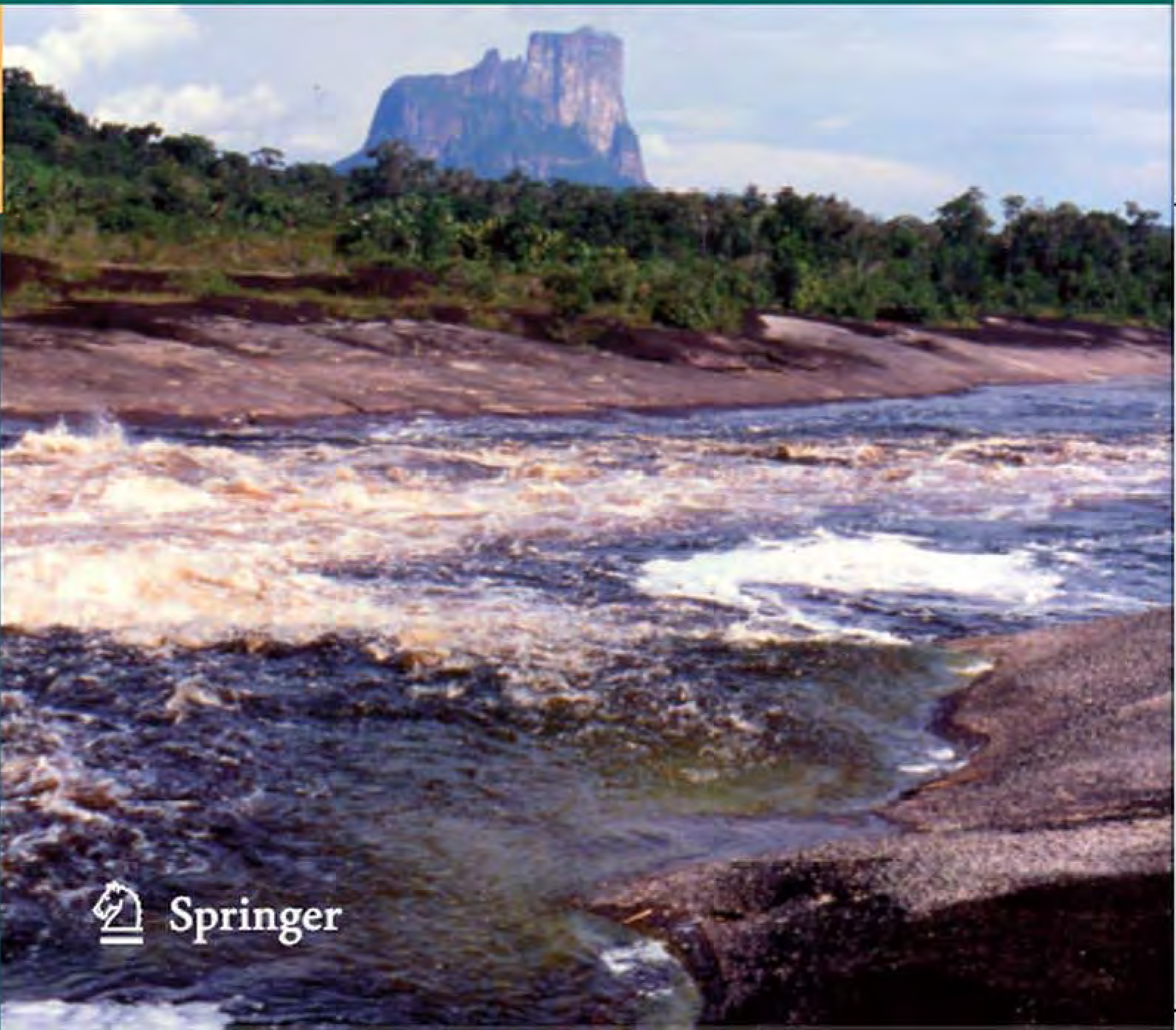
J. David Allan
María M. Castillo

Stream Ecology

Structure and Function of Running Waters

Second Edition



Springer

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The cover photograph shows the Autana River, a blackwater river in the Orinoco basin of Venezuela. In the background is the Autana Mountain, sacred to the Piaroa people, whose culture and livelihood are closely connected to the river. Photograph by M M Castillo

Dedicated to our families, with gratitude for their support

Contents

Preface to the Second Edition

The diversity of running water environments is enormous. When one considers torrential mountain brooks, large rivers of lowlands, and great rivers whose basins occupy subcontinents, it is apparent how location-specific environmental factors contribute to the sense of uniqueness and diversity of running waters. At the same time, however, our improved understanding of ecological, biogeochemical, hydrological, and geomorphological processes provides insight into the structural and functional characteristics of river systems that brings a unifying framework to this field of study. Inputs and transformations of energy and materials are important in all river systems, regional species richness and local species interactions influence the structure of all riverine communities, and the interaction of physical and biological forces is important to virtually every question that has been asked. It seems that the processes acting in running waters are general, but the settings are often unique.

We believe that it helps the reader, when some pattern or result is described, to have some image of what kind of stream or river is under investigation, and also where it is located. Stream ecology, like all ecology, depends greatly on context: place, environmental conditions, season, and species. This text includes frequent use of descriptors like "small woodland stream," "open pastureland stream," or "large lowland river," and we believe that readers will find these useful clues to the patterns and processes that are reported. For most studies within the United States we have included further regional description, but have done so less frequently for studies from elsewhere around the globe. We apologize to our international readers for this pragmatic choice, and we have made every effort to include examples and literature from outside of North America.

Some locations have established themselves as leading centers of study due to the work of many researchers carried out over decades. The Hubbard Brook Experimental Forest in New Hampshire, Coweeta Hydrologic Laboratory in North Carolina, and some individual streams including Walker Branch in Tennessee, Sycamore Creek in Arizona, Río las Marías in Venezuela, and the Taeri and Whatawhata in New Zealand are locations that appear frequently in the pages that follow. Knowing what these places are like, and how they may or may not be typical, in our view justifies the frequent use of place names and brief descriptions. The names of organisms also appear frequently and may at first overwhelm the reader. It may be easiest to pay them little attention until they gradually become familiar. Ultimately, it is difficult to really comprehend the outcome of a study without some appreciation for the organisms that were present.

As is true for every area of ecology at present, the study of streams and rivers cannot be addressed exclusive of the role of human activities, nor can we ignore the urgency of the need for conservation. This is a two-way street. Ecologists who study streams without considering how past or present human modifications of the stream or its valley might have contributed to their observations do so at the risk of incomplete understanding. Conservation efforts that lack an adequate scientific basis are less likely to succeed. One trend that seems safe to forecast in stream ecology is toward a greater emphasis on understanding human impacts. Fortunately, signs of this trend are already apparent.

We have organized the flow of topics in a way that is most logical to us, but no doubt some readers will prefer to cover topics in whatever order they find most useful. For this reason, we have striven to explain enough in each chapter so that it is comprehensible on its own. This leads to a certain amount of intentional repetition, which we hope will provide clarification or a reminder that will benefit the reader's understanding.

We are extremely grateful to the many colleagues who shared ideas, provided references, and reviewed chapters in draft form. Space does not permit us to thank everyone who answered a query with a helpful explanation and suggestions for source material; however, we do wish to acknowledge the persons who carefully read and improved our chapters. Any remaining shortcomings or errors are the authors' responsibility, but hopefully these are few, thanks to the efforts of Robin Abell, Brian Allan, Fred Benfield, Barb Downes, David Dudgeon, Kurt Fausch, Stuart Findlay, Alex Flecker, Art Gold, Sujay Kaushal, Matt Kondolf, Angus McIntosh, Peter McIntyre, Rich Merritt, Judy Meyer, Pat Mulholland, Bobbi Peckarsky, LeRoy Poff, Brian Roberts, Doug Shields, Al Steinman, Jan Stevenson, Jen Tank, Paul Webb, Jack Webster, Kevin Wehrly, and Kirk Winemiller. All were generous with their time and knowledge, and we are indebted to them.

We also wish to thank those who provided helpful reviews of chapters in the first edition of this book, including Fred Benfield, Art Benke, Art Brown, Scott Cooper, Stuart Findlay, Alex Flecker, Nancy Grimm, David Hart, Chuck Hawkins, Bob Hughes, Steve Kohler, Gary Lamberti, Rex Lowe, Rich Merritt, Diane McKnight, Judy Meyer, Bobbi Peckarsky, Pete Ode, Walt Osterkamp, ML Ostrofsky, Margaret Palmer, LeRoy Poff, Karen Prestergaard, Ike Schlosser, Len Smock, Al Steinman, Scott Wissinger, and Jack Webster.

Others provided invaluable assistance with important aspects of manuscript production. Jennifer Allan, Mary Hejna and Jamie Steffes did extensive proofreading and arranged all the figure permissions. Haymara Alvarez, Susana Martinez, and Dana Infante assisted with production of figures, and Jesus Montoya did a superb job of taking figures made in many different styles and redrafting them to a common style and high quality. Funding for MMC release time and travel to Michigan was provided by Dirección de Desarrollo Profesoral of Universidad Simón Bolívar, and the Horace H. Rackham School of Graduate Studies of the University of Michigan. We also wish to thank our editors at Springer, Suzanne Mekking and Martine van Bezooijen, and our prior editor Anna Besse-Lototskaya, for their support, encouragement, and patience. It has been a pleasure to work with them all.

Lastly, our deepest thanks go to our families for their love and support, and especially for their help and understanding during the time this edition was completed. David wishes to express his appreciation to Susan for the unflagging encouragement that has been a constant throughout our lives together. María Mercedes wishes to thank her parents for their unconditional support in the development of her career. It has been an enjoyable experience for both of us, and we hope that this edition will serve as a useful guide for the next generation of stream ecologists.

Chapter one

An introduction to fluvial ecosystems

This chapter provides an overview of the diversity of rivers and streams, including some of the causes of this diversity, and some of the consequences. The intent is to provide a road map for the individual chapters that follow, rather than define terms and explain principles in detail. By sketching out the broadest patterns of fluvial ecosystems and providing at least a glimpse of the underlying processes, we hope this introduction will serve as a framework for the entire book. Some of these generalizations may later be qualified to recognize their exceptions and limitations. Yet, it is through this effort to elucidate the working principles of fluvial ecosystems and how environmental context governs their expression that river ecologists hope to comprehend the enormous variety of streams and rivers, and provide the needed guidance to ensure their sustained well-being.

1.1 Fluvial Ecosystem Diversity

Streams and rivers occur in almost bewildering variety. There is no real distinction between streams and rivers, except that the former are smaller. Some use the term "great river" to distinguish rivers such as the Mekong, the Amazon, and the Mississippi from rivers of more usual size. Partly because the vast majority of river length is in the smaller headwater streams, and partly because these smaller systems have received considerably more study, many and perhaps most researchers consider themselves "stream ecologists." Attempting to understand how the principles of fluvial systems are manifested across scale is one of the primary themes of this book.

Fluvial ecosystems vary in many additional features. Some have the color of tea due to high concentrations of dissolved plant matter, while others have fewer chemical constituents and so remain clear; these are known as blackwater and clearwater rivers, respectively. Rivers can tumble and cascade down steep slopes over large boulders, meander through gentle valleys, or flow majestically across broad flats as they approach the sea. Food webs in forested streams derive much of their food base from autumn leaf fall, whereas streams that are open, shallow, and stony typically develop a rich film of algae and microbes. Rivers that still have an intact floodplain exchange organic matter and nutrients with the adjacent land, and all fluvial ecosystems exhibit high connectivity laterally, longitudinally, and vertically (Figure 1.1).

River science attempts to catalog this diversity, reveal the underlying processes that are responsible for the variety of patterns that we observe, and understand how those processes interact with different environmental settings and across scale from the smallest headwater streams to great rivers. Numerous classification systems for rivers have been developed to better comprehend natural patterns of variation, as well as guide management activities including restoration and assessments of river health. At the time of this writing it is not possible to describe one, overarching river classification. Indeed, this may not be an attainable goal: the variation of fluvial ecosystems is continuous, the variables often are too independent to form recognizable clusters, and different classifications have different purposes (Kondolf et al. 2003a, b). With these limitations in mind, however, a number of broad generalizations can be made that help to organize the variety and variability of fluvial ecosystems.

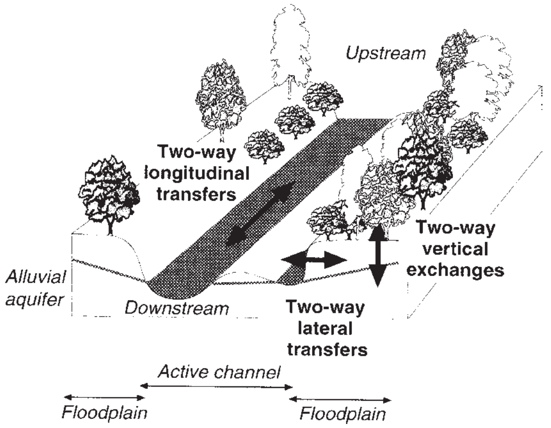

FIGURE 1.1 The fluvial ecosystem with its three major axes: upstream/downstream, channel/margins, and surficial/underground environments. (Reproduced from Piégay and Schumm 2003.)

1.1.1 The fluvial hierarchy

Streams and the landscape units they drain form nested hierarchies. The smallest permanently flowing stream is referred to as first order. The union of two first-order streams results in a second-order stream, the union of two streams of second order results in a third-order stream, and so on (Figure 1.2). Stream order is an approximate measure of stream size, conceptually attractive, and correlates with a number of other, more precise size measures including the area drained, volume of water discharged, and channel dimensions. As a simple classification system it provides an informative tally of the numbers of small streams and large rivers (Table 1.1). The great majority of the total length of river systems is comprised of lower-order or headwater systems, each of short length and small drainage area. Rivers that we might consider to be of medium size, fourth through sixth order, are

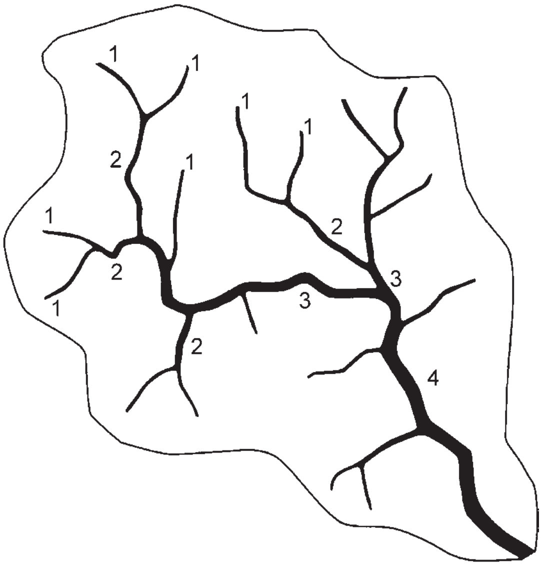

FIGURE 1.2 A drainage network illustrating stream channel order within a fourth-order catchment. The terminus may be a lake or the junction with a larger river. Intermittent streams occur upstream of the first-order tributaries, and often extend nearly to the catchment divide.

TABLE 1.1 Number and lengths of river channels of various sizes in the United States (excluding tributaries of smaller order). (From Leopold et al. 1964.)

Order	*Number*	*Average length (km)*	*Total length (km)*	*Mean drainage area (km^2)*
1	1,570,000	1.6	2,510,000	2.6
2	350,000	3.7	1,300,000	12.2
3	80,000	8.8	670,000	67
4	18,000	19	350,000	282
5	4,200	45	190,000	1,340
6	950	102	98,000	6,370
7	200	235	48,000	30,300
8	41	540	22,999	144,000
9	8	1,240	9,900	684,000
10	1	2,880	2,880	3,240,000

Of the approximately 5,200,000 total river kilometers in the contiguous United States, nearly half are first order, and the total for first- to third-order combined is just over 85%. Examples of large rivers include the Allegheny (seventh order), the Gila (eighth order), the Columbia (ninth order), and the Mississippi (tenth order).

TABLE 1.2 The 25 largest rivers of North America, ranked by their virgin (corrected for withdrawals) discharge. (From Benke and Cushing 2005.)

River name	*Discharge (m^3 s^{-1})*	*Basin area (km^2)*
1 Mississippi	18,400	3,270,000
2 St. Lawrence	12,600	1,600,000
3 Mackenzie	9,020	1,743,058
4 Ohio	8,733	529,000
5 Columbia	7,730	724,025
6 Yukon	6,340	839,200
7 Fraser	3,972	234,000
8 Upper Mississippi	3,576	489,510
9 Slave (Mackenzie Basin)	3,437	606,000
10 Usumacinta	2,687	112,550
11 Nelson	2,480	1,072,300
12 Liard (Mackenzie Basin)	2,446	277,000
13 Koksoak (Quebec)	2,420	133,400
14 Tennessee (Ohio Basin)	2,000	105,870
15 Missouri	1,956	1,371,017
16 Ottawa (St. Lawrence Basin)	1,948	146,334
17 Mobile	1,914	111,369
18 Kuskokwim	1,900	124,319
19 Churchill (Labrador)	1,861	93,415
20 Copper	1,785	63,196
21 Skeena	1,760	54,400
22 La Grande (Quebec)	1,720	96,866
23 Stikine	1,587	51,592
24 Saguenay (St. Lawrence Basin)	1,535	85,500
25 Susitna	1,427	51,800

Note that drainage area alone is a rough predictor of volume of flow.

not uncommon – they include over 20,000 river channels in the contiguous United States. About 250 US rivers are of order seven and higher, and only a handful are great rivers (Table 1.2). Of these, only the Mississippi ranks among the 15 largest rivers of the world based on the annual volume of its discharge.

Each stream or river drains an area of land that is proportional to its size. This area is its drainage basin, and includes the topographically determined region that contributes all the water that passes through the stream. Although it is common to define drainage area for the entire river system from origin to mouth, one can also determine the drainage area for individual tributaries. Clearly, then, just as the stream network forms a hierarchy of low-order streams nested within higher-order rivers, their drainages likewise are nested hierarchically. As with rivers and streams, there are overlapping terms in wide use. Drainage basin and river basin tend to be applied to large units, whereas smaller units are referred to as watersheds and subwatersheds, or catchments and subcatchments.

Worldwide, rivers are classified by their hierarchic position within river basins and within regions. The US Geological Survey Hydrologic Unit Cataloging (HUC) system (Seaber et al. 1987) catalogs watersheds at different geographical scales based on 1:100,000 mapping (Table 1.3). It first divides the United States into 21 major regions that contain either the drainage area of a single river or the combined drainage area of a series of rivers. Smaller units are nested within regions. An eight-digit HUC is standard, and typically corresponds to a drainage area in the order of 10^3-10^4 km^2. Further subdivisions exist or are under development, resulting in 11- or 14-digit watersheds.

The view of river systems as a hierarchically arranged, nested series of units provides a powerful organizing framework in which to examine the patterns and processes of fluvial ecosystems (Frissell et al. 1986) (Figure 1.3). The largest scale is the river basin and drainage network. River segments, typically extending between an upstream and downstream tributary juncture, are nested within the network. Individual segments may be from one to tens of kilometers in length, and are the scale at which one would observe major floodplain and channel features. Individual reaches are recognizably homogeneous units within a valley segment. In practice, they often are defined as a repeating sequence of channel units (such as a riffle–pool–run sequence) or by a sampling convention, such as a distance equal to 25 stream widths. A reach can be 100 m or less in length in a small stream, and several kilometers in a larger river. Macrohabitats such as a pool or riffle occur within a reach, and microhabitats may include a gravel patch or a leaf accumulation along the stream margin.

The hierarchical view of river systems also emphasizes that processes acting at upper levels of the hierarchy control features expressed lower in the hierarchy, but not vice versa. Climate, source of flow, geology, and landform exert particular control on the river basin and network development, and set the domain of

TABLE 1.3 Hydrologic Unit Cataloguing illustrated for a specific watershed, Mill Creek (04173500), which enters the Huron River upstream of Ann Arbor, Michigan.

Code segment	*Name*	*Number in the United States*	*Average area (km^2)*
04	Water resource region	21	460,000
0417	Subregion	222	43,500
041735	Accounting code	352	27,500
04173500	Cataloging unit	2,150	1,820

The accounting code is sometimes referred to as basin, and the cataloging unit as subbasin or watershed.

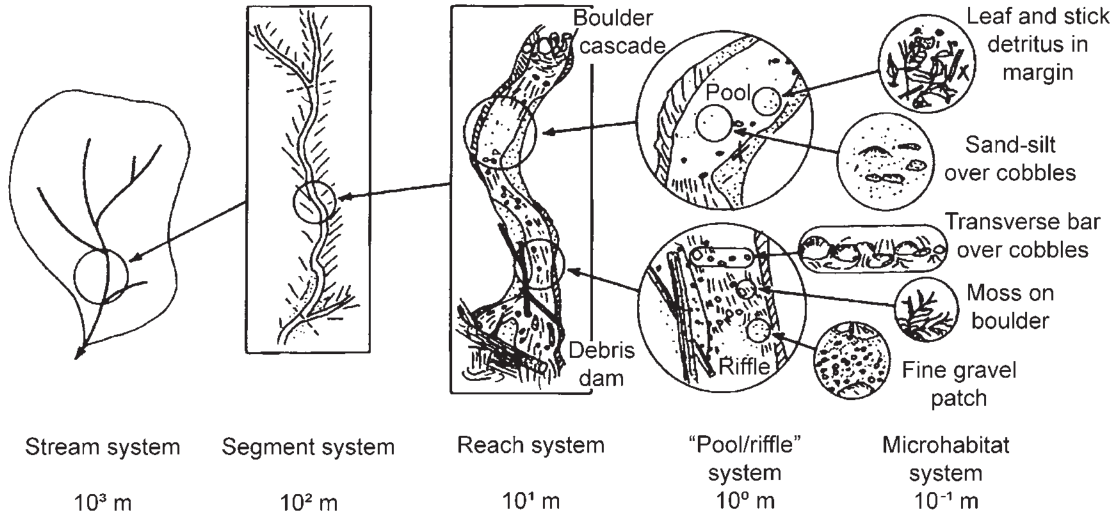

FIGURE 1.3 The hierarchical organization of a stream system illustrating how smaller units are repeating elements nested within larger units. Upper hierarchical units exert considerable influence over lower hierarchical units, but not vice versa. (Reproduced from Frissell et al. 1986.)

interacting geomorphic processes that shape channels and features at the segment to reach scale. More locally, the stability of banks and supply of pool-forming wood strongly influence details of channel features and habitats.

1.1.2 Longitudinal patterns

Some changes that occur along a river's length have already been noted. An increase in size and volume of water will occur as tributaries join and the network's drainage area increases. Rivers have a characteristic longitudinal profile in which they typically are steeper in the uplands where they originate and have a more gradual slope in the lowlands near their terminus. The longitudinal profile of a river can be divided roughly into three zones: erosion, transfer, and deposition of sediments (Schumm 1977). In addition to their steeper gradients, headwaters often have deep, V-shaped valleys, rapids and waterfalls, and export sediments. The midelevation transfer zone is characterized by broader valleys and gentler slopes. Tributaries merge and some meandering develops. Sediments are received from the headwaters and delivered to lower sections of the river system. In the lower elevation depositional zone, the river meanders across a broad, nearly flat valley, and may become divided into multiple channels as it flows across its own deposited sediments.

This description adds another perspective to our view of rivers, that of sediment erosion, transport, and deposition. Because the river's power to transport sediment is a function of gradient and volume of flow, and more power is required to move large versus small particles, the river also is a sediment sorting machine. Indeed, many of the channel types and features that contribute to the variety of rivers, such as boulder cascades, rapids, riffle–pool sequences, and so on can be seen to exhibit a longitudinal progression determined by sediment supply, stream power, and additional factors considered in Chapter 3 (Figure 1.4).

1.1.3 The stream and its valley

Stream ecologists have long recognized the profound influence that surrounding lands have on the stream ecosystem ("in every respect, the valley rules the stream", Hynes 1975). Rain and snow that fall within the catchment reach the stream by myriad flow paths. Some, notably surface and shallow subsurface flows, reach the stream rapidly and so high flows quickly follow storms. Others, primarily groundwater flows, are so gradual that streamflow barely responds to rain events. Geology, slope, and vegetation strongly influence these flow paths in natural systems, and human land use adds further complications. Precipitation that flows quickly over surfaces can wash sediments and organic matter into streams, whereas water that has a longer residence time in the ground has more opportunity to dissolve minerals and take on the chemical signature of the underlying geology. The valley slope is the source of much of the sediment inputs in the headwaters, which exports all but the largest particles downstream, and the channel walls become increasingly important as a sediment source in middle and lower river sections as the river's meandering and flooding drives endless cycles of erosion and deposition. Thus, key aspects of the river's hydrology, its channel shape, and its chemistry are the consequences of climate and the geology, topography, and vegetation of the valley.

Land that borders the stream undoubtedly has the greatest influence, affecting multiple stream functions. Called the riparian zone, and including the floodplain in locations where the river frequently overflows its banks, the influence of the stream margin and its vegetation cannot be overstated. Roots stabilize banks and prevent slumping, branches and trunks create habitat diversity wherever they fall into streams, shade from the canopy prevents excessive warming, and the infall of vegetation and invertebrates are major sources of energy to stream food webs. When vegetation changes along a river's length, across

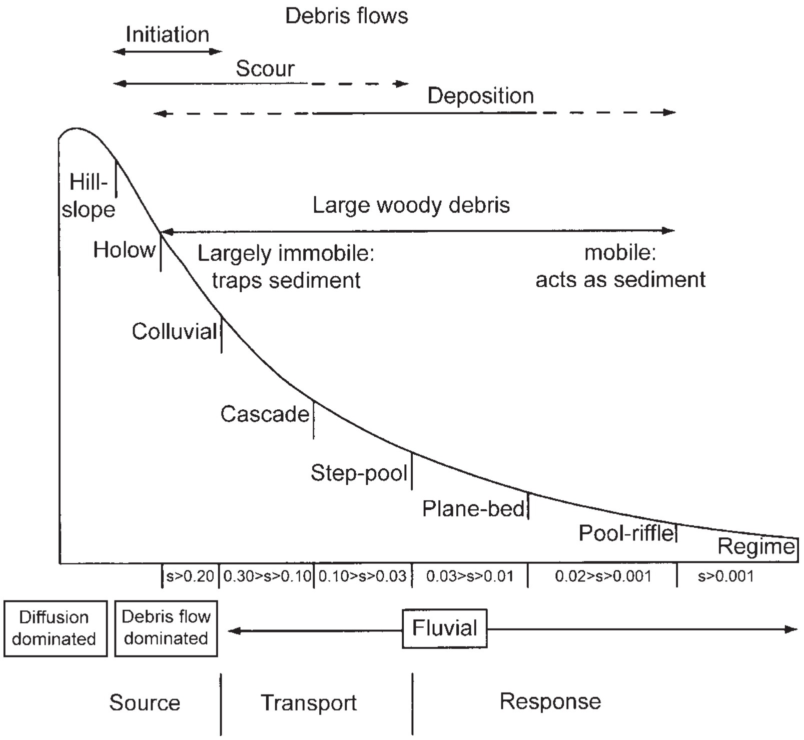

FIGURE 1.4 River channel types occur in succession along the river's profile due to complex interactions governed by slope (s), sediment supply, trapping of sediments by large wood in the channel, and other factors. Although thresholds may be difficult to detect, certain channel features prevail over a substantial distance, referred to as a process domain. This model was developed for small mountain streams in the Western United States. (Reproduced from Montgomery and Buffington 1997.)

ecological regions or due to human activities, the stream is affected in multiple ways.

1.2 The Fluvial Ecosystem

The fluvial ecosystem integrates the biota and biological interactions with all of the interacting physical and chemical processes that collectively determine how systems function. Certain properties can be recognized that characterize the whole system: its overall production and metabolism, how efficiently nutrients are used, the diversity of energy supplies, and the number of species and feeding roles represented. All ecosystems have some flux across their boundaries, but fluvial ecosystems are especially open, exhibiting high connectivity longitudinally, laterally, and vertically (Figure 1.1). Ecosystems include people, and rivers have always been magnets for human settlement, providing water for drinking and to grow crops, harvestable resources, transportation, and hydropower. In ways both subtle and obvious, almost all running waters today show some evidence of modification due to human activities.

1.2.1 Energy sources

In fluvial food webs, all energy available to consumers ultimately originates as primary production, but not necessarily from aquatic plants or within the stream itself. The primary producers of greatest significance, especially in small streams, include algae, diatoms, and other microscopic producers. These are found on stones, wood, and other surfaces and occur where light, nutrients, and other conditions are suitable for their growth. Organic matter that enters the stream from the surrounding land, such as leaf fall and other plant and animal detritus, is an important energy source in most streams, and is of primary importance in many. Bacteria and fungi are the immediate consumers of organic substrates and in doing so create a microbe-rich and nutritious food supply for consumers, including biofilms on both inorganic and organic surfaces, and autumn-shed leaves riddled with fungal mycelia.

Rivers typically receive organic matter from upstream and also laterally, depending upon the nature of the riparian vegetation and the river's connectivity with a floodplain. In forested headwater streams and large floodplain rivers, most energy is received as external inputs, termed allochthonous sources. Streams flowing over a stony bottom in an open meadow often develop a rich algal turf on the substrate, and so most of the energy is produced internally, that is, from an autochthonous source. Typically, the food webs of streams and rivers are fueled by a complex mixture of allochthonous and autochthonous energy sources, and unraveling their relative contributions to higher trophic levels is a considerable challenge.

1.2.2 Food webs and biological communities

Just as they are adapted to their physical environment, the organisms of fluvial ecosystems exhibit specific food-gathering abilities and feeding modes that are shaped by the food supplies available to them and the habitats in which they forage. The macroinvertebrates of streams, including insects, crustaceans, mollusks, and other taxa, are organized into functional feeding groups based on similarities in how food is gathered as well as the food type. Grazers and scrapers consume algae from substrate surfaces, stones in particular; shredders consume autumn-shed leaves enriched with microbes; predators consume other animals; and collector-gatherers feed on the abundant and amorphous fine organic particles originating from the breakdown of leaves and everything once living. Because functional feeding groups place primary emphasis on how the food is obtained rather than from where it originated, they may imply greater distinctiveness in trophic pathways than actually is the case. This is especially true in the case of biofilms, which appear to be ubiquitous and likely make a direct contribution to the trophic needs of all consumers.

The vertebrates of fluvial ecosystems likewise exhibit considerable diversification in their feeding roles and their adaptations to exploit available resources. The various trophic categories, often termed guilds, include algivore, detritivore, omnivore, invertivore, and piscivore; and feeding location (e.g., streambed versus water surface) may also be distinguished. Many fishes consume primarily an invertebrate diet, and so do salamanders, and some birds and mammals. Algae are the primary diet of a number of fish species, especially in the tropics, and of some larval anurans. Other fishes with elongated guts are able to digest detritus, including leaf matter and ooze. In addition to omnivores, a term generally used to describe species whose diet include plant (or detritus) and animal matter, and piscivores, which are invertivores early in their life histories, many species feed more broadly than these categories imply.

The biological communities of fluvial ecosystems are assembled from the organisms that are adapted to regional conditions, including the physical environment and food resources, and are further refined through interactions with other species. Similar to the way that large-scale aspects of climate, vegetation, and geology influence local-scale physical and chemical features of the stream environment, a series of hierarchically nested environmental factors also influences the assemblage of species at progressively more localized spatial scales (Figure 1.5).

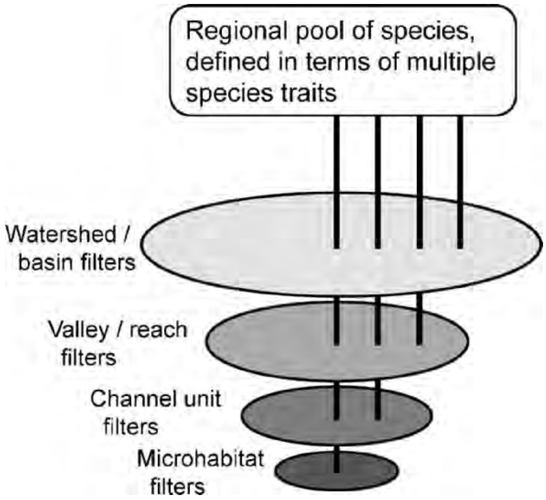

FIGURE 1.5 The number and types of species at a site reflects their possessing traits (trophic, habitat, life history, etc.) that allow them to pass through multiple biotic and abiotic filters at hierarchical spatial scales. The species assemblage found within a particular microhabitat possesses traits suitable for prevailing watershed/basin, valley bottom/stream reach, and channel unit and habitat conditions. (Reproduced from Poff 1997.)

Species able to colonize and survive within a particular stream network are those that occur within the region and are tolerant of the hydrologic and thermal regimes and water chemistry. Persistence at the valley reach level requires a more refined match of species adaptations to physical habitat, food resources, and specific temperature and flow conditions. Additional filters at the channel unit and microhabitat level further restrict the pool of suitable species to those with traits suited to finer-scale conditions such as space within the interstices of the substrate, local hydraulic conditions, and habitat and food resources. Lastly, interactions among species can serve as a powerful additional filter, as when one species competitively displaces another, a critical food resource is lacking, or a top predator eliminates all but the most cryptic or elusive of prey.

1.2.3 The river ecosystem

The river ecosystem includes its hydrology, diversity of channel and habitat types, solutes and sediments, and biota. Certain processes and properties emerge at the level of the whole ecosystem, including the flow of energy through food webs, the cycling of carbon (C) and nutrients such as nitrogen (N) and phosphorus (P), and the origin, processing, and transport of materials from headwaters to sea. Rivers are not only important links in the hydrologic cycle and "the gutters down which run the ruins of continents" (Leopold et al. 1964), but also ecosystems that use and reuse biologically reactive elements.

In any ecosystem, nutrient cycling describes the uptake of some nutrient, usually from a dissolved inorganic phase, and its subsequent incorporation into biological tissue. That material resides for some time in organic form within the plant or microbe, and likely passes through other consumers, but eventually is remineralized by excretion or respiration, thus completing the cycle (Figure 1.6). In running waters, downstream transport occurs in both the inorganic and organic phases, but especially in the former, stretching the cycle into a spiral. Thus, uptake distance rather than time becomes a useful measure of biological availability and demand.

At the catchment scale, mass balance analysis complements reach-scale uptake studies by computing all inputs to the landscape and exports from the river mouth. The difference is an estimate of all the nutrients removed by ecosystem processes or stored within soils and sediments, and this can be viewed as a measure both of the services provided by an ecosystem and of their limitations. For example, it appears that roughly 25% (but occasionally as much as 50%) of the total N inputs to a catchment are exported at the river mouth; the difference is attributed mostly to denitrification that takes place in terrestrial ecosystems, wetlands, and the river itself (Howarth et al. 1996). Such analyses were

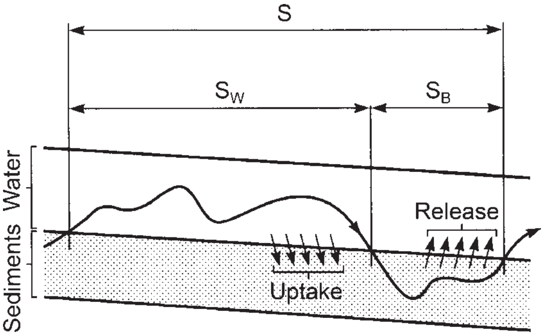

FIGURE 1.6 Nutrient uptake and release in streams is coupled with downstream transport, stretching cycles into spirals. Spiraling length is the sum of the distance traveled by a nutrient atom in dissolved inorganic form in the water column, called the uptake length (S_W, in meters), and the distance traveled within the biota before being mineralized and returned to the water column, called the turnover length (S_B). Arrows show uptake and release of nutrient retained within the streambed. (Modified from Newbold 1992.)

critical in establishing the link between fertilizer use in the Upper Mississippi Basin and the Gulf of Mexico's anoxic zone, where nutrient enrichment has harmed fisheries over a large region. Nutrient exports are a fairly constant percentage of inputs, which differ among catchments largely because of human influences over agricultural activities, food and crop imports and exports, and atmospheric deposition. Reductions in the mass of nutrients exported by rivers will require either a reduction of inputs, or finding ways to increase internal removal.

The river continuum concept integrates stream order, energy sources, food webs, and to a lesser extent nutrients into a longitudinal model of stream ecosystems (Figure 1.7). In a river system flowing through a forested region, the headwaters (order 1–3) are heavily shaded and receive abundant leaf litter, but algal growth often will be light-limited. Streams of order 4–6 are expected to support more plant life because they are wider and less shaded, and in addition receive organic particles from upstream. The headwaters have more allochthonous inputs, indicated by a ratio of primary production to respiration well below unity, whereas the mid reaches have more autochthonous production and a higher P/R ratio. Higher-order rivers are too wide to be dominated by riparian leaf fall and too deep for algal production on the bed to be important. Instead, organic inputs from upstream and the floodplain, along with river plankton, play a greater role.

1.3 The Status of Rivers Today

Today, few rivers are pristine, and most have a long history of alteration. In regions of extensive human settlement the changes may be so profound and so lost in antiquity that even the best ecological detectives are unable to specify historic conditions with much certainty. Thus, it is instructive to look to areas that have a recent history of human disruption and that we might erroneously consider scarcely altered from their original state. Mountain rivers of the Front Range of the Colorado Rockies provide such an example (Wohl 2001). Particularly in the high country, resplendent with flowers and rich with trout and other wildlife, visitors may suppose they gaze upon streams as natural as when Native Americans occupied the landscape. However, this is far from the truth (Figure 1.8). By the time the first expeditions reported of these valleys and rivers in the 1840s, beaver trappers had already been at work. Due to the decimation of perhaps the foremost example of an "ecological engineer" – a species that manipulates habitat and ecosystem processes through its activities – mountain streams had fewer beaver dams, different flow regimes, less wetland and channel habitat, and fewer locations in which young trout could rear. The discovery of gold and silver in 1859 set off a mining rush that transformed valleys and resulted in acidification of streams that continues to the present. By the 1860s, lower valleys were being settled, forests harvested, and streams diverted into irrigation ditches. Even the water law in the

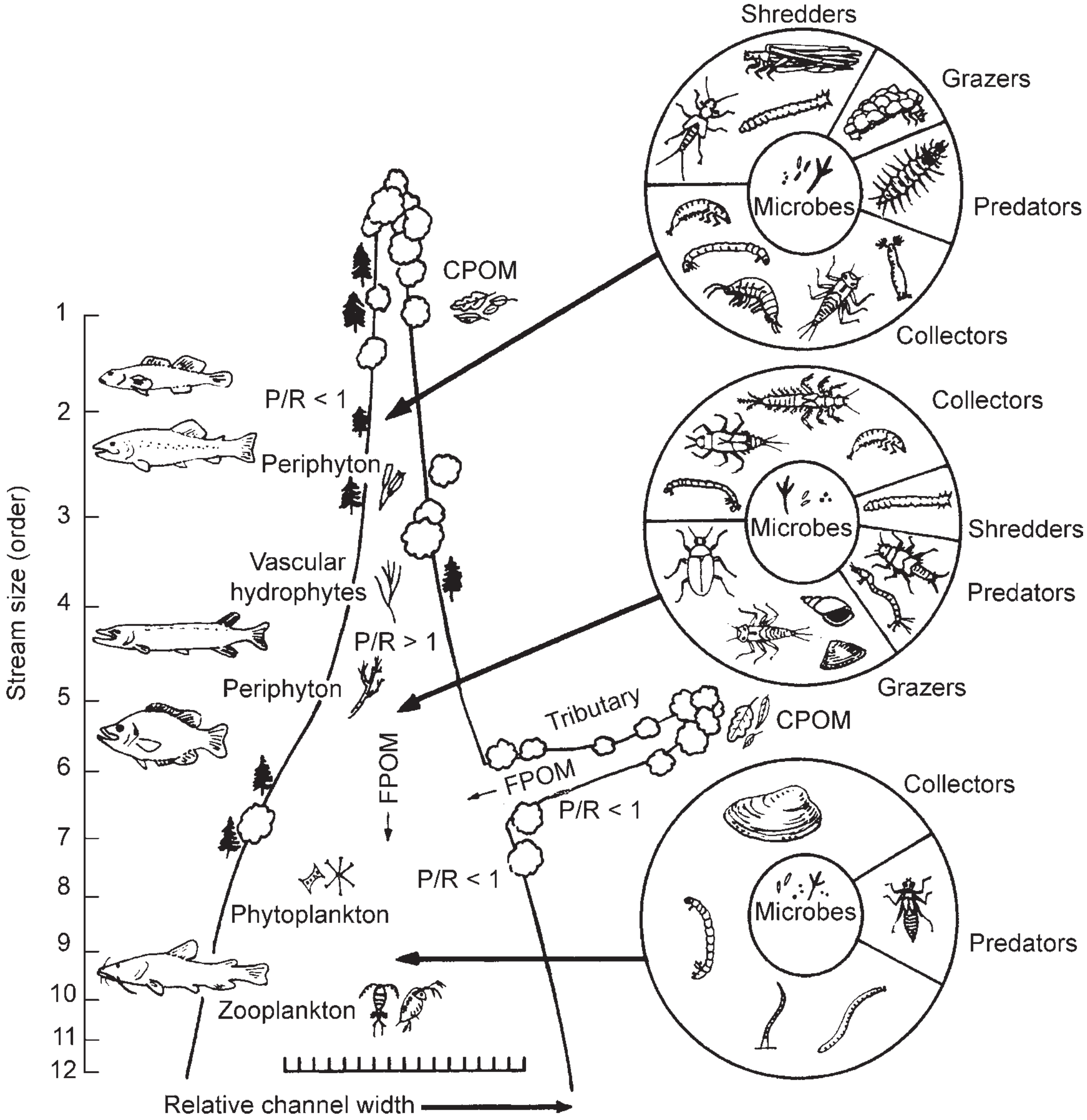

FIGURE 1.7 The river continuum concept summarizes expected longitudinal changes in energy inputs and consumers as one proceeds from a first-order stream to a large river. A low P/R ratio indicates that the majority of the energy supplied to the food web derives from organic matter and microbial activity, and mostly originates as terrestrial production outside the stream channel. A P/R approaching 1 indicates that much more energy to the food web is supplied by primary production within the stream channel. An important upstream–downstream linkage is the export of fine particulate organic matter (FPOM) from the headwaters to locations downstream. (Reproduced from Allan 1995 after Vannote et al. 1980.)

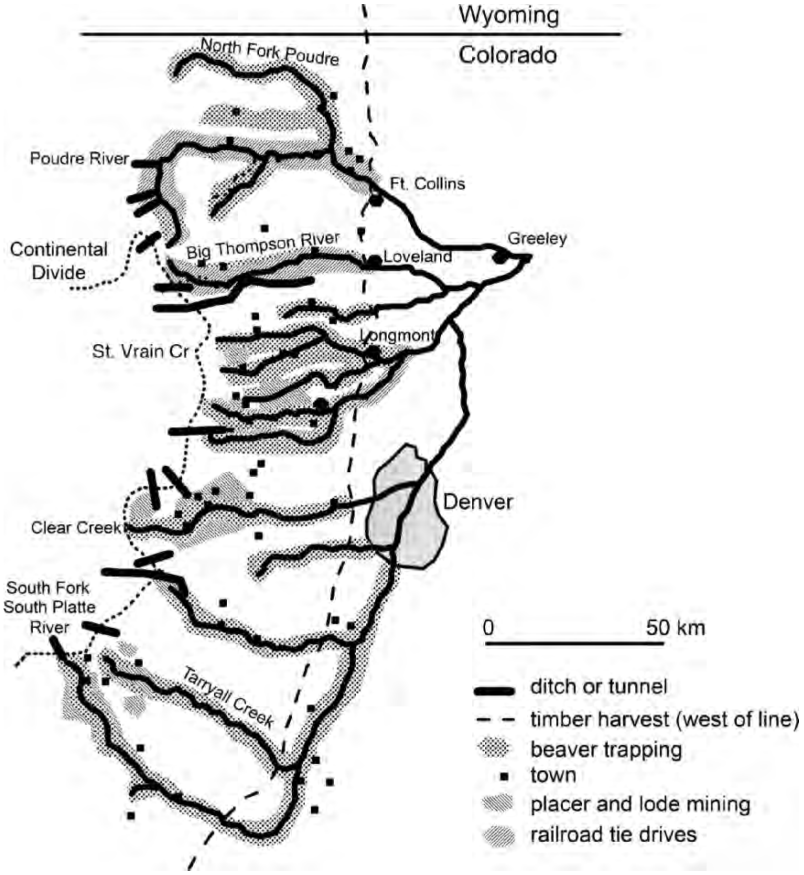

FIGURE 1.8 The extent of various human land use activities in the Upper South Platte River Basin, Colorado. Beaver trapping was the earliest influence, followed by mining, which brought railroads and the need for tie drives, where timber was floated down rivers to make railroad ties. Timber harvest, grazing animals, and agricultural crops brought further changes, and a growing population on the eastern slope of the Continental Divide led to tunnels that divert water from the western slope. (Reproduced from Wohl 2001.)

western United States, with its emphasis on the priority of upstream users, reflects this period of early settlement. Native herbivores were replaced with cattle and sheep, and local instances of severe overgrazing occurred. Then came more and more people, attracted to this "Switzerland of the West" with its abundance of recreational opportunities throughout the back country and mountain valleys. Yet, still one can marvel at the scenic beauty of this area and imagine that it is as it always has been. This is an example of what has become known as the "shifting baseline," where humans define what is natural from their perceptions and memories of the present and very recent past.

What is the status of rivers today? Many responses to that question will appear throughout this book, yet a definitive answer is lacking. Global and national assessments are very approximate, but nonetheless indicate that most rivers are influenced by human activities, often to a substantial extent (Revenga et al. 2000). To be sure, some regions are as untouched as one could reasonably imagine, including the great salmon-producing rivers of the Kamchatka Peninsula, remote tropical rivers of the Amazon and Orinoco basins, and a few other places. As new methods of biological assessment are becoming standardized and widely deployed, river surveys are beginning to produce comprehensive evaluations of river health for basins and regions, and eventually these will be stitched together into national assessments of the status and trends of fluvial ecosystems.

There can be little doubt that most streams and rivers will continue to face a daunting array of threats. Foremost is the increase in human population in all of its manifestations: urban areas with impervious surfaces and piping, housing sprawl into farmland and increasingly remote areas, and the intensification of agriculture. Often summed up as changing urban and agricultural land use, these trends result in altered supplies of water and sediments and increasing concentrations of nutrients and contaminants. Immediate consequences include habitat fragmentation and degradation, sedimentation, the enrichment of some systems, and the poisoning of others. Tolerant species multiply and spread, and sensitive species decline. Coupled with the invasion of nonnative species, some of which are very adaptable and thrive in disturbed conditions, the stream biota undergoes simplification and homogenization. Dam construction may actually be on the wane globally, due in part to the recognition of social and environmental costs and in part to the exhaustion of best sites, but for some regions this era is far from over. As concern grows over the ecological effects of climate change, which for rivers portends significant hydrologic impacts, the desire to replace fossil fuels with renewable energy favors more dams on more rivers. In areas that are seasonally or regularly water-stressed, water storage, withdrawal, and transfers exert virtually continuous pressure on river managers to define and defend the water needs of ecosystems against the water needed for human population and development.

In order to protect and restore rivers, managers will need recourse to the best science to justify their recommendations, and the public must be informed of the values provided by healthy fluvial ecosystems (Baron et al. 2002). Flowing waters provide critically important goods and services upon which humans depend. This is evident in the protected status that numerous cities give to the catchments that supply their drinking water. The river ecosystem plays a fundamental role in global cycles, transporting water from land to sea, along with vast quantities of sediments, C, N, and other materials. Rivers provide harvestable resources, particularly in Asia and Africa where river fisheries are a major source of protein and employment for large number of people (Allan et al. 2005a). Rivers are transportation corridors and sources of hydropower, providing most of the energy consumed in a number of countries and in some regions of the United States. Rivers provide irrigation water that is critical to crops and livestock. Rivers provide recreation, aesthetic enjoyment, and spiritual renewal.

The great challenge facing those who study rivers is to contribute to the reconciliation between the needs of humankind and the needs of the ecosystem. Driven by population and economic growth, human demands can only increase. However, increasing efficiencies, redirection of water to higher priority uses, and an improved understanding of human benefits derived from healthy rivers offer pathways toward a better balance among competing needs. To understand the workings of fluvial ecosystems depends not only upon exciting, conceptual scientific advances, but also on their management, protection, and restoration. We hope that the pages that follow contribute to both objectives.

Chapter two

Streamflow

Fluvial ecosystems exhibit a wide range of natural variability in the quantity, quality, timing, and temporal variability of river flow. How much water does a river need, and what is the importance of natural variation? To answer these questions, an understanding of flow and its far-reaching consequences for the physical, chemical, and biological condition of rivers is essential. This chapter shows how a basic appreciation of the water cycle is critical to understanding the magnitude and timing of streamflow, and discusses how natural variation in flow often has been altered by human actions. Increasingly today, the tools of hydrologic analysis are being combined with other elements of river science to ensure that "environmental flows" are sufficient to protect and restore stream ecosystems.

Human societies extract great quantities of water from rivers, lakes, wetlands, and underground aquifers to meet agricultural, municipal, and industrial demands. Yet freshwater ecosystems also need enough water, of sufficient quality and at the right time, to provide economically valuable commodities and services to society. The benefits of functionally intact and biologically complex freshwater ecosystems include flood control, transportation, recreation, purification of human and industrial wastes, provision of habitat for plants and animals, and production of fish and other foods and marketable goods (Baron et al. 2002). Unfortunately, however, existing and projected future increases in water demand are resulting in intensifying conflicts between these human uses and the conservation and management of intact, functioning fluvial ecosystems (Postel and Richter 2003).

The human impact on rivers and other surface fresh waters is staggering. Over half of the world's accessible runoff presently is appropriated for human use, and that fraction is projected to grow to 70% by 2025 (Postel et al. 1996). Impoundments, surface and groundwater abstractions, interbasin water transfers, and a vast number of small dams, weirs, and diversions alter flow patterns, reduce surface flows, and fragment river channels. With more than 75,000 dams >2 m in height in the United States and approximately 2.5 million smaller water control structures (Poff and Hart 2002), it is unsurprising that a river inventory of the 48 contiguous states found that only 42 high-quality, free-flowing rivers >200 km in length remain (Benke 1990). Worldwide, the number of large dams (defined as >15 m in height, or >5 m and of large reservoir capacity) exceeds 45,000 (WCD 2000) (Figure 2.1), and the number of small dams is put at 800,000 (McCully 1996). Slightly more than three fourths of the 139 largest river systems of North America, Europe, and former USSR are highly or moderately affected by fragmentation of their main channels by flow-control structures (Dynesius and Nilsson 1994). Revenga et al. (2000) estimated that 60% of the world's rivers are fragmented by hydrologic alteration.

Increases in the size and affluence of the human population will place even greater demands on surface water supplies in the future,

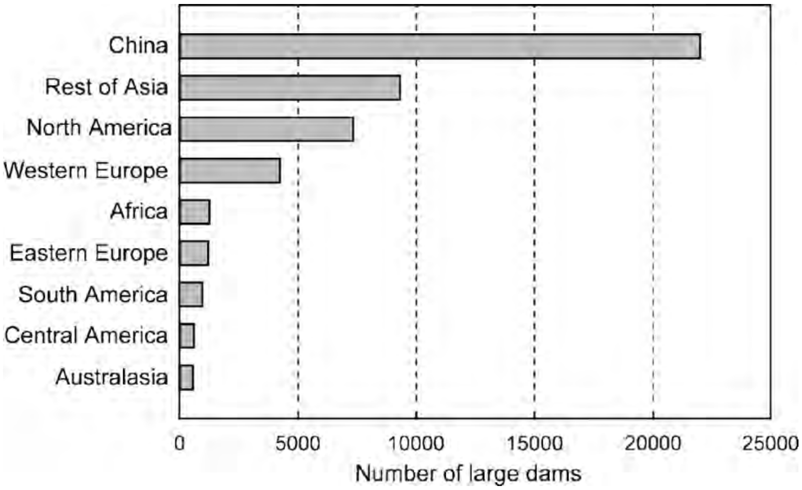

FIGURE 2.1 Distribution of large dams by region. China and Australasia (Australia, New Zealand, Papua New Guinea, and Fiji) were treated separately from the rest of Asia, and Central America including Mexico was separated from North America (United States and Canada). Large dams are >15 m in height or, if between 5 and 15 m in height, have a reservoir capacity $>3 \times 10^6$ m^3 (Reproduced from Tharme 2003, adapted from WCD 2000.)

some aquifers will become exhausted, and climate change introduces further uncertainty into water availability. A recent projection of water demand through 2025 indicated that ensuring a sustainable water supply will become increasingly challenging for large areas of the globe (Vörösmarty et al. 2000). To understand how water appropriation and flow modifications will influence fluvial ecosystems in the future, the analysis of streamflow is of central importance.

2.1 The Water Cycle

Until the 16th century, oceans were thought to be the source of rivers and springs via underground seepage. Palissy and others suggested that storage of rainwater was the real source, based on several lines of reasoning. It was noted that springs would not dry up in summer if oceans were the source, since the oceans do not decrease noticeably. Springs should be more common at low elevations if they derive from oceanic water. However springs often do dry up in summer, they are more common on mountain slopes, and finally, springs are fresh. In 1674, measurements by Perrault showed that precipitation into the Seine basin was six times greater than discharge (Morisawa 1968). This finding changed the focus from whether rainfall is sufficient to provision rivers, to where does the rest of the rainfall go.

The hydrologic cycle describes the continuous cycling of water from atmosphere to earth and oceans, and back to the atmosphere (Figure 2.2). Conceptually this cycle can be viewed as a series of storage places and transfer processes, although water in rivers is both a storage place, however temporary, and a transfer between land and sea. The hydrologic cycle is powered by solar energy. This drives evaporation, transferring water from the surface of the land and especially from the oceans, into the atmosphere, and also the water loss that plants experience as a consequence of gas exchange necessary for photosynthesis. Together these are referred to as evapotranspiration (ET). Precipitation, primarily as rain and snow, transfers water from the atmosphere to the land surface. These inputs immediately run off as surface water, or follow a number of alternative subsurface pathways, some of which (e.g., groundwater) release to the stream channel much more slowly and so are, in effect, storage places as well.

Despite the enormous significance of rivers in the development of civilizations and the shaping of land masses, the amount of water in rivers at any one time is tiny in comparison to other stores. Only 2.8% of the world's total water occurs on land. Ice caps and glaciers make up the majority (2.24%), and groundwater (0.61%) also is a sizable percentage. Only 0.009% of the total water is stored in lakes, about 0.001% is stored in the atmosphere, and rivers contain ten times less, 0.0001% of the world's water. Because the volume in the atmosphere and rivers at any instant in time is small, the average water molecule cycles through them rapidly, residing only days to weeks, compared with much longer residence times of water in other compartments.

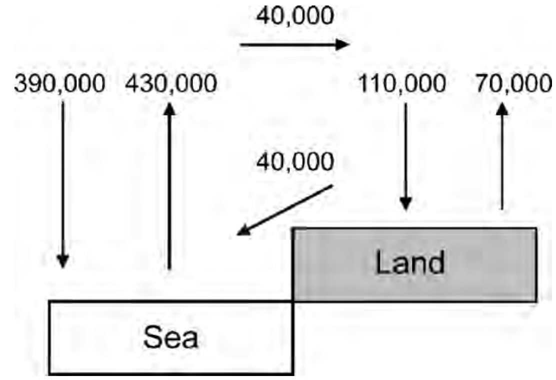

FIGURE 2.2 A simplified depiction of the global water cycle. Flows are approximate, in cubic kilometers per year. Downward arrows signify precipitation, upward arrows evapotranspiration (ET). The upper horizontal arrow represents the transfer of moisture from sea to land; the lower arrow represents runoff from land to sea. (Reproduced from Postel et al. 1996, after Gleick 1993.)

Estimates of the amount of water discharged annually by rivers to the world's oceans vary, but the value of $40,000\,\mathrm{km}^3$ is widely used. The world's 16 largest rivers in terms of runoff volume account for nearly one third of the total, and the Amazon alone contributes nearly 15% (Dingman 2002). Within the United States, the Mississippi contributes some 40% of total US discharge, while the Columbia, Mobile, and Susquehanna together contribute an additional 20%. Globally, the greatest runoff occurs in tropical and subtropical areas, because these latitudes also receive the greatest rainfall (Milliman 1990). By continent, South America is the wettest, Antarctica the driest, and Australia has the lowest runoff per unit area (Table 2.1).

TABLE 2.1 Water balances of the continents. (From Dingman 2002.)

Continent		*Precipitation*		*Evapotranspiration*		*Runoff*	
	Area (10^6 km^2)	*(km^3 year^{-1})*	*(mm year^{-1})*	*(km^3 year^{-1})*	*(mm year^{-1})*	*(km^3 year^{-1})*	*(mm year^{-1})*
Europe	10.0	6,600	657	3,800	375	2,800	282
Asia	44.1	30,700	696	18,500	420	12,200	276
Africa	29.8	20,700	695	17,300	582	3,400	114
Australia[a]	7.6	3,400	447	3,200	420	200	27
North America	24.1	15,600	645	9,700	403	5,900	242
South America	17.9	28,000	1,564	16,900	946	11,100	618
Antarctica	14.1	2,400	169	400	28	2,000	141
Total land[b]	148.9	111,100	746	71,400	480	39,700	266

[a] Not including New Zealand and adjacent islands

[b] Including New Zealand and adjacent islands

2.1.1 Global water cycle

The global water cycle depicted in Figure 2.2 emphasizes the importance of the transfer of atmospheric moisture from sea to land. Oceans receive 79% of global precipitation and contribute 88% of global ET (Dingman 2002). Precipitation on the earth's land surfaces exceeds ET by 40,000 km^3, and this is balanced by an equal amount that is runoff from land to sea. The annual runoff of $40,000\,\mathrm{km}^3$ is the total amount of water potentially available for all human uses, including drinking and other municipal needs, for industry, and for irrigated agriculture (non-irrigated agriculture is fed by rain and returns most of this water to the atmosphere as ET over land). However, only about $12,500\,\mathrm{km}^3$ of runoff is truly accessible, because the majority occurs in lightly populated areas or in seasonal floods that are only partly captured (Postel et al. 1996).

2.1.2 Water balance of a catchment

For any catchment or region, a water balance equation can be written as follows:

$$P + G_{\mathrm{in}} - (Q + \mathrm{ET} + G_{\mathrm{out}}) = \Delta S \qquad (2.1)$$

Where P is precipitation, G_{in} is groundwater inflow to the area, Q is stream outflow, ET is water loss by evapotranspiration, G_{out} is groundwater outflow, and ΔS refers to change in storage (Dingman 2002). When averaged over a period of years with no significant climate trends or anthropogenic influences, changes in storage can be assumed to be zero (but this is not true over short time intervals), and so we can rewrite this equation as:

$$P + G_{\mathrm{in}} = Q + \mathrm{ET} + G_{\mathrm{out}} \qquad (2.2)$$

Runoff includes both surface flow and groundwater outflow, but the latter is usually small and unmeasured, and so the two terms are not always distinguished in common use.

If groundwater inflows and outflows are roughly in balance or small enough to ignore, then precipitation leaves the system as streamflow and ET. These terms vary both spatially and temporally, and thus are primarily responsible for the variability in streamflow that we shall discuss at length later in this chapter. First, it will be helpful to describe each term in more detail.

Precipitation includes rain and snow. Its rate varies more on hourly and daily timescales than over months or years, and we are all familiar with patterns in the average values of the latter, recognized as wet and dry months, and from annual mean values that help define the climate of a region and cause us to remark on unusually wet or dry years. Rain infiltrates the land surface or runs off rapidly, but snow is stored on the earth's surface for hours to months before melting. In many areas snow is the main source of surface water supply and groundwater recharge, and melt water is influential in spring flood cycles and in maintaining summer base flows. In the High Sierras of the western United States, gradual warming since the 1950s has reduced the winter storage of precipitation as ice and snow, and shifted the peak of snowmelt runoff to earlier in the spring (Service 2004). Because winter storage acts as a natural reservoir, melting gradually to provision spring and summer river flows, some have suggested the need for new reservoirs to replace the storage capacity formerly afforded by the snowpack.

ET includes all processes by which water at or near the land surface is returned to the atmosphere (Dingman 2002). Mainly, it includes evaporation from land surfaces and water lost by plants during the exchange of carbon dioxide (CO_2) and oxygen for photosynthesis. Globally, about 62% of precipitation that falls on land becomes ET, and ET exceeds runoff for most rivers and for all continents except Antarctica (Table 2.1). Water loss by plant transpiration constitutes a major flux back to the atmosphere. When an experimental forest in New Hampshire was clear-cut and subsequent regrowth was suppressed with herbicides, stream runoff increased 40% on an annual basis, and 400% during summer (Likens and Bormann 1995). This represented the water that would have returned to the atmosphere primarily via transpiration in an intact forest. Subsequently, when herbicide treatment was suspended, the forest rapidly regenerated with species with high transpiration rates, and streamflow declined to levels below that of the mature forest.

Seasonal variation in ET, due to the combined effects of temperature and water demand by plants, often is greater than seasonal variation in precipitation. This can be seen in comparisons of monthly averages for precipitation and runoff for a series of North American rivers (Figure 2.3), in which ET can be inferred as the difference. In Mediterranean climates, both ET and precipitation can show marked seasonal declines during summer months, creating large precipitation deficits that virtually eliminate groundwater recharge and base flow. In cold climates ET is reduced and so a larger fraction of precipitation leaves the catchment as runoff, as Figure 2.4 illustrates for rivers along the Atlantic Coast from Canada to the southeastern United States.

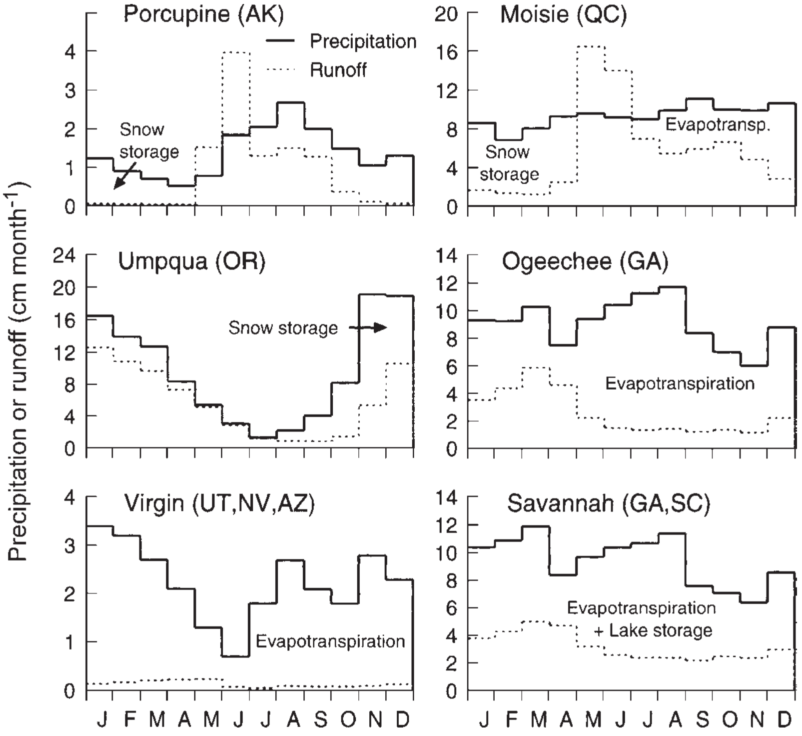

FIGURE 2.3 Patterns of precipitation and runoff for rivers from a diversity of regions in North America. Porcupine River, Alaska, showing snowmelt peak of runoff during low precipitation. Moisie River, Quebec, showing snowmelt peak of runoff. Umpqua River, Oregon, showing runoff peak following seasonal precipitation. Ogeechee River, Georgia, showing runoff pattern caused by seasonal changes in evapotranspiration. Virgin River, Utah, Nevada, Arizona, showing very low runoff due to low precipitation and high evapotranspiration. Savannah River, Georgia and South Carolina, showing flattened runoff pattern due to regulation (compare to Ogeechee). (Reproduced from Benke and Cushing 2005.)

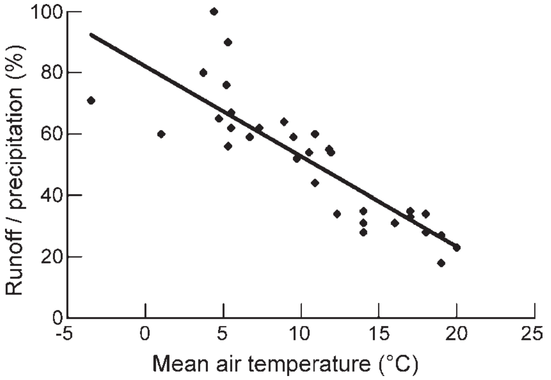

FIGURE 2.4 Annual runoff as a percentage of precipitation versus mean annual air temperature for rivers draining into the Atlantic Ocean from Canada to the southeastern United States. (Reproduced from Allan and Benke 2005.)

2.1.3 Surface versus groundwater pathways

Precipitation destined to become runoff travels by a number of pathways that are influenced by gradient, vegetation cover, soil properties, and antecedent moisture conditions. Some rainwater evaporates from the surface of vegetation immediately during and after a rainstorm, never reaching the ground or being absorbed by plants. This is referred to as interception and is included within ET. Some rainfall passes through spaces in the canopy (throughfall), some runs down stems and trunks (stemflow), and some intercepted water later falls to the ground (canopy drip). The latter two pathways may play a role in nutrient transfers, and will be discussed later.

Once rain or melt water encounters the ground, it follows several pathways in reaching a stream channel or groundwater (Figure 2.5). Approximately three fourths of land-area precipitation infiltrates into the soil. In unsaturated,

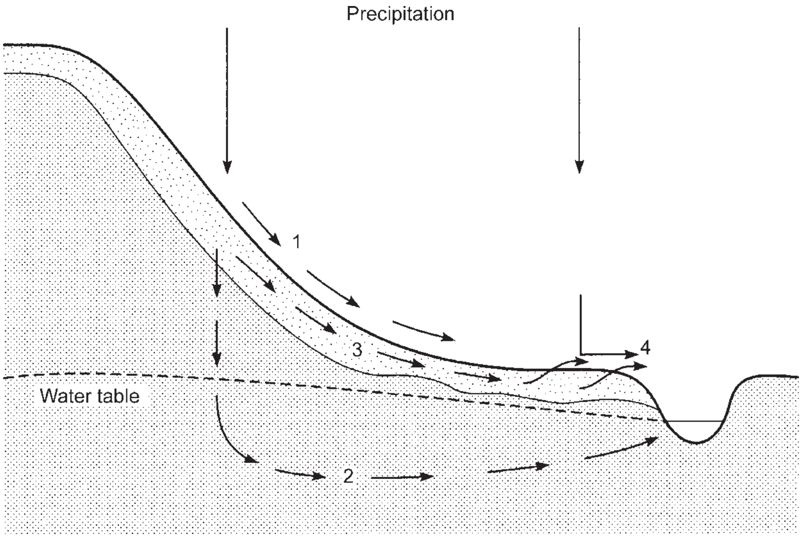

FIGURE 2.5 Pathways of water moving downhill. Overland flow (1) occurs when precipitation exceeds the infiltration capacity of the soil. Water that enters the soil adds to groundwater flow (2) and usually reaches streams, lakes, or the oceans. A relatively impermeable layer will cause water to move laterally through the soil (3) as shallow subsurface stormflow. Saturation of the soil can force subsurface water to rise to the surface where, along with direct precipitation, it forms saturation overland flow (4). The stippled area is relatively permeable topsoil. (Reproduced from Dunne and Leopold 1978.)

porous soils, water infiltrates at some maximum rate, termed the infiltration capacity. This capacity declines during a rain event, normally approaching a constant some 0.5–2 h into the storm (Free et al. 1940). The downward percolation of water results in a series of hydrologic horizons. The unsaturated (vadose) zone lies above the saturated (groundwater, phreatic) zone whose upper limit is the water table surface. Soil moisture usually is least in the rooted zone, which is the uppermost horizon of the unsaturated zone, due to evaporation, plant uptake, and downward infiltration. The water table is the fluctuating upper boundary of the groundwater zone. These horizons fluctuate seasonally depending on rainfall, and generally rise at the end of the growing season when ET is low. Soil moisture thus varies with prior rainfall and season, and the degree of soil saturation influences whether new moisture percolates downward to recharge groundwater, moves laterally through the soil, or rises vertically above the soil surface.

Rain that reaches the groundwater will discharge to the stream slowly and over a long period of time. Base flow or dry-weather flow in a river is due to groundwater entering the stream channel from the saturated zone. Above the saturated zone, some infiltrated water will move downslope as interflow, which is subsurface runoff in response to a storm event (Figure 2.5). Interflow is lowest in unsaturated soils and when grain size (and thus pore size) is small; it can reach 11 m day^{-1} through sandy loam on a steep hill (Linsley et al. 1958). Rainfall in excess of infiltration capacity accumulates on the surface, and any surface water in excess of depression storage capacity will move as an irregular sheet of overland flow. In extreme cases, 50–100% of the rainfall can travel as overland flow (Horton 1945), attaining velocities of 10–500 m h^{-1}. Overland flow tends to occur in semiarid to arid regions, where human activities have created impervious surfaces or compacted the soil, when the surface is frozen, and over smoother surfaces and steeper slopes (Dingman 2002). However, overland flow rarely occurs in undisturbed humid regions because their soils have high infiltration capacities. Lastly, when there is a large rainstorm or a shallow water table, the water table may rise to the ground surface, causing subsurface water to escape from the saturated soil as saturation overland flow. This is composed of return flow forced up from the soil and direct precipitation onto the saturated soil (Dunne and Leopold 1978). Velocities are similar to the lower range of Horton overland flow.

Most rivers continue to flow during periods of little rainfall. These are perennial, as opposed to intermittent, and most of the water in the channel comes from groundwater. In humid regions the water table slopes toward the stream channel, with the consequence that groundwater discharges into the channel. Discharge from the water table into the stream accounts for base flow during periods without precipitation, and also explains why base flow increases as one proceeds downstream, even without tributary input. Such streams are called gaining or effluent (Figure 2.6a). Streams originating at high elevation sometimes flow into drier areas where the local water table is below the bottom of the stream channel. Depending upon permeability of materials underlying the streambed, the stream may lose water into the ground. This is referred to as a losing or influent stream (Figure 2.6b). The same stream can shift between gaining and losing conditions along its course due to changes in underlying lithology and local climate, or temporally due to alternation of base flow and stormflow conditions. The exchange of water between the channel and groundwater will turn out to be important to the dynamics of nutrients and the ecology of the biota that dwells within the substrate of the streambed.

2.2 Streamflow

The volume of flow moving past a point over some time interval is referred to interchangeably as discharge or flow. Usually it is calculated from measurements of width (w), depth (d), and current velocity (v), and expressed in $m^3\ s^{-1}$ or $ft^3\ s^{-1}$ (cfs).

$$Q = wdv \qquad (2.3)$$

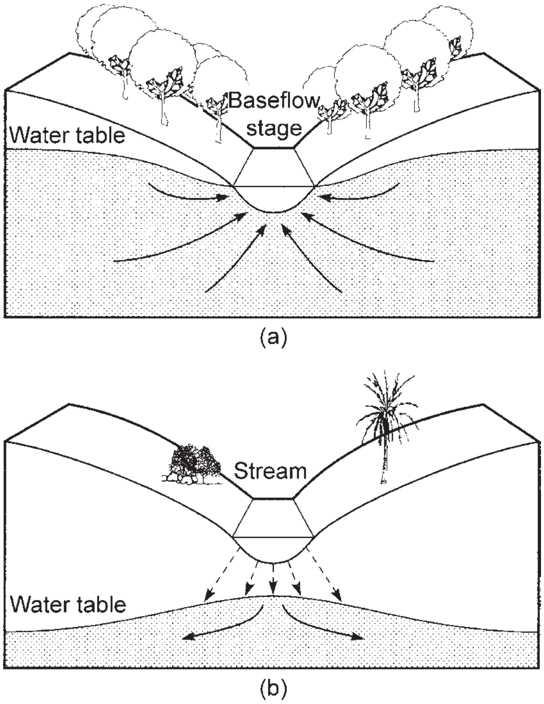

FIGURE 2.6 (a) Cross section of a gaining stream, typical of humid regions, where groundwater recharges the stream. (b) Cross section of a losing stream, typical of arid regions, where streams can recharge groundwater. (Reproduced from Fetter 1988.)

In practice, discharge is estimated by dividing the stream cross section into segments, measuring area and velocity for each, and summing the discharge estimates for the segments (Figure 2.7).

$$Q = \sum a_i v_i \qquad (2.4)$$

Velocity is measured at the midpoint of the segment and (in shallow streams) at 0.6 depth below the surface. At least ten subsections are required, and none should have more than 10% of the total flow (Whiting 2003).

Current velocity varies considerably within a stream's cross section owing to friction with the bottom and sides, and to sinuosity and obstructions. Highest velocities are found where friction is least, generally at or near the surface and near the center of the channel. In shallow streams, velocity is greatest at the surface due to attenuation of friction with the bed, and in deeper rivers, it is greatest just below the surface because of friction with the atmosphere (Gordon et al. 2004). Velocity then decreases as a function of the logarithm of depth (Figure 2.8), approaching zero at the substrate surface. In streams with logarithmic velocity profiles, one can obtain an average value fairly easily by measuring current speed at 0.6 of the depth from the surface to the bottom. At depths >0.75 m, velocities measured at 0.2 and 0.8 beneath the surface can be averaged, and in very turbulent water it may be necessary to measure velocity

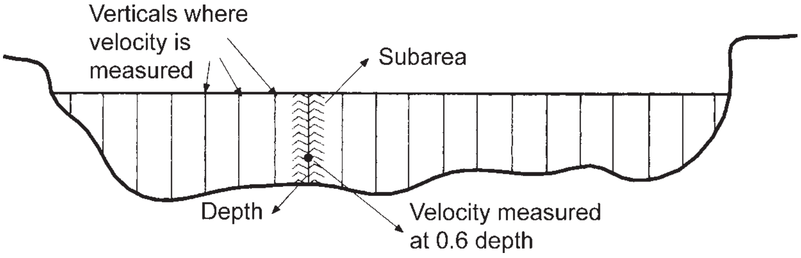

FIGURE 2.7 Estimation of discharge from the integration of point measurements of velocity and associated area of flow in subsections of the channel cross section. Velocity is measured at 0.6 depth from the surface in shallow streams. (Reproduced from Whiting 2003.)

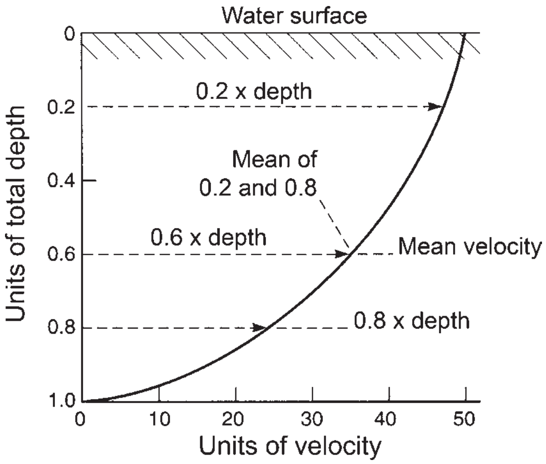

FIGURE 2.8 Current velocity as a function of depth in an open channel. Mean velocity is obtained at a depth of 0.6 from the surface when depth is <0.75 m, and from the average of measurements at 0.2 and 0.8 depth in deeper rivers.

at 0.1 depth intervals. In the absence of an appropriate current meter, floats give a rough measure of surface velocity, which when multiplied by 0.8–0.9 provides an estimate of mean velocity.

Methods of discharge estimation are numerous, but the integration of point measurements of velocity and associated areas of flow is most common (Whiting 2003). Many rivers have permanent gauges consisting of a well on the stream bank, which is connected by a horizontal pipe to the deepest part of the channel to measure river height, or stage. Discharge is then estimated from Equation 2.3 for a range of flow conditions, and a stage-discharge rating curve is constructed for that location. Thereafter, discharge is estimated hourly or continuously by monitoring stage.

Discharge varies over all timescales, from hourly and daily responses to a storm event, through seasonal, annual, and decadal intervals, as well as over historic and geologic time. It usually increases along a stream network due to inputs from tributaries and groundwater. Over a stream reach of a few hundred meters, assuming that inputs from tributaries and groundwater are negligible, discharge should be the same at any of several transects, even though the channel shape and water velocity vary from transect to transect. This is known as the continuity relationship.

2.2.1 The hydrograph

A continuous record of discharge plotted against time is called a hydrograph. It can depict in detail the passage of a flood event over several days (Figure 2.9), or the discharge pattern over a year or more. A hydrograph has a number of characteristics that reflect the pathways and rapidity with which precipitation inputs reach the stream or river. Base flow represents groundwater input to river flow. Rainstorms result in increases above base flow, called stormflow or quickflow. The rising limb will be steepest when overland and shallow subsurface flows predominate, and more gradual when water reaches the stream through deeper pathways. The magnitude of the hydrograph peak is influenced by the severity of the storm and the relative importance of various pathways by which rainwater enters the stream (Figure 2.5). The lag to peak measures the time between the center of mass of rainfall and the peak of the hydrograph. The recession limb describes the return to base flow conditions.

Hydrographs exhibit wide variation over all timescales, from small stream to large river, and among geographic regions, influenced by the amount and distribution of precipitation throughout the year, its storage as snow, the size and topography of the basin, and soil and vegetation characteristics. Substantial overland flow causes a rapid and pronounced rising limb to the hydrograph and can result in significant sediment erosion from the land surface. Such streams are called “flashy”; arid-land streams often are good examples. Since little or no overland flow occurred in a humid New Hampshire forest even after deforestation (Likens and Bormann 1995), it is clear that soil permeability,

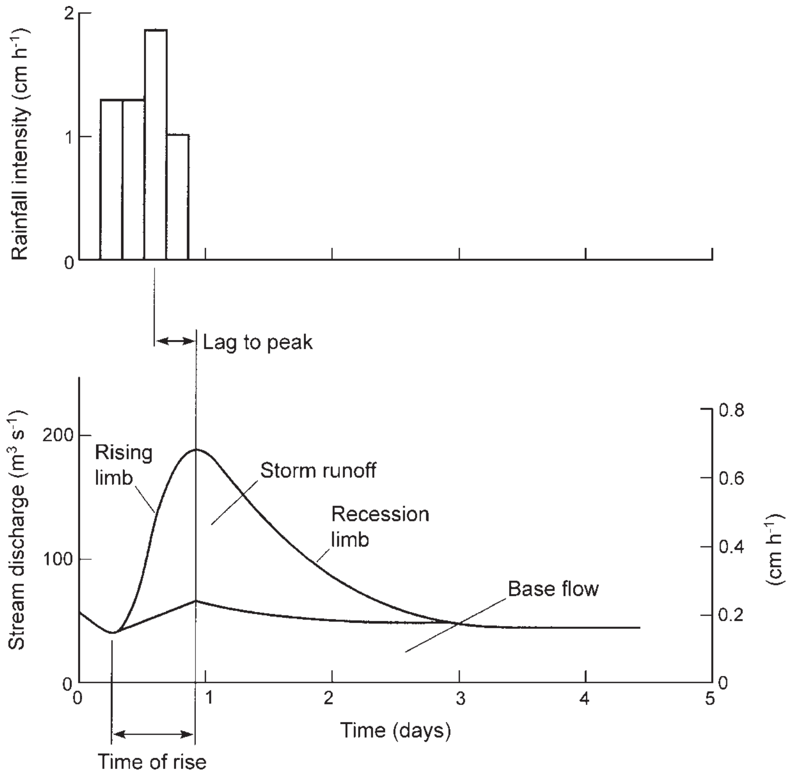

FIGURE 2.9 Streamflow hydrograph resulting from a rainstorm. (Reproduced from Dunne and Leopold 1978.)

enhanced by litter, other organic matter, and root structure, provides an infiltration capacity that rarely is exceeded in forested catchments of humid areas. Because flow is slower in subsurface pathways, this should result in a less pronounced rising limb of the hydrograph. Furthermore, the likelihood of sediment transport from the landscape is reduced, while the transport of dissolved materials is enhanced.

Another general pattern is for flood hydrographs to become broader and less sharp as a river gathers tributaries in a downstream direction. This is due to differences among tributary subbasins in the amount and intensity of precipitation received, causing the sum of tributary inputs to a larger river to be less well defined than the individual events. In addition, a flood peak attenuates as it travels downstream owing to friction and temporary storage. This attenuation will be greatest when a river is connected to its floodplain and has natural bends and channel roughness. However, when a river is straightened and separated from its flood plain by levees, floods will pass very quickly downstream, where they may cause significant damage. The Upper Mississippi experienced a major flood in 1993 in response to a 1-in-200 year rainfall, with an orientation along the river channel that favored the convergence of flood waters, and that occurred during a period of above-normal soil moisture conditions and below-normal ET (Kunkel et al. 1994).

2.3 Flow Variation

The characterization of streamflow has practical application for the design of flood-control structures, evaluation of channel stability, and in determining whether sufficient water is available at the appropriate time to meet the needs of both people and the ecosystem. Abundant data often are available for gauged sites – as much as a century of continuous monitoring – and methods exist that allow extrapolation to ungauged sites. This has led to a great deal of hydrologic analysis of the spatial and temporal variation in streamflow.

Ecologists stress that one must consider five elements of streamflow to ensure that the needs of the stream ecosystem are met. These include the magnitude of flow, its frequency of occurrence, duration and timing of the event, and the rate of rise and fall (Richter et al. 1996). Because these five components are determined by natural variation in climate, vegetation, geology, and terrain, it is argued that rivers of a region have a characteristic flow regime, much like a region has a characteristic climate.

2.3.1 The likelihood of extreme events

Often we wish to know how frequently a flow of a given magnitude is exceeded in an average year, or the likelihood of an extreme annual flood such as one that we might characterize as a 10- or 50-year event. Several methods are available for estimating the probability of extreme events, whether flood or drought. The magnitude of events is inversely related to their frequency (or probability) of occurrence, a relationship captured in a flow-duration curve. These typically are constructed using daily streamflows over many years, so they include both seasonal and interannual variability. A flow-duration curve plots the cumulative frequency of daily records that equal or exceed a given value of average daily discharge against flow magnitude (Figure 2.10). Low flows are equaled or exceeded on most days, whereas high flows are equaled or exceeded only a small percentage of the time.

Several useful metrics are easily obtained from a flow duration graph. The median flow ($Q_{0.50}$) is that exceeded 50% of the time. Because of the influence of a few large floods on the mean value, in humid regions the mean is exceeded only on 20–30% of the days (Dingman 2002). The $Q_{0.05}$ is a streamflow exceeded only 5% of the time (18 days in an average year), so is a reasonable value for high flows that occur infrequently. Similarly $Q_{0.95}$ is a streamflow exceeded 95% of the time. This value indicates how much water is available most of the time, and also provides a threshold below which we can identify extremely low flows. The flow-duration method is an excellent indicator of water availability, but does not by itself provide information on the timing of high and low flows, which may be ecologically significant.

If one wishes to compare among streams, it is usual to normalize flow to drainage area by plotting flow divided by drainage area. Such

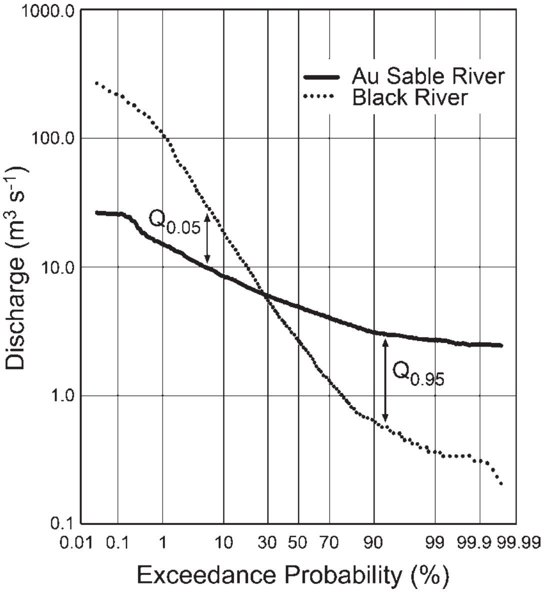

FIGURE 2.10 Flow duration curves for two rivers in Michigan, showing the high flow discharge ($Q_{0.05}$) that is exceeded only 5% of the time, and the low flow discharge ($Q_{0.95}$) that is exceeded 95% of the time. Because the two watersheds are of similar area, discharge was not normalized to drainage area. Graphs were constructed from daily records for 1990–2000.

comparisons distinguish “flashy” from stable streams, as Figure 2.10 illustrates for locations in Michigan. The relatively flat curve of the Au Sable River indicates stable flow throughout the year compared to the much more variable Black River.

Estimating the probability of an extreme annual flood, such as one that might occur on average once in 10 or 50 years, also is useful. Typically one estimates the probability of a “1-in-*N*-year” flood event of a given size or larger. Thus, a 1-in-100-year flood has a 1% likelihood of occurring in any year and the average recurrence interval is 100 years between two floods of that magnitude or larger. Flood probability (P) and average recurrence (T) are reciprocals:

$$P = \frac{1}{T} \tag{2.5}$$

Given a record of annual maximum flows or other measures of flood events, a number of methods can be used to estimate P and T (Gordon et al. 2004). One begins with a list of the single highest flow of each year, preferably based on the peak of the flood hydrograph rather than average daily discharge. This is especially important in small rivers where the peak flow passes in hours and will be underestimated by the daily average, although this may not be critical for large rivers. By fitting a probability distribution to the data set, it is possible to predict the average recurrence interval for floods of a given magnitude or, conversely, the magnitude of the flood that occurs with a given frequency. The recurrence interval (T) for an individual flood is calculated as:

$$T = \frac{n+1}{m} \tag{2.6}$$

where $n =$ years of record and $m =$ rank magnitude of that flood. The largest event is scored as $m = 1$. Figure 2.11 illustrates flood-frequency curves for Sycamore Creek, Arizona, which experiences irregular flash floods, and for the upper reaches of the Colorado River, with a highly repeatable, snowmelt-driven flow regime. The recurrence interval for floods of a given magnitude is read directly from the graph. One can also determine the likelihood ($1/T$) that the annual maximum flood for a given year will equal or exceed the value of a 10-year, 20-year, or 50-year flood event.

Flood-frequency analysis can also be used to estimate the flood magnitude that has a 1- to 2-year recurrence. This is often considered to be an estimate of the flood that just overtops the banks, the bankfull discharge (Q_{bkf}), which in turn is a surrogate for the effective discharge, the flow that is considered most influential in maintaining channel form (discussed further in Chapter 3).

Estimating the likelihood of rare events obviously is risky, and becomes more so when only a short hydrologic record is available for analysis. In addition to the possibility that any given string of years can include an individual flood whose true recurrence interval is actually much longer than the record, changes in land use or climate can result in a heterogeneous data set. For instance, the flood-frequency curves for a river before and after construction of a major dam, large-scale deforestation, or urbanization likely will be very different.

2.3.2 Effect of land use on streamflow

Human alteration of land use can have major effects on streamflow by altering the balance between ET and runoff, and by altering runoff pathways. In extreme circumstances land-use change can even alter precipitation, as when deforestation reduces ET over a large area, thus lowering atmospheric moisture (of concern for the Amazon Basin, Lean and Warrilow 1989). Owing to their extensive canopy coverage and deeper roots relative to the majority of shorter vegetation, interception and transpiration of water by forests is near maximal. Thus deforestation usually increases streamflow, especially dry-season flow, as noted earlier for Hubbard

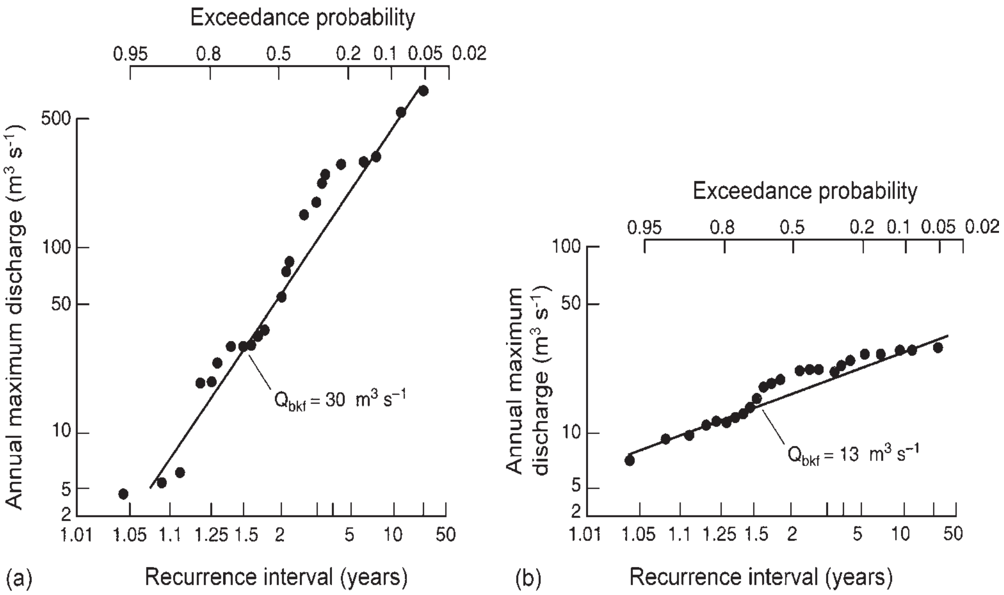

FIGURE 2.11 Example of a flood-frequency analysis for two rivers, based on annual peak instantaneous flows from a 20-plus year gauge record. The bankfull flood (Q_{bkf}) is estimated using $T = 1.5$ years, and the probability or recurrence interval for more extreme events (e.g., 20- and 50-year floods) can be read from the graph. Lines are fitted by eye. (a) Sycamore Creek, Arizona, is an arid land stream subject to flash floods. (b) The Colorado River in its upper reaches, near Grand Lake, Colorado, has a highly regular snowmelt-driven hydrograph. Note the steeper slope of the graph for Sycamore Creek.

Brook. Where agriculture replaces forest with crops, it tends to increase average flow, dry-season flow, and peak flows for smaller floods but has little effect on larger floods (Dingman 2002). Development of drainage systems, such as tiles buried beneath the soil surface, and channel deepening and straightening for flow conveyance, have the further effects of speeding subsurface flows and downstream routing of a rain event. Conversion of wetlands into agricultural usage may also contribute to river flooding, since wetlands naturally are locations of surface storage and frequently of groundwater recharge as well.

Urbanization can have a very strong influence on streamflows (Dingman 2002). Replacement of vegetation with pavement and buildings reduces transpiration and infiltration, and these impervious surfaces substantially increase the amount of runoff that travels by rapid overland flow. Storm sewers and roadways transport water quickly, and so may require the construction of retention ponds in an effort to retard the flood peak. Runoff approximately doubles when impervious surface area is 10–20% of catchment area and triples at 35–50% impervious surface area (Arnold and Gibbons 1996) (Figure 2.12). Flood peaks increase, time to peak shortens, and the peak becomes narrower (Paul and Meyer 2001). Because a greater fraction of the water is exported as runoff, less recharge of groundwater occurs, and so base flows are reduced as well.

2.3.3 The flow regime

Characterization of the spatial and temporal variability of streamflow identifies a limited

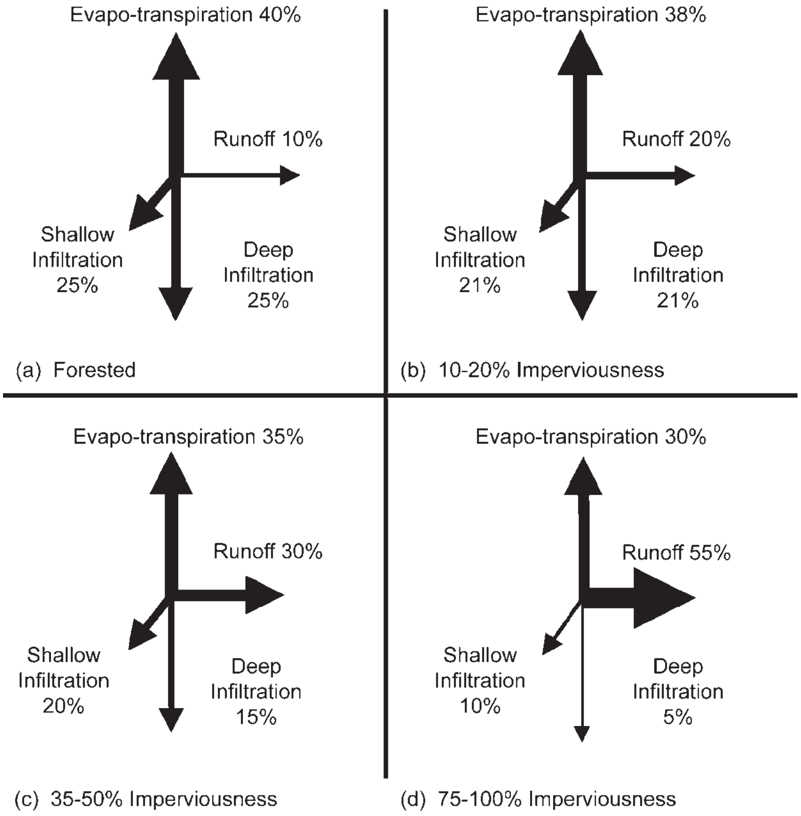

FIGURE 2.12 Changes in hydrologic flows with increasing impervious surface cover in urbanizing catchments. (Reproduced from Paul and Meyer 2001, after Arnold and Gibbons 1996.)

number of flow regimes that show some geographic clustering, referred to as a “hydroclimatology” or “hydrogeography.” Based on a large number of descriptors of flow variability and predictability, Poff and Ward (1989) identified ten distinctive flow regimes within the United States, including seven permanent and three intermittent stream types. Examples include the highly predictable snowmelt regime of the Upper Colorado River; the stable flows of groundwater-fed Augusta Creek, Michigan; the winter rainy hydrograph of McKenzie Creek, Oregon; and the relatively continuously variable Satilla River, Georgia (Figure 2.13). Further analysis using 420 stream gauges distributed across the coterminous United States and selected to represent minimal human modification of streamflow documented a regional clustering indicative of differences in climatic and geologic features (Poff 1996). In a separate analysis of 559 gages for the period 1941–1988, Lins (1997) identified 11 distinct regional streamflow regimes. Interestingly, these did not correspond well to the 18 hydrologic accounting units (HUCs, see Table 1.3) within the United States.

Although the characterization of flow regimes into regionally distinct groups may continue to be refined, the concept that each individual river has a natural flow regime upon which its ecological integrity depends has become firmly established (Poff et al. 1997) (Figure 2.14). The magnitude of flow is the volume of water

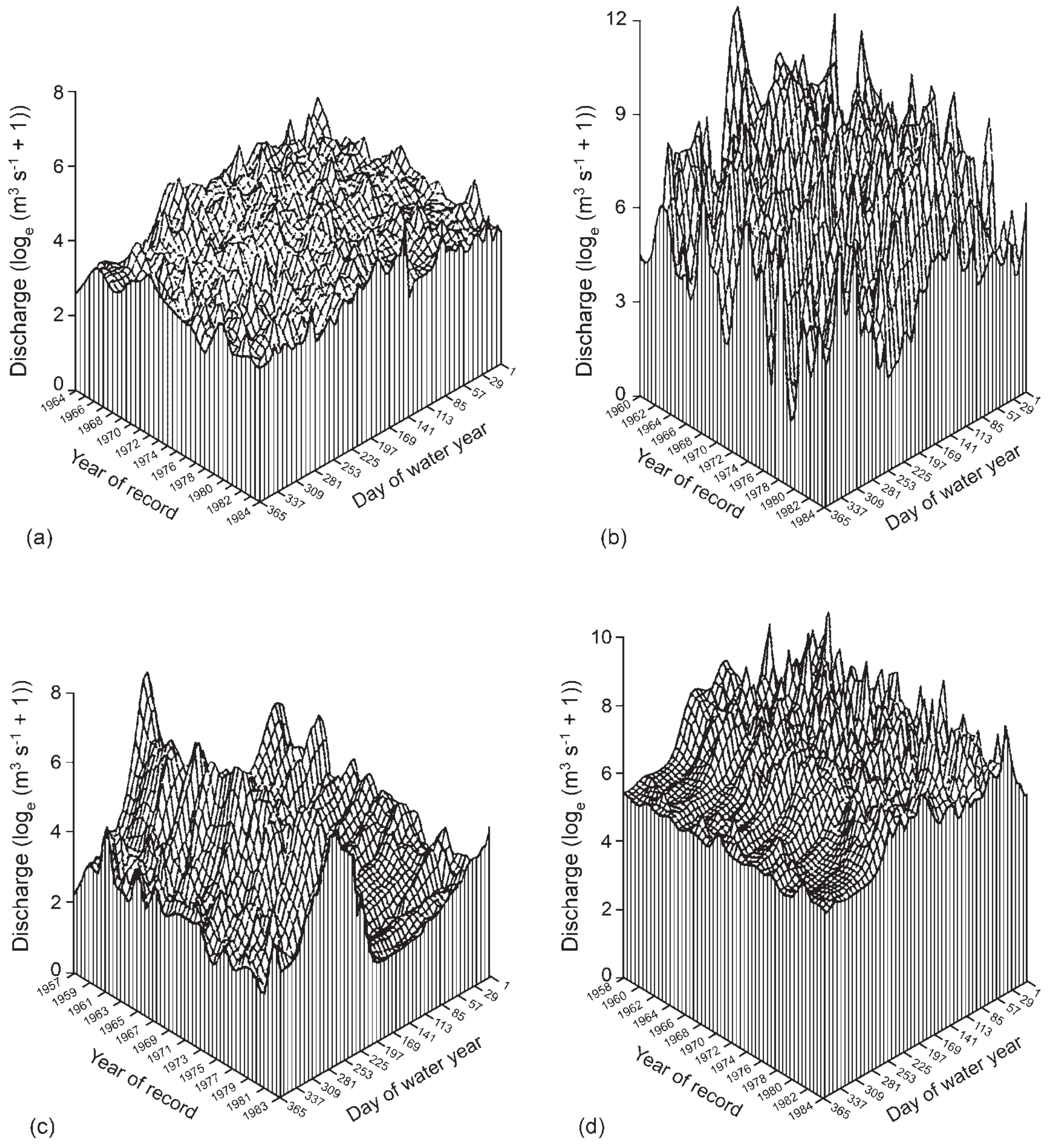

FIGURE 2.13 Patterns in streamflow variability based on long-term daily mean discharge records for four different stream "types." Water year is 1 October–30 September. Four of nine flow categories of Poff and Ward (1989) are shown: (a) "mesic groundwater" Augusta Creek, Michigan; (b) "perennially flashy" Satilla River, Georgia; (c) "snowmelt" Colorado River, Colorado; (d) "winter rain" South Fork of the McKenzie, Oregon. (Reproduced from Poff and Ward 1989.)

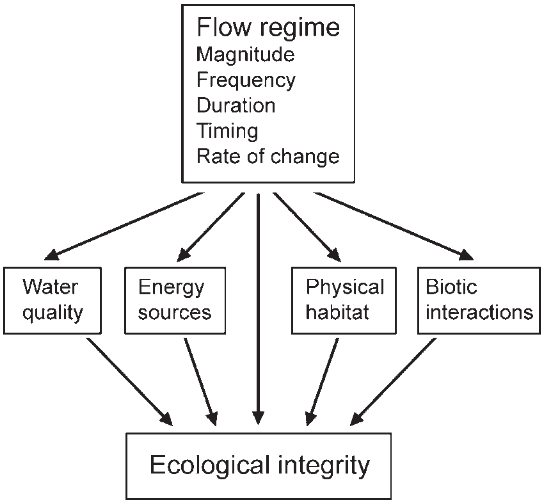

FIGURE 2.14. Streamflow as a master variable. (Reproduced from Poff et al. 1997.)

moving past a point per unit time. Frequency is a measure of how often a flow of a given magnitude occurs, and is inversely related to magnitude. Duration, timing (predictability), and rate of change all describe temporal aspects of flow events. Climate, vegetation, geology, and terrain determine the natural flow regime, as discussed earlier; and humans alter flow regimes by changing flow pathways and response times, and even by altering climate. In highly regulated rivers, once-seasonal flows have become nearly constant due to impoundment of water during seasons of high flow and its later release during periods of low flows. Based on 21 sites with adequate long-term hydrologic records, Magilligan and Nislow (2005) found that dams generally caused increases in low-flow and decreases in high-flow statistics, reduced seasonality, and caused a decline in the mean rate of rise and fall. Many other changes occur as a consequence, in both channel features and ecology, and in response river managers have experimentally released large volumes of water to test the restoration potential of artificial floods (Figure 2.15). At the other extreme, rivers become much flashier when changes to the landscape including drainage tiles, ditches, stormwater conveyances, and impervious surfaces all result in more event-responsive runoff (Figure 2.16). Stream responses to altered flow regimes include channel adjustments, interruption of the recruitment cycle of riparian plants, loss of spawning cues for fishes and numerous habitat changes (Poff et al. 1997). Low flow events

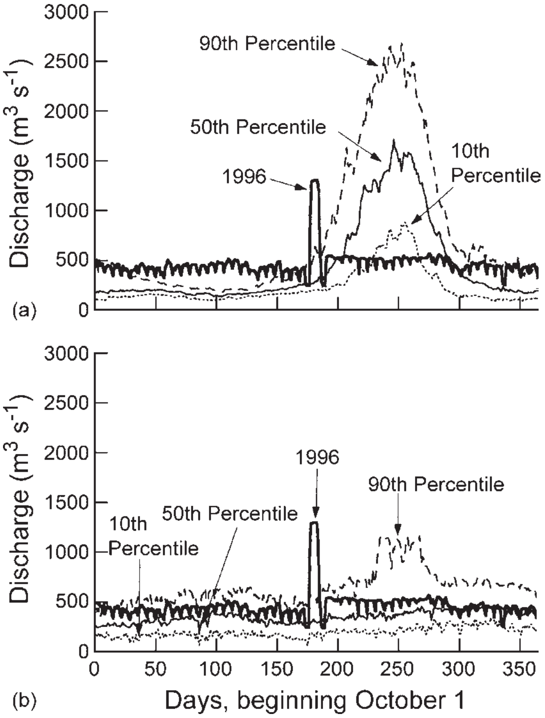

FIGURE 2.15 The Glen Canyon Dam (closed in 1963) transformed the lower Colorado River from a spring-pulse system (a) to a regulated system (b). An experimental flood in March 1996 was a high flow event for the regulated river, but below average for the unregulated Colorado. The 1996 hydrograph (heavy black line in both panels) is compared to long-term average hydrographs for the Colorado River at Lee's Ferry, Arizona, for the (a) pre-dam (1922–1962) and (b) post-dam (1963–1995) periods. The dashed, solid, and dotted lines connect the mean daily discharge values below which 90%, 50%, and 10% of the years, respectively, occur. (Reproduced from Schmidt et al. 1998.)

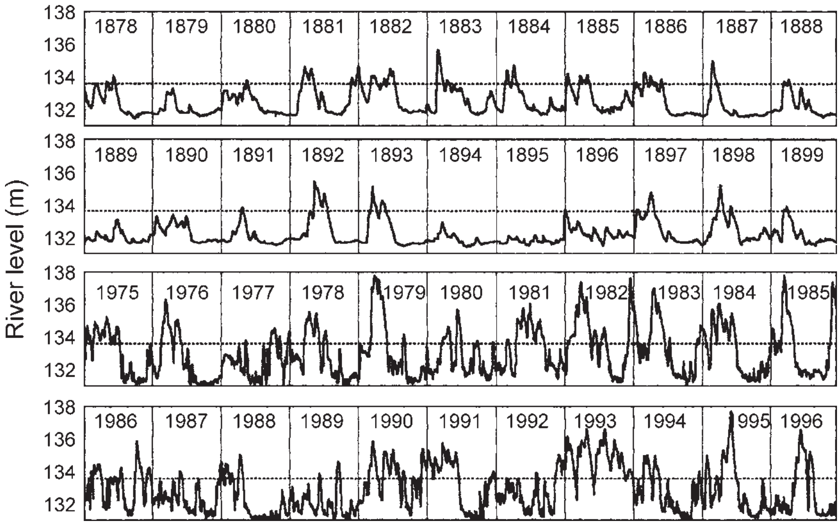

FIGURE 2.16. River stage (in meters above mean sea level [msl]) at Illinois River mile 137 before water diversions and modern navigation dams (1878–1899) and after many alterations in the catchment and river (1975–1996). Each block shows a year from January to December. The horizontal line indicates a flood at which economic damage occurs. (Reproduced from Sparks et al. 1998.)

including droughts have received less attention than high-flow events and altered variability. Direct and indirect responses include dewatering, deterioration of water quality, loss of longitudinal connectivity, and changes to habitat and food resources (Lake 2003).

Patterns in streamflow have been shown to be good indicators of biological attributes of streams. Stream fish assemblages totaling 106 species from 34 sites in Wisconsin and Minnesota were clustered into two groups based on functional traits describing their habitat, trophic, morphological, and tolerance characteristics (Poff and Allan 1995). Independent hydrological analysis of streamflow variability and predictability clearly separated the two ecologically defined fish assemblages. In support of theoretical expectations, streams with more variable flows tended to support resource generalists, and streams with more stable flows had a higher proportion of specialist species. When small streams in the Etowah River Catchment, Georgia, were separated into groups based on impervious surface and then characterized hydrologically, increased imperviousness was correlated with several measures of "flashiness," and with decreased richness of endemic, cosmopolitan, and sensitive fish species, and decreased abundance of slow-water species (Roy et al. 2005). The extreme flow conditions associated with urbanization can have very strong effects on the biota. Degradation of macroinvertebrate communities of urban streams in and around Melbourne, Australia, was well explained by the degree of imperviousness and was especially severe where stormwater drainage systems were highly connected to stream channels, even at low urban densities (Walsh et al. 2001).

The reasons that individual species are associated with particular flow regimes obviously will be very specific, but it has been argued that four key flow-related processes underlie the decline in biological condition of flow-modified streams (Bunn and Arthington 2002). These are loss or alteration of habitat, disruption of life history processes and recruitment of young, loss of lateral and longitudinal connectivity, and greater susceptibility to invasive species. Because many organisms have specific adaptations that enable them to persist under the environmental conditions associated with specific flows, and some are adapted to exploit historical cycles of floods and droughts, changes to the predictability and variability of streamflow are likely to test the organism's adaptability and thus its ability to survive (Lytle and Poff 2004).

2.3.4 Environmental flows

The science of environmental flow assessment has developed in response to the recognition of the extent of flow alteration worldwide, and the need to assess ecological degradation and set acceptable levels. At present, there are many different methods to assess environmental flows as well as a wide range of flow recommendations. Consider these extremes: 10% of the mean annual flow (MAF) is used in some countries in Europe (Tharme 2003), and the need for as much as 80% of the MAF is supported by research in some rivers in Queensland, Australia (Arthington and Pusey 2003).

Tharme (2003) identified some 207 methodologies for environmental flow assessment recorded from 44 countries within six world regions. Some methods are as simple as setting an annual or minimal flow volume, but increasingly a comprehensive combination of monthly and event-based (low flows and flood pulses) allocations is preferred. The most common approach is hydrological, using daily or monthly flow records and some threshold, often a minimum flow. The most widely used method worldwide, the Tennant method (Tennant 1976), uses a percentage of MAF, adjusted seasonally to recommend minimum flows. Many variants and thresholds are used (Reiser et al. 1989, Tharme 2003), some as low as 5% and 10% of MAF. Exceedance percentiles based on flow duration curves are a similar approach, often applied for a daily or 7-day interval by season to set minimal flows. A more comprehensive statistical characterization of flow is captured using the indicators of hydrologic alteration (IHA) software that uses 32 different hydrologic indices derived from long-term, daily flow records and grouped into the five categories of the flow regime (Richter et al. 1996, 1997). Although these methods are all intended to characterize ecologically relevant flows, evidence that these indices protect ecological attributes of streams needs to be strengthened (Tharme 2003).

Another common approach, employed mainly in the northern hemisphere, uses hydrodynamic habitat modeling, usually to set a minimum flow considered sufficient to sustain target species or the entire biological community. The instream flow incremental methodology (IFIM, Stalnaker and Arnette 1976) was an early example of this approach, intended to model the quantity and suitability of biological habitat using hydraulic variables such as depth, velocity, and substrate. Hydraulic and habitat simulation models then are combined to predict changes in available habitat in response to changes in flow on a species-specific basis. Tharme (2003) reports that this approach is used in at least 20 countries, despite extensive criticisms of the model approach and the often poor or untested ecological predictive capability of IFIM output. Estimating the wetted perimeter as an indication of available habitat is simpler than IFIM and is widely used (Reiser et al. 1989). The relationship between discharge and wetted perimeter is estimated, often for riffles because they tend to be areas of high macroinvertebrate production and are first to go dry. Streams in Montana showed clear breakpoints such that flows at 10% of the MAF protected about half of the maximum wetted perimeter and flows >30% of MAF protected nearly all of the maximum wetted perimeter (Tennant 1976). In an Australian application of this approach, Gippel and Stewardson (1998) showed that breakpoints sometimes are hard to identify, and questioned whether the resultant flow recommendation is sufficient for either macroinvertebrates or fish.

A holistic, ecosystem approach is now at the forefront of environmental flow methodologies, drawing upon hydrological, hydraulic, and habitat analyses, and expert judgment to construct a suitable flow regime for a managed system. These are increasingly complex and interdisciplinary undertakings, allowing the evaluation of alternative scenarios, and designed with the intent to protect the river ecosystem while meeting human needs (Postel and Richter 2003) (Figure 2.17).

The answer to the question, "how much water does a river need?" is beginning to take shape. Rivers and their floodplains need most of the spatial and temporal variability of their natural flow regime to maintain their ecological integrity (Poff et al. 1997, Richter et al. 2003). More research is needed to verify the ecological outcomes of flow management scenarios, and to identify the critical thresholds for environmental flows that will ensure low risk of environmental degradation. Because the ability to connect ecological outcomes to specific flow recommendations is central to the development of environmental water requirements and their adoption by water managers, we require long-term hydrologic experiments to fully understand the ecological consequences of various flows.

2.4 Summary

Fluvial ecosystems exhibit tremendous variability in the quantity, timing, and temporal patterns of river flow, and this profoundly influences their physical, chemical, and biological condition. Vast quantities of fresh water are extracted to meet agricultural, municipal, and industrial demands, yet freshwater ecosystems also need enough water, of sufficient quality and at the right time, to remain ecologically intact and provide economically valuable commodities and services to society. Increasingly today, the tools of hydrologic analysis are being combined with other elements of river science to address the

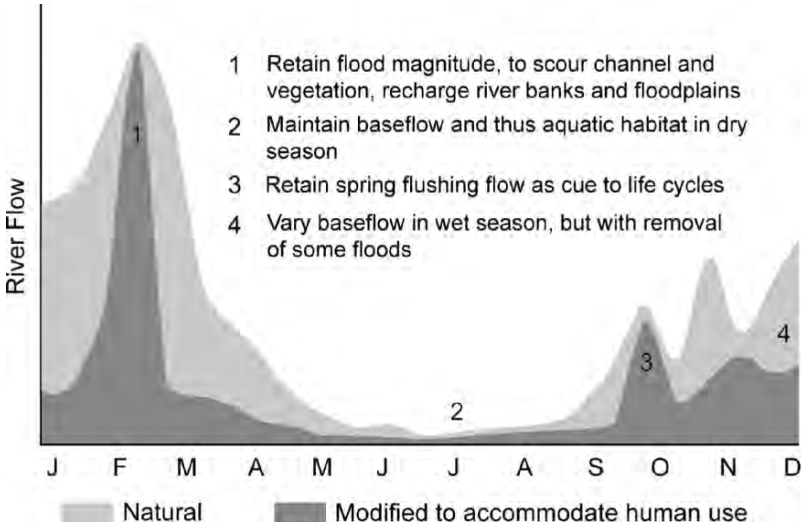

FIGURE 2.17 Natural (light shading) and modified (dark shading) hydrographs for selected rivers in South Africa, illustrating a flow scenario that provides only half as much water as the natural hydrograph and is intended to accommodate human uses while keeping the river as healthy as possible. This scenario illustrates some key principles identified by a panel of scientists. (Reproduced from Postel and Richter 2003, after Tharme and King 1998.)

question, "How much water does a river need?" and ensure that flows are sufficient to protect and restore stream ecosystems.

The hydrologic cycle describes the continuous cycling of water from atmosphere to earth and oceans, and back to the atmosphere. Evaporation from the oceans exceeds that over land, while precipitation on the earth's land surfaces exceeds evaporation and plant water loss. This excess provides the runoff from land to sea that is primarily river discharge, but includes groundwater as well. At the scale of an individual catchment and averaged over years, a water budget consists of inputs from precipitation and groundwater inflow, and outputs due to streamflow, ET (water loss from evaporation and by plants), and groundwater outflow. Over short time intervals, imbalances between inputs and outflows result in increases or decreases in storage. Globally, almost two thirds of precipitation that falls on land becomes ET, and ET exceeds runoff for most rivers and for all continents except Antarctica. Both precipitation and ET vary with climate and vegetation, resulting in seasonal and regional differences in the amount and timing of streamflow.

Precipitation destined to become runoff travels by a number of pathways that are influenced by gradient, vegetation cover, soil properties, and antecedent moisture conditions. Surface and shallow subsurface flows reach streams much more quickly than water that percolates to the water table and discharges into the stream as groundwater. Thus the stream hydrograph, which describes the rise and fall of streamflow over time, will exhibit a strong or a more gradual response to a rain event depending on soils, slopes, and human actions that affect flow paths. Most rivers continue to flow during periods of little rainfall, and this base flow comes from groundwater that discharges into the channel more or less continuously, depending on fluctuation in the level of the water table.

The characterization of streamflow has practical application for the design of flood-control structures, evaluation of channel stability, and in determining whether sufficient water is available at the appropriate time to meet the needs of both people and the ecosystem. One can estimate the frequency with which flows of a given magnitude are expected to occur, or the probability of occurrence of a flow of a given magnitude. The flood magnitude that has a 1- to 2-year recurrence is often used as an estimate of the flood that just overtops the banks, which is the flow considered most influential in maintaining channel form.

Flow analyses tell us that each individual river has a natural flow regime characterized by the magnitude of flows and their frequencies, as well as duration, timing, and rate of change. Climate, vegetation, geology, and terrain place broad constraints on natural flow regime, conditions at the catchment scale make each river to some degree unique, and a wide range of human influences further alter flow regimes by changing flow pathways and response times, and even by altering climate. In highly regulated rivers, once-seasonal flows have become nearly constant due to impoundments, whereas other rivers have become much flashier owing to changes in stormwater conveyance and impervious surfaces. The science of environmental flow assessment has developed in response to the recognition that river flows are being altered everywhere, causing widespread ecological degradation. Present evidence suggests that rivers and their floodplains need much of the spatial and temporal variability of their natural flow regime to maintain their ecological integrity. Our ability to prescribe environmental flows that protect the fluvial ecosystem and meet human needs is in its infancy, but promises to make important contributions to river health.

Chapter three

Fluvial geomorphology

Before the close of the 18th century, the erosive capabilities of running water were not appreciated. Streams were believed to flow in valleys because the valleys were already there, not because the stream cut the valley. Catastrophism, with its emphasis on the biblical flood as the final stage in the shaping of the earth's surface, obviously influenced this perspective (Morisawa 1968). By the late 1700s, however, geologists reasoned that the dendritic pattern of drainage nets gave evidence of erosion, as did the observation that valleys in headwaters are smaller than valleys downriver. Modern study of geomorphology focuses on the linkages among channel, floodplain, network, and catchment, and employs such diverse approaches as stratigraphic analyses, experimental studies of sediment transport in flumes, modeling of physical processes, comparisons of landforms, and sophisticated statistical approaches to gain greater understanding of the physical dynamics of river systems (Kondolf and Piégay 2003). The field of fluvial geomorphology is the study of landforms generally, but in particular the study of river channels and drainage networks, emphasizing the dynamic interplay between rivers and landscapes. This chapter summarizes some of the main ideas of this field; readers wishing more depth should consult the books of Leopold et al. (1964), Leopold (1994), Kondolf and Piégay (2003), and Gordon et al. (2004). Fluvial geomorphology is important to stream ecologists for several reasons. It helps make sense of the enormous variety of rivers and streams introduced in Chapter 1, revealing how stream channels are shaped and suggesting useful ways to classify stream types. Variability in riverine features over space and time is responsible for the diverse range of habitats in which organisms live. In addition, quantification of the relationships among river features and analysis of the underlying processes contribute to a deeper understanding of how rivers and riverine habitats change in response to environmental influences, both natural and anthropogenic. This knowledge can in turn be used to avoid unwise management choices and inform the design of healthier rivers in anthropogenic landscapes.

A central theme in fluvial geomorphology is that alluvial rivers determine the location and shape of their channels through complex interactions among hydrology, geology, topography, and vegetation (Leopold et al. 1964, Richards 1982). The development of stream channels and entire drainage networks, and the existence of various regular patterns in the shape of channels, indicate that rivers are in dynamic equilibrium between erosion and deposition, and governed by common hydraulic processes. However, because channel geometry is three dimensional with a long profile, a cross section, and a plan view (what one would see from the air), and because these mutually adjust over a timescale of years to centuries, cause and effect are difficult to establish. Leopold and Maddock (1953) argue that discharge, sediment load, and the elevational extent of the stream are extrinsic variables that the river cannot control, and therefore must adjust to. For a particular reach, slope exerts significant control over channel characteristics because it adjusts more slowly than other variables including channel width and depth, velocity, grain size of sediment load, bed roughness, and the degree of sinuosity and braiding. In concept, the mutual adjustment of these variables results in a graded stream, one whose shape exhibits a balance between its transporting capacity and the sediment load available to it. In reality, changing climatic and other factors may prevent a reach from achieving or remaining in such an ideal state for a long time. The usefulness of this concept lies in the fact that streams tend to respond to perturbation by moving in the direction of some equilibrium state.

We begin by describing the shape and form of rivers – along their length, as seen from above, and as viewed across the channel and the valley. Rivers exhibit a number of remarkably predictable relationships among key hydrologic and geometric variables, and we will explore the underlying processes that account for these patterns. The central idea guiding this chapter is that streams seek a state of dynamic equilibrium, which is a function of the flow and sediment associated with a main channel and a flood-prone area (Leopold et al. 1964). Stream channels tend to develop a stable dimension, pattern, and profile, features that are maintained in the face of episodes of high flows, sediment transport, and channel movement, and so it is the relationships that are predictable even though particular channel features may change. We begin by describing the patterns in channel shape, and later consider the processes responsible for these patterns.

3.1 The Drainage Network

Water on the ground surface moves downhill, creating small channels or rills that, over time, become persistent channels. The channels join others, forming a treelike network of increasing drainage area. In reality, each additional tributary causes drainage area to increase in steps, rather than smoothly, but as an approximation, channel length increases as the 0.6 power of drainage area[1] increases. Stream networks generally increase in length more than width, and develop particular shapes depending on topography and the erodibility of the land surface. A stream draining a narrow valley often results in a central channel with numerous, short tributaries entering almost at right angles, whereas more gentle terrain can lead to a rounder drainage basin. Various descriptive terms (dendritic, radial, rectangular, trellis) are used to describe these patterns. Drainage density (the sum of channel length divided by drainage area, in km/km^2) is a measure of how finely dissected the network is, and tends to be lower in more xeric (drier) locations. Relief ratio is the elevation difference divided by river length along the main axis, and thus is related to gradient and the pathway that the river takes.

At the upstream origin of the drainage network, near the drainage divide, a very large number of very small channels carry water only during storms, but at some point the upstream area is sufficient to generate year-round flow. This is the point where perennial flow begins, and defines the beginning of a first-order stream. Above the first-order stream lies an ephemeral stream flowing only during wet periods (and shown as dashed blue lines on topographic

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[1] Drainage area is the term commonly used when discussing the river network, and refers to the total area drained by the multitude of tributaries that feed the main channel or set of channels. It is interchangeable with catchment and (in American usage) watershed area. River basin can also be substituted, although the convention is to restrict its use to very large rivers.

maps). The exact transition between an ephemeral and first-order perennial channel is indistinct, and migrates up- and downslope depending on precipitation.

Stream order is a useful measure because it describes the position of a stream in the hierarchy of tributaries (Table 1.1). The union of two first-order streams forms a second-order stream, defined as having only first-order channels as tributaries. A third-order stream is formed by the coalescence of two second-order streams, and so on (Figure 1.2). This system, originated by Horton (1945) and later refined by Strahler (1952), is perhaps the most widely used classification system for streams and rivers, but it has limitations (Hughes and Omernik 1983, Richards 1982). The identification of first-order streams is challenging, and if done using maps, will vary with map scale (1:24,000 or 1:25,000 is recommended), thereby affecting all higher-order designations. Because of differences in drainage density across regions, stream size and stream order may not correlate well. In addition, this approach ignores the entry of streams of order n into order $n + 1$. Link classification incorporates the addition of first-order streams into higher-order branches of a drainage network, but shares the other failings.

Nonetheless, stream order has been a durable concept because of its simplicity and its usefulness. In addition, stream order classification is useful as a correlate of other catchment variables. Mean length, total number, and to a lesser degree mean slope all form straight lines when their logarithmic values are plotted against stream order. There are usually some three to four times as many streams of order $n - 1$ as of order n (the bifurcation ratio), each of which is roughly less than half as long as the stream of next higher order, and drains somewhat more than one fifth of the area. These ratios can be verified by inspection of Table 1.1, which summarizes the number, lengths, and drainage areas of US streams of order 1–10. This table shows convincingly that the vast majority of streams are of low order. Typically, first- to third-order streams comprise 70–80% of the total length of perennial channels in a catchment, emphasizing how land–water connections are tightly coupled in headwaters. The river continuum concept (Figure 1.7) uses stream order as its physical template, and many stream ecologists find stream order to be a convenient indicator of size and longitudinal position.

3.2 The Stream Channel

The shape of the cross section of a stream channel is a function of the interaction between discharge and sediment, the erodibility of its bed and banks, the stabilizing influence of vegetation, and any large structure (boulders, large wood [LW]) that can influence local channel conditions. A cross-sectional survey maps the shape of the channel and measures depth at multiple points, effectively creating a series of cells of known width and depth, whose product is summed to determine the area (Figure 2.7). Mean depth can then be estimated as area divided by width. The location of maximum depth within the channel is known as the thalweg.

Channel shape and cross-sectional area will differ from transect to transect even within a reach, as some locations are wide and shallow, others narrow and deep. Water discharge must be the same at each transect, barring tributary inputs and groundwater exchange, but area and shape need not. Channel cross sections are more regular, often trapezoidal, in straight stretches but are asymmetric at curves or bends, where the greatest depth and velocity usually are at the outer bank (Figure 3.1). Sediment deposition forms point bars along the inner bank due to reduced velocity and the helicoidal flow within the bend, in which near-bed current flows from the outside toward the inside of the bend. Anglers make use of these shallow and gently sloping regions of streambed to cast toward the deeper water on the far bank. In steep, narrow valleys, channels are confined by topography, whereas flat, wide valleys allow more lateral movement and meandering (Figure 3.2).

The bankfull stage, or depth of water where overbank flooding occurs, can be determined by direct observation if a well-developed floodplain is present. Often this boundary is less apparent, and so it is estimated in various ways. A change in the topography, the elevation of point bars, the level of woody vegetation on the bank, and obvious signs of scouring are useful clues in establishing the bankfull channel. The dimensions of the wetted channel are of obvious importance to the aquatic biota and change frequently with fluctuations in discharge, whereas the bankfull dimensions are of particular importance in interpreting fluvial processes.

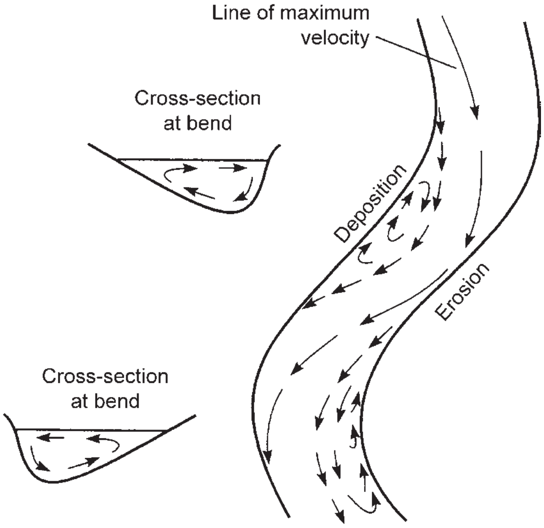

FIGURE 3.1 A meandering reach, showing the line of maximum velocity and the separation of flow that produces areas of deposition and erosion. Cross sections show the lateral movement of water at bends. (Reproduced from Morisawa 1968.)

3.2.1 Hydraulic geometry

Rivers generally increase in size as one proceeds downstream, because tributaries and groundwater add to the flow. Since discharge $Q = wdv$ (see Equation 2.3), any increase in discharge must result in an increase in width, depth, velocity, or some combination of these. Figure 3.3 illustrates these relationships for the Powder River and its tributaries in Wyoming and Montana. A similar graph can be constructed from the fluctuations in river discharge over time at a single station. Hydraulic geometry, as defined by Leopold and Maddock (1953), describes the relationships among hydraulic characteristics, chiefly width, depth, velocity, and discharge. Power equations provide good fits to empirical data.

$$w = aQ^{b} \tag{3.1}$$

$$d = cQ^{f} \tag{3.2}$$

$$v = kQ^{m} \tag{3.3}$$

Because $Q = w \times d \times v$, it follows that $a \times c \times k = 1$ and $b + f + m = 1$.

Early work suggested that a fixed set of coefficients related changes in width, depth, and velocity to discharge along a river's length, while

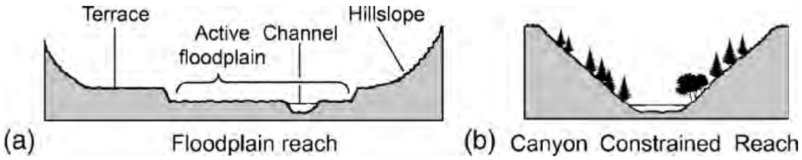

FIGURE 3.2 (a) Diagrammatic cross section of a valley showing present channel, the floodplain occupied in modern time, and a terrace representing a previous floodplain. (Reproduced from Dunne and Leopold 1978.) (b) A constrained river channel with little opportunity to develop a floodplain. (Reproduced from Ward et al. 2002.)

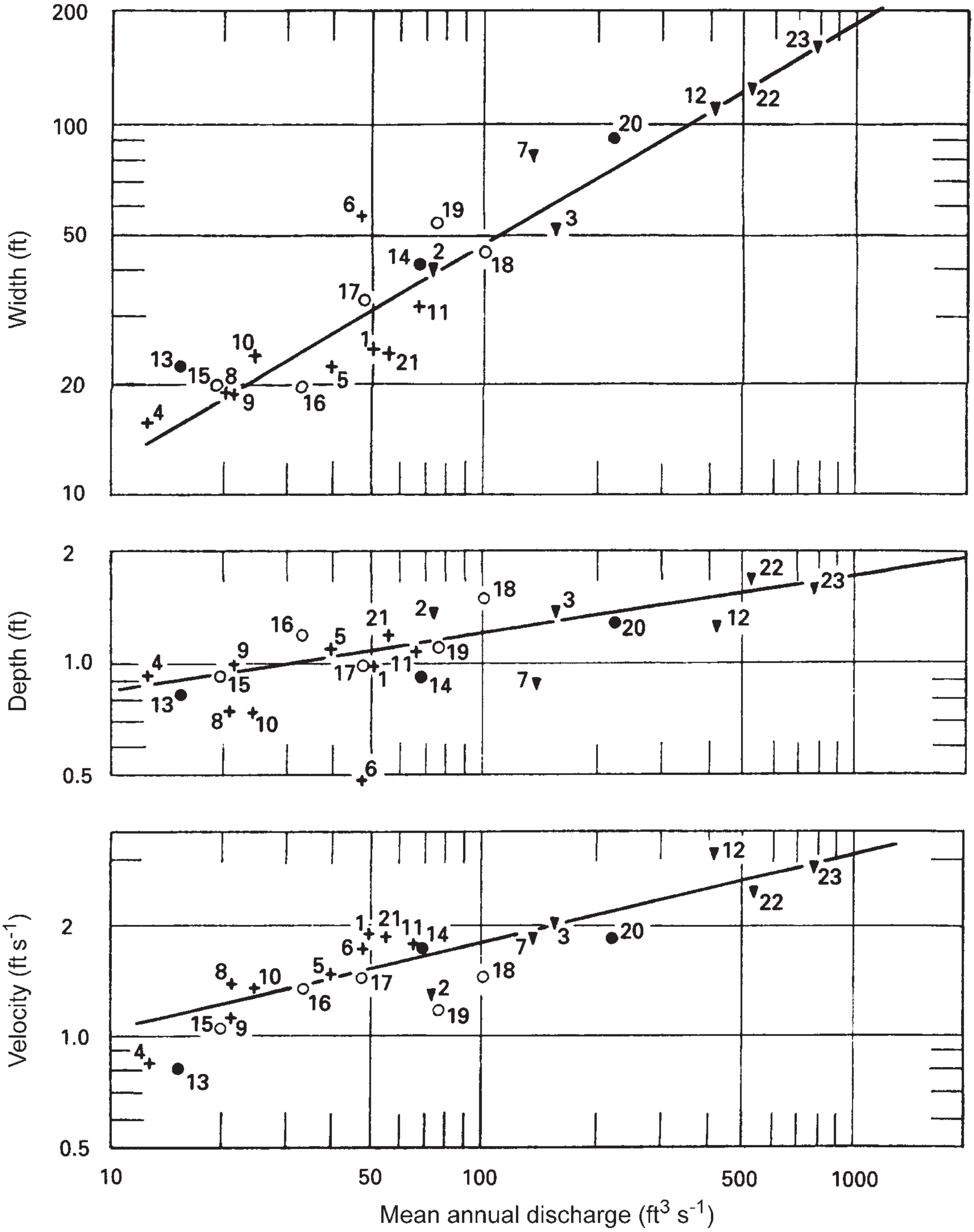

FIGURE 3.3 Width, depth, and velocity in relation to mean annual discharge as discharge varies downstream. Numbers refer to sites on the Powder River and tributaries, Wyoming and Montana. (Reproduced from Leopold 1994.)

another set of coefficients held "at-a-station." This turns out to be an overgeneralization because coefficients vary with the nature of the material forming the channel perimeter, as Osterkamp et al. (1983) showed using data from the western United States. Bearing in mind that Equations 3.1–3.3 describe general trends, and there is considerable variation in these regressions (less apparent in the figures because of the logarithmic scale), some broad generalizations can be made.

At a station, increases in Q are the result of a rain event and are accommodated mostly by increases in d and v until the river overflows its bank (if there is a floodplain), and then width increases greatly. As one proceeds downstream for a given flow stage, increases in Q are the result of tributary and groundwater inputs. Width, depth, and velocity all increase log-linearly with mean annual discharge. The increase of width with discharge is greater than the increase of depth, while velocity increases least with discharge and can remain almost constant (Leopold 1962). The modest downstream increase in velocity may seem surprising, because we might expect velocity to decrease downstream due to a general decline in gradient. However, because channel depth generally is greater and substrates are finer as one proceeds downstream, resistance decreases longitudinally and this offsets the effects of reduction in slope. The River Tweed in Scotland illustrates this nicely (Ledger 1981). At most flows, the highest velocities are found at the lower and flatter end of the river system. Only in some situations, involving floods, does mean velocity not exhibit an increase in the downstream direction.

3.2.2 Sinuosity

Flowing water will follow a sinuous course, whether it is melt water on the surface of a glacier, the Gulf Stream, which is unconstrained by banks, or a river channel. Most rivers are sinuous or meandering when viewed from above. However, the degree of meandering varies considerably, from relatively straight channels with a sinuous thalweg, to channels with pronounced and regular curvature (Leopold 1994). The sinuosity of a reach is easily quantified as:

$$\text{Sinuosity} = \frac{\text{Channel distance}}{\text{Straightline downvalley distance}} \tag{3.4}$$

Many variables affect degree of sinuosity, and so values range from near one in simple, well-defined channels to four in highly meandering channels. Meandering usually is defined as an arbitrarily extreme level of sinuosity, typically >1.5 (Gordon et al. 2004).

Flow through a meander stretch follows a predictable pattern and causes regular regions of erosion and deposition, as described above (Figure 3.1). A superelevation of water at the outside of a bend causes a helical flow of water toward the opposite bank. In addition, a separation of surface flow causes a back eddy. The result is zones of erosion and deposition, and explains why the features known as point bars develop in a downstream direction in depositional zones.

The consistency of channel bends is such that if one scales a small stream and a large river to fit on the same page, their similarity is striking. Small channels wind in small curves and large channels wind in large curves (Leopold 1994). The wavelength of a meander averages about 10–14 times the channel width, whether one measures a stream in a small experimental flume or the Gulf Stream meandering in the Atlantic Ocean (Figure 3.4). The radius of curvature of the channel bend averages 2–3 times the channel width. Models of channel meandering have reasonable predictive ability but are still under development (Darby and van de Wiel 2003), and it is important to realize that most meanders are asymmetric (Carson and LaPointe 1983).

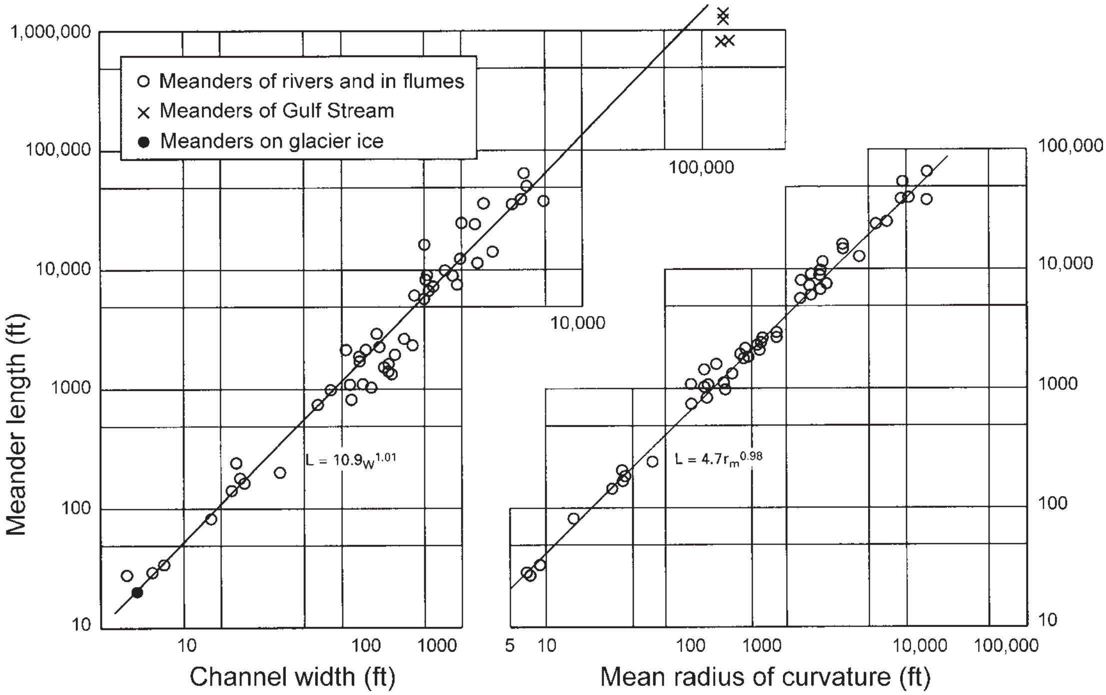

FIGURE 3.4 Relations between meander length and channel width, and between meander length and mean radius of curvature (Reproduced from Leopold 1994)

3.2.3 Pool–riffle features

Pool-riffle channels typically are found in moderate to low gradient, unconfined, gravel-bed streams. At the scale of the stream reach, perhaps a few hundred meters in length, one can observe a more or less regular alternation between shallow areas of higher velocity and mixed gravel-cobble substrate, called riffles, and deeper areas of slower velocity and finer substrate, called pools (Figure 3.5). The riffle is a topographical hillock and the pool a depression in the undulating streambed. In self-formed pool-riffle channels, riffles are formed by the deposition of gravel bars in a characteristic alternation from one side of the channel to the other, at a distance of approximately 5-7 channel widths (Leopold et al. 1964). Pool-riffle sequences are the result of particle sorting and require a range of sediment sizes to develop. At low flows, riffles have a high slope, tend to be shallow relative to pools, and have higher velocities. At high flows the water surface slope becomes more uniform between riffles and pools, although pools remain deeper, and velocities increase more in pools than in riffles. This results in changes in the distribution of forces on the streambed. At flood stage, when flows are high enough to mobilize the bed, riffles are the locations of lowest transport capacity and thus the locations of gravel deposition.

Pools also form on the outside of bends and where LW or other obstructions force pool development. In these circumstances the regular alternation of riffle-pool sequences may not be apparent. In high gradient, gravel-bed streams of the Pacific Northwest, the presence of pools is strongly dependent on LW, and streams with a high loading of wood typically have closer

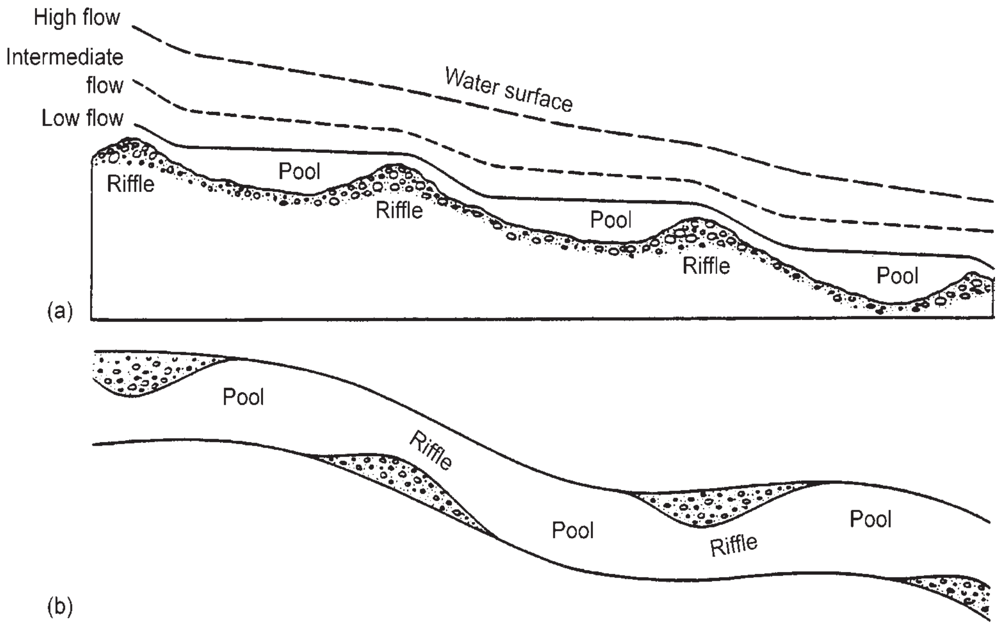

FIGURE 3.5 A longitudinal profile (a) and a plan view (b) of a riffle–pool sequence. Water surface profiles in (a) depict high-, intermediate-, and low-flow conditions. (Reproduced from Dunne and Leopold 1978.)

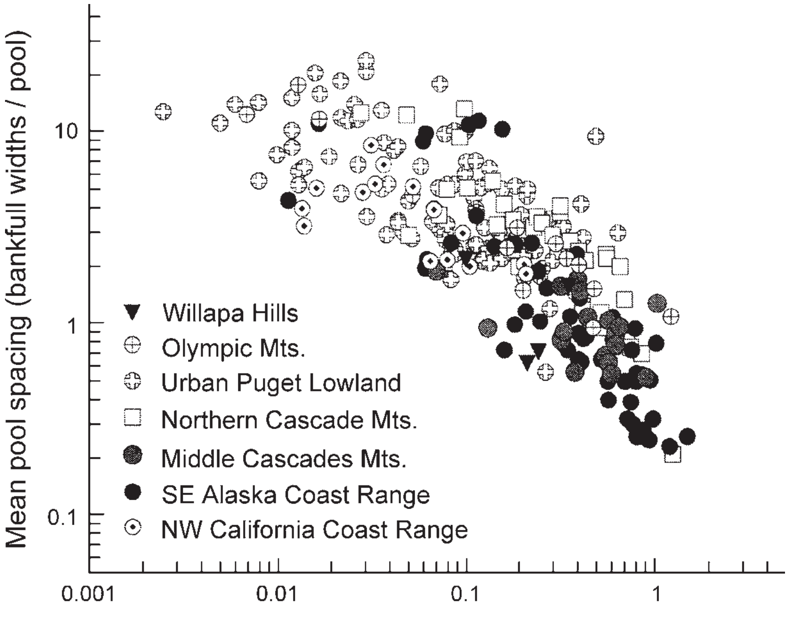

FIGURE 3.6 Average pool-spacing as a function of the frequency of pieces of wood in pool–riffle and plane-bed channels, from various locations in the western United States. (Reproduced from Buffington et al. 2003.)

pool spacing (Figure 3.6). LW has its greatest influence on first through fourth-order streams, where it has been found to increase width, form waterfalls, and stabilize gravel bars, as well as create pools (Bilby and Bisson 1998). Physical diversity in sand-bed channels is often depressed in reaches where wood has been removed (Shields and Smith 1992).

3.2.4 The floodplain

A floodplain is a level area near the stream channel that is inundated during moderate flow and is constructed by the river under present climatic conditions by deposition of sediments during overbank flooding (Leopold 1994). Unconfined, flat valleys, which occur most commonly in lowland rivers, permit considerable meandering and lateral migration, and so tend to have well developed floodplains. In contrast, in highly confined channels floodplain development is correspondingly restricted (Figure 3.2).

Channel movement and valley flooding are regular and natural behaviors of the river. The bankfull level of a river can be recognized by field observations as described previously or by directly observing the flood where the river just overflows its banks. In practice, however, this is not always easily done. A widely used rule-of-thumb is for overbank flows to occur about every 1–2 years (the 1.5 year recurrence event in Figure 2.11), but actually the floodplain along a given stream reach may be inundated many times annually, or much less frequently. As a corollary to this statement, the river constructs a channel that is large enough to contain most discharges that it experiences; only less frequent, larger discharges spill out of the channel onto the floodplain.

Owing to changes in climate or basin conditions, a river can change its bed level upward (aggradation) or downward (degradation). Over long periods of degradation, the old floodplain, abandoned as the river cuts downward, remains as a terrace.

3.3 Sediments and their Transport

The supply and transport of sediments are important because they strongly influence channel dynamics, affect habitat quality experienced by the biota, and can be costly to manage. The dynamic equilibrium that rivers seek is between the twin supplies of sediments and water, which together determine whether erosion and deposition are in balance and thus how the channel responds. Too much sediment, or too little, can be harmful to the biota and have costly consequences for human populations and infrastructure. Many rivers have a long history of human-induced erosion and sedimentation, causing habitat degradation and altering their ecology to the point where restoration will be extremely challenging (Gore and Shields 1995). Some 13% of all rivers in the United States, and 40% of impaired rivers, were considered to be impaired by excessive sedimentation as of 1998 (USEPA 2000). Excess sediment in drinking water requires expensive filtration treatment, which is why New York City now focuses on riparian management in the watersheds that supply its reservoirs. Sediments delivered from rivers can cause serious damage to estuaries and reefs, whereas an insufficient sediment supply can cause river deltas and coastal shorelines to retreat, resulting in loss of habitat and inadequate protection from storm surges.

3.3.1 Bed material

The grain size of bed material in a stream reach is determined by the sizes introduced to the channel from upstream, from local tributaries and from hillslopes, and by abrasion and sorting. Bed material is one of the imposed conditions to which channel form is adjusted. A convenient size classification (Table 3.1), based on a progressive doubling of sizes, helps us be precise in our use of terms such as gravel, pebble, boulder, etc. Grain and particle describe a particle of any size,

TABLE 3.1 The Wentworth grain size scale defines size classes in intervals that increase by powers of two.

Size category	*Particle diameter (range in mm)*
Boulder	>256
Cobble	
Large	128–256
Small	64–128
Gravel	
Very coarse	32–64
Coarse	16–32
Medium	8–16
Fine	4–8
Very fine	2–4
Sand	
Very coarse	1–2
Coarse	0.5–1
Medium	0.25–0.5
Fine	0.125–0.25
Very fine	0.0625–0.125
Silt	<0.0625

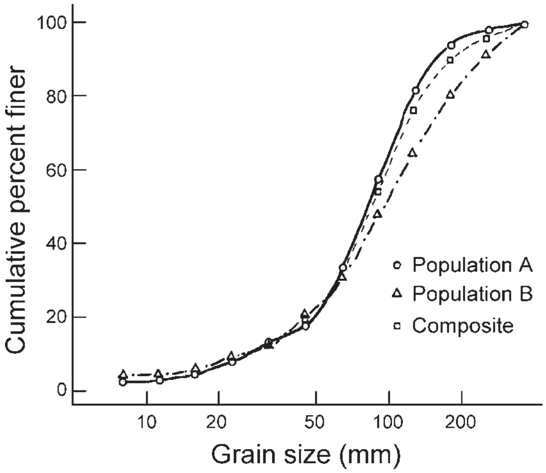

FIGURE 3.7 The distribution of grain sizes obtained by pebble count for two locations on the streambed identified as distinct local depositional environments from a site on Rush Creek, California. The median particle size is approximately 80 mm, in the size range of small cobbles, and slightly smaller at the location referred to as Population B. (Reproduced from Kondolf et al. 2003a.)

and clast usually refers to larger particles. Streambeds typically include a mix of particle sizes. The composition of the bed surface determines material available for transport, which is the main focus here. It also influences bed roughness and thus the near-bed hydraulic environment, as well as bed permeability and its suitability as habitat for biota, which will be dealt with later.

Because the bed surface typically is composed of a mix of particle sizes, it is useful to quantify the average particle size as well as the size range. The pebble count (Wolman 1954) is a simple and widely used method to quantify grain size of the surface layer and predict bed mobilization thresholds. The usual approach is to measure the intermediate axis of approximately 100 grains that are >4 mm diameter by randomly selecting stones from the streambed or a gravel bar of a reasonably homogeneous stream reach. However, when the streambed contains significant amounts of material smaller than 10–15 mm in diameter, samples of bed material must be passed through sieves of various sizes. A plot of the cumulative frequency distribution against a geometric progression of particle sizes (Figure 3.7) allows one to quickly estimate the median particle size, or D_{50}. The D_{16} and D_{84} often are reported as well, as they encompass one standard deviation on either side of the mean in a normal distribution.

The surface layer of a gravel-bed stream usually has coarser grains than subsurface layers. Streambed armoring refers to the vertical layering of substrate, where coarser grains overlay finer material and may prevent the latter from being entrained in the water column. This can be quantified as the ratio of surface D_{50}: subsurface D_{50}.

Bed sediment measurement employs many methods in addition to the pebble count (Kondolf et al. 2003a). A less quantitative, but still useful, approach preferred by some biologists is to report the dominant and subdominant particle size. If the interest is in fish biology rather than in sediment transport, the fraction of gravel within a certain size range preferred by fish for spawning may be the most useful measure, and if fine sediments are limiting the intergravel flow of oxygenated water necessary for incubating fish embryos or benthic invertebrates, then their quantification is important.

3.3.2 Bank and bed erosion

All sediments ultimately derive from erosion of basin slopes and water flowing across the land surface, but the immediate supply usually derives from the river bed and banks (Richards 1982). Episodes of high flow scour and transport sediments, eventually depositing them farther down the channel as flow subsides. The erosion of stream banks is an important source of sediments and of channel instability. It occurs naturally as channels meander, and can become severe when peak flows are increased. Thus, increases in impervious surface area and stormwater conveyance can enhance erosion. The process begins when streamflows cause the bank to steepen by eroding material at its base (the “toe”). As tension cracks begin to form in the upper, horizontal bank surface and water infiltration raises pore-water pressure (and increases mass), shearing begins, leading to bank failure. Soil debris is deposited at the foot of the bank, and streamflow removes the failed debris, increasing the sediment load of the stream. Bank steepening starts again, resulting in a vertical bank face and another cycle of bank erosion.

Most channel banks include finer material and this provides some degree of cohesion. The root systems of plants help to hold soil in place. Grass has been found to be particularly effective at stabilizing stream banks, relative to trees, owing to a deeper and denser root system (Lyons et al. 2000). Indeed, along a stream passing between pasture and woodland, the channel has been observed to narrow and deepen in the grassy stretches, and become shallower and wider in forested stretches (Sweeney 1993). Because some land managers apparently prefer woody vegetation, the planting of trees in grassy riparian area has the potential to cause streams to become wider and shallower as their shape adjusts to the change in bank stability (Davies-Colley 1997).

Bank stability can be increased in several ways. Vegetation on the bank surface both stabilizes the soil with its roots and removes soil water by uptake and evapotranspiration. Drainage tiles can be installed to remove infiltration water, which reduces the likelihood of mass wasting. Toe protection by various devices can prevent bank steepening. Bank stabilization is an important management activity, and varies from “hard” solutions such as riprap (slabs of concrete) and gabions (wire baskets of stones) to more environment-friendly approaches using vegetation. However, efforts to stabilize banks will be ineffective if incision of the streambed takes place.

Urban streams present a different scenario than agricultural settings. Peak flows typically increase with urban infrastructure, and banks often are hardened because channel shifts can undermine roads and houses. Bed erosion and downcutting are the expected consequences, with considerable sediment exported to lower reaches.

Bed material is transported when discharge reaches a sufficient level to initiate motion and transport particles generally of larger size than fine sand. Not surprisingly, the size of particle that can be eroded and transported varies with current velocity (Figure 3.8). The competence of a stream refers to the largest particle that can be moved along the streambed at some flow, and the critical erosion (competent) velocity is the lowest velocity at which a particle of a given size, resting on the streambed, will move (Morisawa 1968). Sand particles are the most easily eroded, having a critical erosion velocity of about 20 cm s^{-1}. Due to their greater mass, larger particles require higher current velocities to initiate movement, for example, at least 1 m s^{-1} for coarse gravel. However, grains smaller than sands, including

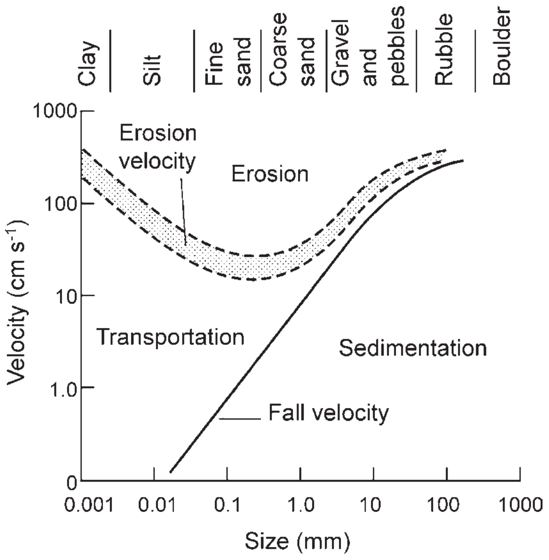

FIGURE 3.8 Relation of mean current velocity in water at least 1 m deep to the size of mineral grains that can be eroded from a bed of material of similar size. Below the velocity sufficient for erosion of grains of a given size (shown as a band), grains can continue to be transported. Deposition occurs at lower velocities than required for erosion of a particle of a given size. (Reproduced from Morisawa 1968.)

silts and clays, have greater critical erosion velocities because of their cohesiveness.

Once in transport, particles will continue in motion at somewhat slower velocities than was necessary to initiate movement (Figure 3.8). As velocities decrease, grains settle out of suspension, beginning with the largest and heaviest. This occurs when discharge declines following a flood, in reaches of lower gradient, at the inside of bends and behind obstructions.

The shear stress or tractive force (τ_o, force per unit area) exerted by the flow of water on the streambed is estimated as:

$$\tau_o = \rho g R S \tag{3.5}$$

where ρ is fluid density, g is gravitational acceleration, the hydraulic radius R equals channel cross-sectional area divided by its wetted perimeter, and S is the water surface slope. For natural channels with a width much larger than mean flow depth, mean depth is a good approximation of the hydraulic radius.

This equation is important because it relates the resistance of the channel bed and banks to the downstream gravitational tractive force of the water: when the former is exceeded, sediment transport is initiated. Critical shear stress (τ_c) refers to the shear stress necessary to mobilize a given grain size. For mobile, gravel-bed rivers with bed materials >1 cm diameter, the particle size near the threshold of motion at bankfull flow is approximately equal to the median bed material size (cm). In other words, the D_{50} is a good indicator of the tractive force on the streambed at bankfull flow.

3.3.3 Sediment load

Sediment load is the amount of sediment passing a point over some time interval. It is estimated by multiplying sediment concentration by water discharge. Matter carried by fluvial systems can be separated into three components (Knighton 1998). These are the dissolved load, which consists of material transported in solution; the wash load, consisting of material between 0.5 µm (the upper limit for dissolved material) and 0.0625 mm (the boundary between silt and sand); and solid load, consisting of material >0.0625 mm. Terms that describe the total sediment load refer either to the source of the material or the mode of transport (Hicks and Gomez 2003) (Figure 3.9).

The dissolved load consists of solutes derived from chemical weathering of bedrock and soils. The dissolved constituents of river water are discussed more fully in Chapter 4. Their contribution is greatest in nonflashy hydrologic regimes where most flow is subsurface, and in regions of limestone geology (Richards 1982). The relative amount of material transported as solute versus solid load depends upon basin

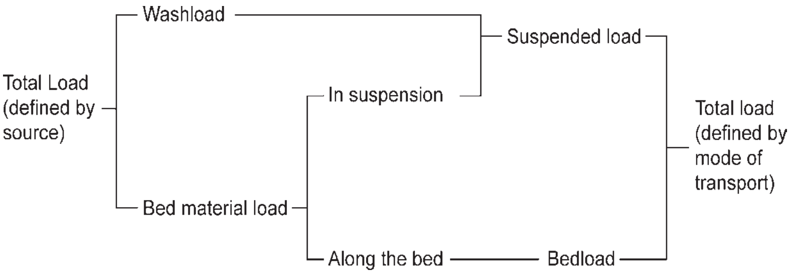

FIGURE 3.9 The components of stream sediment load shown in terms of sediment source and mode of transport. (Reproduced from Hicks and Gomez 2003.)

characteristics, lithology, and hydrologic pathways. In dry regions, sediments make up as much as 90% of the total load, whereas the contribution of solutes is substantially more in areas of very high runoff (Richards 1982). Worldwide, it is estimated that rivers carry approximately 15 billion tons of suspended materials annually to the oceans, which is roughly five times the dissolved load (Holeman 1968, Martin and Meybeck 1979).

By source, the total sediment load is split between wash load and bed material load (Hicks and Gomez 2003). The wash load (so named because this load is "washed" into the stream from banks and upland areas) consists of very fine particles including clay and silt up to very fine sand. It requires only low velocities and minor turbulence to remain in suspension, thus this material may never settle out. The amount of the wash load is determined by its supply from uplands and stream banks rather than by the stream's transport capacity, and is likely to be high where stream banks have a high clay and silt content. The bed material load is derived from the river bed, typically sand or gravel, and its concentration is directly related to the river's transport capacity.

By mode of transport, the sediment load is divided into suspended load and bed load. The flow of water in rivers generally is turbulent, and exerts a shearing force that causes particles to move along the bed by pushing, rolling, and skipping, referred to as the bed load. This same shear causes turbulent eddies that entrain particles into suspension, called the suspended load. The distinction between bed load and suspended load is based on sampling method, and the same material that is transported as bed load at low discharge may become suspended load at higher discharge. Bed load transport is difficult to measure, and often involves a trap or tracer particles (Gordon et al. 2004). Suspended load is fairly easy to sample – a simple grab sample will suffice – but varies with depth and can change rapidly with discharge, and so sampling that integrates across depth and takes place frequently over the rise and fall of the hydrograph is preferred. Because fine sediments tend to be washed into the stream at the beginning of a rain event and entrained by rising water, their concentrations usually are greater during the rise of the hydrograph, and decline during the falling hydrograph due to exhaustion of the sediment supply. As a consequence, sediment concentrations can be different at identical discharges of the rising and falling hydrograph. This is referred to as hysteresis.

Suspended sediments cause turbidity by restricting the transmission of light through water due to scattering and absorption. By measuring light transmission through a water sample, turbidity meters provide a simple approximation of suspended sediment loads. These usually are reported as nephalometric turbidity units (NTUs), which can be calibrated against measured sediment concentrations (mg L^{-1}). There are additional sources of turbidity, however, including algae and colloidal matter, and so turbidity is not solely a measure of suspended sediments.

The majority of sediment transport is due to the suspended load, which typically exceeds bed load by a factor of 5–50 (Gordon et al. 2004). The bed load will be a lower fraction in bedrock streams than in alluvial streams where channels are composed of easily transported material. However, bed load transport increases substantially during floods, and is particularly important in determining channel shape. For a stream channel in equilibrium, the transport of bed material requires that it be replaced by material derived from upstream banks and channel, in a cycle of scour and fill that accompanies the rise and fall of flood waters; if not, the bed will be downcut. For example, a flood in the Colorado River at Lees Ferry increased bed depth by approximately 1.5 m. Redeposition of sediment as the flood receded reestablished bed elevation at very close to its previous value (Leopold 1962), further evidence of the dynamic equilibrium between erosion and deposition. Since the closing of the Glen Canyon Dam the Colorado River immediately downstream has been downcut by more than 9 m, demonstrating the consequences of the loss of its upstream sediment supply (Postel and Richter 2003).

3.3.4 Factors influencing sediment concentrations and loads

A stream's capacity is the total load of bed material it can carry. This increases with velocity and discharge unless the supply of sediment becomes depleted; the larger the flow, in general, the larger the quantity of sediment transported (Richards 1982). Throughout most of the year discharge usually is too low to scour, shape channels, or move significant quantities of sediment, although sand-bed streams can experience change much more frequently. Although one might suppose that extreme events also account for the greatest proportion of total sediment transport, flow events of intermediate frequency actually move more sediment over the years. The discharge at which sediment transport peaks is called the effective or dominant discharge, and it is found from the product of the discharge frequency curve and the curve describing sediment transport rate as a function of discharge (Figure 3.10). Because the effective discharge accomplishes the most geomorphic work compared to other flows, it follows that fluvial landforms are shaped by frequently occurring moderate floods, rather than by rare, cataclysmic floods (Wolman and Miller 1960).

The effective discharge often is very close to the bankfull discharge estimated from the 1.5 year flow ($Q_{1.5}$), as Andrews and Nakervis (1995) report for 17 gravel-bed rivers of the western United States, and the D_{50} closely approximates the particle size that is mobilized at the effective discharge. Given the difficulty of directly determining effective discharge, the usefulness of bankfull discharge and the D_{50} is clear as both are field measurements that provide estimates of the discharge responsible for transporting most of the annual sediment flux, and thus having the greatest influence on channel shape. An analysis of suspended-sediment transport data from more than 2,900 sites across the United States, sorted into ecoregions, supported the use of the $Q_{1.5}$ as a measure of the effective discharge (Simon et al. 2004). Median values of the recurrence interval of the effective discharge for 17 ecoregions ranged from 1.1 to 1.7 years, and the detection of differences among regions argues for the use of regionalized curves. The concept of a channel-forming discharge is widely used in river restoration designs because it suggests ways to estimate, fairly easily, the equilibrium channel dimensions. These efforts have met with both successes and failures; reasons for the latter include application to an area where conditions may be different, inadequate

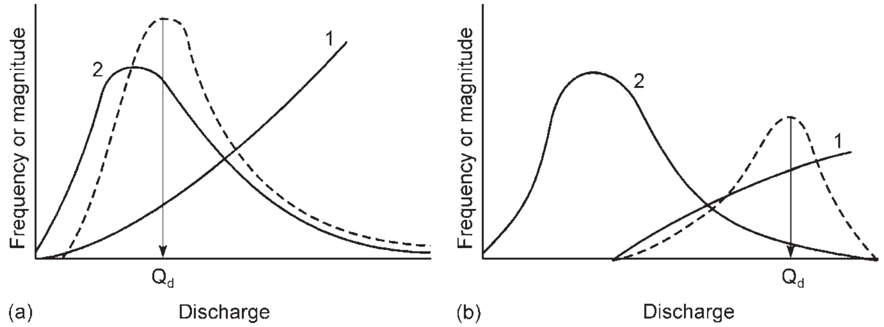

FIGURE 3.10 The relationship between frequency and magnitude of discharge events responsible for sediment transport: (a) suspended load, (b) bedload. Curve 1 depicts the increase in sediment transport rate with increasing magnitude of discharge, and curve 2 describes the frequency of discharge events of a given magnitude. Their product (dashed line) is the discharge that transports the most sediment, referred to as Q_d, the dominant or effective discharge. Q_d is approximately Q_{bkf} for suspended sediments, and is in the range $Q_{1.5}-Q_{10}$ for bedload. (Reproduced from Richards 1982.)

consideration of past history, and the problems inherent in applying general relationships to specific cases (Smith and Prestegaard 2005, Doyle et al. 2006).

Concentrations of suspended sediments vary greatly depending on the factors described above that influence sediment supply, and with discharge and velocity, which determine how much sediment is in transport at any time. Based on some 400–600 stations sampled from 1970–1983 across the United States, site-specific measurements of total suspended sediments (TSS) had a median value of 63 mg L^{-1}, but varied by more than three orders of magnitude (Dodds and Whiles 2004). Sediment concentrations and yields vary greatly with region, with human activities leading to erosion, and whether the channel is in a stable or unstable state. Using a model of channel evolution that recognized equilibrium conditions both for predisturbance and disturbance-accommodated channel forms, Simon et al. (2004) estimated that the median values (for suspended-sediment yields at $Q_{1.5}$) at stable sites within a given ecoregion are generally an order of magnitude lower than for nonstable sites.

Nearly 90% of the variation in TSS in the large data set analyzed by Dodds and Whiles (2004) was explained by turbidity, indicating that the latter is a reasonable surrogate measure, at least to within an order of magnitude. TSS was negatively correlated with catchment land area in forest, and highest values were found at forest covers <20%. Relationships with urban land were less clear, presumably because impervious surfaces result in less erodible soil, so high TSS values were rare in urban catchments. TSS also exhibited pronounced differences associated with ecoregion. Lower sediment concentrations were seen in Eastern Deciduous Forests, and higher values in the Great Plains and North American Desert ecoregions.

Sediment yields from individual rivers are calculated as loads divided by catchment area, and provide a useful comparison of variation in sediment export among rivers and over time. Water discharge alone is a poor predictor of sediment load except within a region. Rivers in just 10% of the world's drainage basins account for over 60% of sediment discharge (Milliman 1990). The Hwang Ho (Yellow River) of northern China is believed to carry the highest suspended load of any river, as much as 40% sand, silt, and clay by weight, during high discharge (Cressey 1963). The great rivers of South America make a significant but nonetheless much smaller contribution to the world sediment flux, and large northern rivers account for considerably less.

Human activities can increase or reduce sediment yields. Deforestation and poor agricultural practices greatly increase erosion, perhaps as much as fivefold in Asia and Oceania. On the other hand, sediment flux is greatly reduced in rivers by thousands of large and millions of small impoundments. Although prior work in the United States has emphasized sediment storage in stream channels and floodplains (Trimble 1983), Renwick et al. (2005) estimate that, at least for the later part of the 20th century, much of the sedimentation in the United States actually is occurring in impoundments. Both the Nile and the Colorado have experienced a complete cessation of sediment export, and the Rhône is estimated to export approximately 5% of its load of a century ago. Thus in a number of large rivers we have the apparent paradox of increased erosion within the drainage basin coupled with reduced export to the oceans.

The global consequences of these trends can be seen in Table 3.2, which summarizes discharge and sediment fluxes for prehuman and modern times by continent. Combining data and models, Syvitski et al. (2005) estimated the global total prior to human influence to be 14 billion tons annually (15.5 billion tons year^{-1} when bed load is included). Asia produces the greatest quantity of fluvial sediment, whereas Oceania and Indonesia have the highest sediment yields as well as the highest runoff (discharge divided by area). By latitude, warm areas produce the highest sediment yields, accounting for nearly two thirds of global delivery. Modern sediment loads are a moving target because land use has generally accelerated erosion (although reforestation and other improvements have brought about declines in some regions), and impoundments retain sediments. The modern sediment flux is estimated to be 12.6 billion tons year^{-1}, about 10% less than the prehuman value. Using the additional information that large impoundments trap 20% of the sediment load of rivers and small impoundments an additional 6%, the current flux would be 16.2 billion tons year^{-1} of suspended sediment in the absence of dams. Thus sediment flux into global rivers due to erosion has increased, while sediment yields to the world's coasts have declined. Coastal retreat that may affect inhabited areas, subsidence of

TABLE 3.2 Landmass area, discharge, predicted sediment flux to the world's coastal zones from world rivers under prehuman and modern conditions, and percentage of sediment load retained in reservoirs. Uncertainty estimates for sediment fluxes and sediment retained in reservoirs have been omitted for simplicity, but range from 15% to 30% of stated values. See Syvitski et al. (2005) for details.

Landmass	*Area (M km^2)*	*Discharge (km^3 year^{-1})*	*Prehuman suspended load Q_s(MT year^{-1})*	*Modern suspended load Q_s(MT year^{-1})*	*Load retained in reservoirs*
Africa	20	3,800	1,310	800	25%
Asia	31	9,810	5,450	4,740	31%
Australasia	4	610	420	390	8%
Europe	10	2,680	920	680	12%
Indonesia	3	4,260	900	1,630	1%
North America	21	5,820	2,350	1,910	13%
Ocean Islands	0.01	20	4	8	0%
South America	17	11,540	2,680	2,450	13%
Total	106	38,540	14,030	12,610	20%

river deltas, and loss of coastal wetland habitat are likely consequences.

3.4 Fluvial Processes along the River Continuum

We are now familiar with many of the principal features of streams, including the shape of their channels, the lateral connection to the floodplain, the presence of riffles, pools, and meanders, and the sediments of the streambed and its banks. These features vary along the river's course from headwaters to lowlands, and with regional differences in climate and terrain. As stated earlier, streams seek a state of dynamic equilibrium between the imposed conditions of valley slope, discharge, and sediment supply, and channel adjustments that can include width, depth, velocity, reach slope, roughness, and sediment size. Over historical time, the channel adjusts to changes in discharge and sediment supply due to human activities, climate change, and extreme events. Increasingly, today, it is human activities that destabilize the rivers' equilibrium, often triggering a series of changes that pose problems for our built environment.

The concept of stream power and the relationships between the supply of water and sediments captured in Lane's Law (Figure 3.11) nicely express the key processes at work. Stream power describes the ability of the stream to mobilize and transport material. It is the product of discharge and slope, although additional formulae estimate unit stream power per unit area or length of reach. Thus steeper slopes and higher discharges both increase stream power,

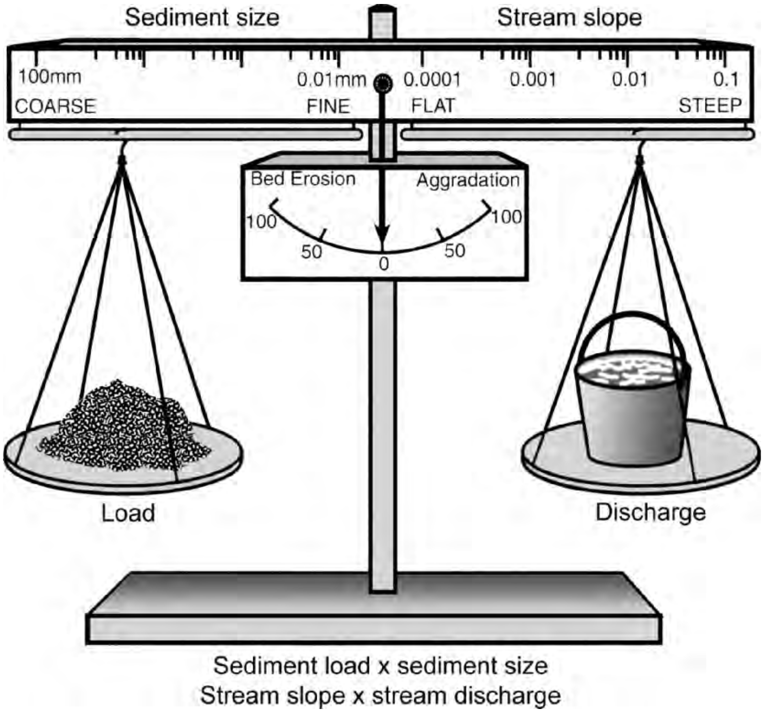

FIGURE 3.11 Lane's Law states that sediment transport is proportional to stream power (streamflow ∗ slope) and inversely proportional to sediment size. Thus stream channels are in equilibrium when: sediment discharge (Q_S) ∗ sediment particle size ($D50$) ∼ streamflow (Q_W) ∗ stream slope (S). (Reproduced from Brierley and Fryirs 2005.)

but because slope tends to decrease downstream while discharge increases, a mountain stream in flood may generate much more power than a large lowland river, and a river that overflows its banks into the floodplain will have lower power than one that stays within its banks (Gordon et al. 2004). Stream power is related approximately to sediment load by:

$$Q_s D_{50} \sim Q_w S \qquad (3.6)$$

where Q_s is the sediment discharge (load), D_{50} is the median particle size, Q_w is water discharge and S is slope (Lane 1955). The relationship is qualitative, hence no units are given. It implies that the channel will remain in equilibrium as long as no major change occurs in any of the variables, or if changes in one are balanced by changes in another.

Equation 3.6 is especially useful for envisioning how a stream will respond to human actions. If sediments are trapped behind a dam, the outflow usually has a low sediment load, resulting in bed coarsening and channel incision as the sediment-hungry river entrains bed material and downcuts. If sediments are introduced by poor land use practices in a tributary catchment, the stream lacks the power to transport that additional material, resulting in deposition and aggradation. If a stream is straightened, its slope is increased (because the same elevation drop now occurs over a shorter distance), and erosion is expected. When as little as 10–20% of a catchment is covered with roofs, pavements or other impervious surfaces, peak discharge typically increases and channels typically widen or deepen in response, a familiar sight in urban areas (Bledsoe and Watson 2001).

3.4.1 Fluvial processes and channel morphologies

We now turn to a process-based analysis of river channels, linking the governing conditions of water and sediment supply to the channel features we have encountered and their changes along the river continuum. This will focus primarily on alluvial channels, defined as those with bed sediments that are transported by the stream. Rearranging Equation 3.6, it is apparent that sediment transport is directly related to stream power ($Q_w S$) and inversely related to grain size D_{50} (also referred to as sediment caliber). The interplay of a stream's capacity to transport sediment with the input of sediments and their caliber results in distinctive channel morphologies (Church 2002). Bank strength, which is influenced by sediment texture and vegetation (LW), and other channel constraints, exerts additional influence over channel shape (Figure 3.12).

As one proceeds from upland, to upland valley to large river, the river changes from primarily a sediment-evacuating to a sediment-accumulating system, and from being coupled to hillslopes for its sediment supply to being largely uncoupled

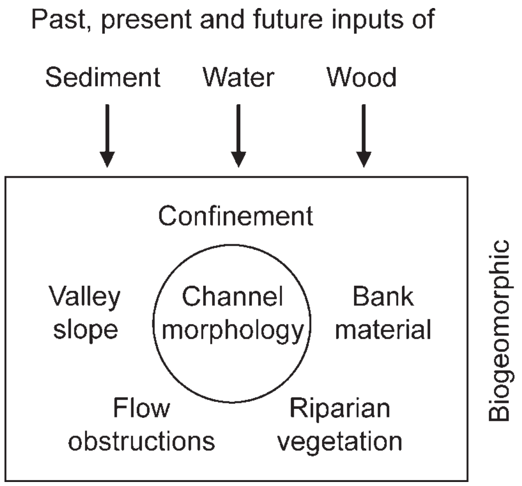

FIGURE 3.12 The principal controls on channel morphology include sediment supply (amount and size), transport capacity (discharge magnitude and frequency), and riparian vegetation. Channel morphology is further influenced by flow obstructions (bedrock outcrops, large woody debris), geomorphic context (confinement and valley slope), and disturbance history. Sediment supply and transport relationships govern channel type. (Reproduced from Montgomery and MacDonald 2002.)

(Church 2002). The upland region is closely associated with hillslopes, from which upland streams receive sediments (Figure 3.13). Much of these sediments, but not the largest clasts, are transported downstream. In the middle section (the upland valley), where gradients are lower, sediments mobilized in upland channels may be deposited, forming an alluvial channel and a floodplain. Material from this section is transported onward, and replenished from upstream, in episodes of erosion and deposition. In large lowland rivers near the distal end of the drainage system, sediment deposition is dominant, resulting in large floodplains, alluvial fans, and deltas.

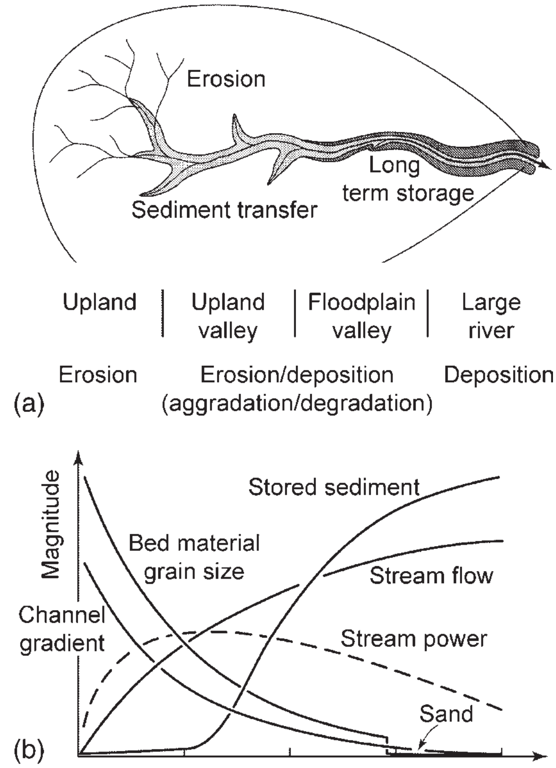

FIGURE 3.13 A drainage basin, illustrating some of the principal longitudinal trends in stream channels. (a) Three principal longitudinal zones: an upland zone where the drainage forms and from which sediments are exported; a middle, transitional zone where erosion and deposition of sediments may be approximately in balance; and a lower floodplain where sediments may accumulate. (b) General patterns of sediment occurrence and transport. Note the longitudinal decrease in bed material grain size. Stream power, the product of slope and discharge, peaks in the middle zone, and the stream's competence (ability to move sediment of a given size) declines downstream. (Reproduced from Church 2002.)

A series of interrelated changes in streamflow and sediment character occur systematically along the river's length. As previously mentioned, channel gradient declines and stream discharge increases. The discharge-slope product, stream power, is greatest in the midrange of the river system. Sediment grain size is largest in the headwaters, where large clasts introduced from hillslopes often have diameters equal to or greater than bankfull depth and are immobile even at highest flows. Smaller material is transported downstream in cycles of erosion and deposition that sort particles and carry farthest those of smallest size. Hence characteristic sediment size becomes finer as one proceeds downstream. Sorting of stones also can result in predicable arrangements that enhance their stability. Gradient and relative roughness (grain diameter divided by depth) can be combined to predict specific details of bed morphology (Montgomery and Buffington 1997, Church 2002). For example, the pool–riffle sequence of gravel-bed streams, with point bars at bends, typically occurs at a slope near 0.01–0.03 and a relative roughness near 0.3. Near the downstream terminus, sand-bed channels are found; because of their small grain size, bed material is mobile over a wide range of flows. Visually this can produce a pleasing picture of ripples and dunes, but for most organisms bed instability makes a hostile environment. As Benke et al. (1985) have shown, most biological production in sand-bed rivers is associated with submerged wood, the only stable habitat for invertebrates.

These ideas underlie a process-based classification of channel morphologies for mountain drainages (Table 3.3). Montgomery and Buffington (1997) recognize three primary channel-reach

TABLE 3.3 A classification of channel-reach morphology for mountain drainage basins recognizes seven distinct reach types. Colluvial channels typically are small headwater streams, receive their sediments from hillslopes, have clasts that are large relative to stream depth, and have insufficient power to transport large boulders but rapidly deliver smaller particles to lower-gradient channels. Bedrock streams have a low sediment supply relative to transport capacity. The five alluvial channel types commonly occur in a downstream sequence of decreasing fluvial transport capacity relative to sediment supply. See Montgomery and Buffington (1997) for further details.

Channel type		*Typical bed material*	*Dominant sediment sources*	*Typical confinement*	*Typical pool spacing*[b]
Colluvial		Variable	Hillslope, debris flows	Confined	Unknown
Bedrock		Rock	Fluvial, hillslope, debris flows	Confined	Variable
Alluvial	Cascade	Boulder	Fluvial, hillslope, debris flows	Confined	<1
	Step–pool	Cobble–boulder	Fluvial, hillslope, debris flows	Confined	1–4
	Plane bed[a]	Gravel–Cobble	Fluvial, bank failure, debris flows	Variable	None
	Pool–riffle	Gravel	Fluvial, bank failure	Unconfined	5–7
	Dune–ripple	Sand	Fluvial, bank failure	Unconfined	5–7

[a] Encompasses runs, glides, and rapids as commonly used in fisheries literature

[b] Pool spacing is expressed in channel widths

substrates: bedrock, alluvium, and colluvium. Bedrock channels lack alluvial deposits and have high transport capacity relative to sediment supply. Colluvial channels typically are small headwater streams that receive sediments from debris flows and hillslopes and have weak capacity for sediment transport. Alluvial channels are further subdivided into five categories that occur along the river continuum owing to threshold changes in the processes summarized above.

In an idealized long profile from upper hillslopes to lowland river, these occur in longitudinal sequence (Figure 1.4). Cascade channels occur on steep slopes, are confined by valley walls and have a substrate that typically consists of cobbles and boulders. Pools commonly are small and spaced less than one channel width apart. Cascade channels retain larger clasts but rapidly transport smaller sediments to lower-gradient channels. In step-pool channels, longitudinal steps are formed by larger clasts, resulting in discrete pools with a spacing of one to four channel widths. Gradients are steep, width to depth ratios are low, and valley wall confinement is evident. At moderate to high gradients and in relatively straight channels, the channel type known as plane bed develops. It usually includes a somewhat featureless combination of riffles, runs, and rapids. The substrate includes gravel, cobbles and small boulders, and may be armored or not. An armored substrate indicates a transport capacity greater than sediment supply, whereas a substrate that is not armored indicates a balance between transport capacity and sediment supply (Dietrich et al. 1989). Thus the plane-bed stream is transitional between supply-limited upper reaches and transport-limited lower reaches (Montgomery and Buffington 1997). Pool–riffle channels with pools spaced at five to seven channel widths occur at moderate gradients. They represent a shift to a more transport-limited system, although this varies with degree of armoring. Dune-ripple channels typically are low-gradient, sand-bed systems experiencing significant sediment mobility under most flow conditions.

The five alluvial channel types just described are referred to as free-formed, meaning they result from the interaction of sediment supply and transport capacity. In forested mountain streams, LW can force channel morphologies where they might not otherwise occur (Figure 3.6). LW can cause local scour and flow divergence, and may result in sediment accumulation in otherwise bedrock streams. A forced pool–riffle system is one where most pools are the result of LW, and a forced step-pool structure can result from regularly spaced, channel-spanning LW.

3.4.2 Channel dynamics over long timeframes

The prior discussion describes how changes in geomorphic processes along the river's length help us understand the development of different channel configurations and features. It emphasizes how adjustments are continually occurring to maintain an approximate equilibrium, and emphasizes events of intermediate magnitude – the dominant discharge – as primarily responsible. In a historical perspective, we should also emphasize the importance of episodes of climate change over the last 15,000 years, and of even older tectonic events and glaciations. For example, the Grand Canyon of the Colorado River is thought to be about 5 million years old and its establishment to depend ultimately on tectonic movements and the opening of the Gulf of California. Both ancient and more recent floods have on occasion had lasting effect on fluvial landscapes, carving channels and placing large clasts that subsequent floods are unable to substantially modify (Knighton 1998). River channels in a large area of the western United States were shaped by a paleoflood estimated to have discharges as high as 10 million $m^3\ s^{-1}$ (Benito 1997), which occurred when an ice dam on glacial Lake Missoula failed some 15,000 years ago. Other ice age floods also had grand effects. Less spectacularly, climatic fluctuations since 10,000 years ago have affected water balances, vegetation patterns, flows, and the supply of materials, resulting in fluctuations in fluvial activity. The postglacial history of a 250 km section of the Mississippi River from the confluence of the Missouri and Ohio Rivers to south of Memphis, Tennessee, illustrates how episodes of major flood influence have resulted in a series of abandoned channels and sedimentary deposits (Blum et al. 2000). More recently, the Mississippi River experienced large floods between AD 1300 and AD 1500 during the period of transition into the Little Ice Age (Knox 1993).

These climatic influences continue into the present and will be important if future climate change takes place as forecast. However, it has become increasingly difficult to isolate climate from the influence of human activity, particularly land clearing. Deforestation in parts of the Huang Ho (Yellow River) catchment in China between 200 BC and AD 600 is estimated to have increased sediment loads by an order of magnitude (Milliman et al. 1987). During the gold rush of the mid-19th century in the Sierra Mountains of California, hydraulic mining mobilized great amounts of waste gravel into the headwaters of the Sacramento River (James 1991). The lower Bear River aggraded as much as 5 m, and is continuing to adjust over 100 years later, which points to the very long time frame of river recovery following human disturbance. In some instances recovery may not be possible, as when river impoundment eliminates flood peaks, or when invading vegetation stabilizes the new configuration, as has occurred in some lower sections of the Bega catchment of Australia (Brierley et al. 1999).

3.4.3 Channel classifications and their uses

There is an extensive literature on river classification resulting in a large number of classification schemes developed for purposes ranging from understanding landscape evolution to engineering design for river restoration (Kondolf et al. 2003). Some have already been discussed. Stream order (Table 1.1) is a useful measure of stream size and position, and is easy to derive. The three longitudinal zones of Schumm (1977) – erosional, transfer, and depositional – identify regions of supply limitation versus transport limitation of sediment movement. Channels can be divided into bedrock, colluvial, and alluvial beds, and the latter further subdivided (at least for mountain drainages) into types determined by transitions in process domains and forcing by LW (Table 3.3). Additional descriptive classifications include whether a channel is straight, meandering, or braided (Leopold 1994). Floodplain rivers have been characterized based on river planforms (Kellerhals and Church 1989). A classification scheme devised by Rosgen (1994, 1996) and widely used in river restoration recognizes seven major and 42 minor channel types based on channel pattern, width to depth ratio, sinuosity, and bed material size.

Why so many classifications, what is their value, and are some better than others? That discussion is likely to continue for some time, and readers should consult Kondolf et al. (2003) for the best current summary. One purpose is to enhance understanding, by providing insights into the processes that are responsible for the great variety of river types. This in turn provides an important framework for further investigations, allowing one to categorize the river types of a region, sample appropriately, and compare like to like. A second purpose is for management and restoration. Reference sites are necessary to set expectations for channel conditions and biological composition, and inventories of the status of streams can be accomplished with greater statistical reliability when the sample universe is appropriately defined. Categories are also useful for communication among specialists working in different fields and regions.

Balanced against these obvious advantages are some limitations, chiefly that classifications are artificial human constructs (Kondolf et al. 2003). Classifications aid our understanding so long as we are suitably cautious in applying them. And whereas scientific understanding is aided by a general model regardless of its ability to exactly define thresholds between categories, managers often need to categorize a particular reach, which may not fall neatly into one category. Especially when classification is used to establish expectations for restoration of a stream reach at considerable expense, it is debatable whether classification is a useful tool or a hindrance. Kondolf et al. (2001) described the failure of a restoration project on a 0.9 km reach of Uvas Creek, near Gilroy, California. Although reconstructed as a single-thread, meandering channel based on estimated bankfull flood and the Rosgen classification system, a flood with a 6-year return interval occurring only months after project completion transformed the constructed channel into a wide, braided channel. Kondolf et al. argued that geomorphological analysis of the reach itself, of historical conditions, and taking into account a longer corridor would have supported a different expectation, more similar to the flood's outcome. Detailed field studies are expensive, of course, which led managers to adopt classification approaches in the first place. An ideal channel classification will both advance scientific understanding and be useful for management, and this requires that classes be process-based (as in Table 3.3).

Whether classification of channel type will commonly be sufficient to set restoration guidelines, versus the need for more technical site-specific analysis by geomorphologists and engineers, continues to be argued. The "river styles" approach illustrates a promising classification of relatively homogeneous reaches into a limited number of categories that can be combined with a prioritization for conservation and management. Employing a nested hierarchical framework of catchments, landscape units, river styles, and geomorphic units, Brierley and Fryirs (2000, 2005) identified nine styles of river character and behavior for the 1,040 km^2 Bega Catchment of New South Wales, Australia. Much of our prior discussion of river types and geomorphic processes is relevant, although Brierley and Fryirs emphasize the distinctive aspects of Australian rivers that are the consequence of a very old, bedrock-dominated landscape with high hydrologic variability. The authors also suggested how to prioritize reach-scale management strategies within an integrative catchment framework: first, conservation should precede restoration; second, we should work to improve sections where natural recovery potential is high; third, we should be thoughtful about investment of effort in reaches with low rehabilitation potential.

3.4.4 Riverine landscape diversity

Fluvial geomorphology provides many insights of value to the stream ecologist: the generation and maintenance of channel types, the dynamic nature of many stream features, and perhaps most of all, how the diversity of riverine landscapes occurs and is maintained. In a broad synthesis of riverine landscape diversity, Ward et al. (2002) argue for a landscape ecology of rivers in which spatial patterns and ecological processes interact across a range of scales. Channel features, habitat units, surface and subsurface zones, floodplains, and riparian corridors form a complex, shifting mosaic, in which the diversity of the physical template provides the setting in which biologically diverse communities flourish. Features of the riverine landscape are both highly predictable in their occurrence and highly dynamic, driven by the fluvial processes that govern river behavior. Through its influence on habitat heterogeneity and temporal succession, natural disturbance creates the opportunity for greater biodiversity than is found under more uniform conditions (Chapter 5). From the perspective of the biota, the environment is spatially heterogeneous, with patches differing in resource quality, permanence, and connectivity across a range of scales, indicating the influence of spatial pattern on ecological processes (Weins 2002). This foreshadows how regulation of river flow and homogenization of habitat, for example, by dams and channelization, causes declines in taxon richness, and argues for management actions that view the entire river basin as an integrated unit.

3.5 Summary

Fluvial geomorphology emphasizes the dynamic interplay between rivers and landscapes in the shaping of river channels and drainage networks. It includes study of the linkages among channel, floodplain, network, and catchment using a diversity of approaches including stratigraphic analyses, experimental studies of sediment transport in flumes, modeling of physical processes, comparisons of landforms, and sophisticated statistical approaches to gain greater understanding of the physical dynamics of river systems. It helps make sense of the enormous variety exhibited among fluvial systems, and thus the habitat and environmental conditions experienced by the biota. Quantification of the relationships among river features and analysis of the underlying processes contribute to a deeper understanding of how rivers respond to human-induced changes in water and sediment supply that can cause rivers to change their shapes.

A central theme in fluvial geomorphology is that the development of stream channels and entire drainage networks, and the existence of various regular patterns in the shape of channels, indicate that rivers are in dynamic equilibrium between erosion and deposition, and governed by common hydraulic processes. Channel width and depth, velocity, grain size of sediment load, bed roughness, and the degree of sinuosity and braiding are other variables that interact as the river adjusts to the variables that it cannot control, including discharge, sediment load, and its elevational extent.

The drainage basin encompasses a network of channels that join with others downstream in a progression of increasing drainage area and stream size. Stream order is a convenient shorthand for stream size, in which the smallest perennial stream is first order, and the union of two stream of order n forms a stream of order $n + 1$. Rivers increase in size as one proceeds downstream because tributaries and groundwater add to the flow. Hydraulic geometry equations describe the relationships of width, depth, and velocity to an increase in discharge, either downstream or as flow varies over time at a station. In the downstream case, width increases more than depth, while velocity increases least.

Many features of river channels are familiar to most of us, including sinuosity or meandering, an alternation of riffles, pools, and runs, and the presence of a floodplain provided the river valley is not so V-shaped that it prevents a floodplain from being formed. These features are formed by the river through cycles of erosion and deposition that in turn are strongly influenced by the balance between the twin supplies of water and sediments. A river's sediment load is the amount of sediment passing a point over some time interval, and includes very fine material that is likely always in transport, and coarser material from the bed and banks that is transported either as suspended load or as bed load, depending on particle size and discharge. The quantity of transported sediment increases with velocity and discharge, but flow events of intermediate frequency actually move more sediment over the years, because extreme events are so infrequent. The dominant or effective discharge is that at which sediment transport is greatest, and it often is approximately the bankfull flood. Human activities can increase or reduce sediment yields. Due to erosion brought about by changing land use, sediment flux into global rivers has increased, while sediment yields to the world's coasts have declined due to the trapping of sediments in impoundments. Some consequences include coastal retreat, subsidence of river deltas, and loss of coastal wetland habitat.

Stream power, the product of discharge and slope, describes the ability of the stream to mobilize and transport material. Sediment transport is directly related to stream power and inversely related to median grain size, and this is a useful relationship for understanding how a stream might respond to changes in sediment and water supply along its length, or due to human interference. As one proceeds from upland, to upland valley, and to large river, the river changes from exporting to accumulating sediments, and from being coupled to hillslopes for its sediment supply to being largely uncoupled. The series of interrelated changes in streamflow and sediment character that occur systematically along the river's length result in a predictable progression of channel types from cascade to step-pool to planform channels, and then to pool–riffle and dune–ripple types. But this classification, like many others, imposes discontinuities on what in reality is continuous change that is still imperfectly understood. River classification as a research topic continues to attract interest because it undeniably can be very useful for management and restoration, and it is a test of our understanding of the processes that are responsible for the great variety of river types.

Finally, to ecologists, geomorphology provides insight into the channel features, habitat units, surface and subsurface zones, floodplains, and riparian corridors that form a complex, shifting mosaic and within which the diversity of the physical template provides the setting in which biologically diverse communities flourish. When this complexity is reduced by dams, channelization, and regulation of river flow, the subsequent homogenization of habitat causes declines in taxon richness, and reminds us of the importance of management actions that view the entire river basin as an integrated unit.

Chapter four

Streamwater chemistry

We all have an intuitive appreciation that river water contains a variety of dissolved and suspended constituents. Mountain streams appear pure, farm creeks often are muddy with sediments, and drainages in limestone-rich regions are fertile while those containing only granitic rocks usually are less so. The rivers of heavily populated areas, and even the rain, are polluted by human activities.

Many factors influence the composition of river water, causing variation from place to place. Rain is one source of chemical inputs to rivers, and a stream flowing through a region of relatively insoluble rocks can be chemically very similar to rain water in its composition. Most streams and rivers contain much more suspended and dissolved material than is found in the rain, however. Ultimately, all of the constituents of river water originate from dissolution of the earth's rocks. The dissolving of rocks commonly is the major determinant of river water chemistry locally as well, but this varies with geology and with the magnitude of inputs via other pathways including precipitation, volcanic activity, and pollution. Materials are concentrated by evaporation and altered by chemical and biological interactions within the stream. Unlike seawater, which is quite constant everywhere and can be approximated with an artificial standard, river water varies considerably in its chemical composition (Livingstone 1963).

The materials transported in river water can be subdivided into dissolved versus suspended, organic versus inorganic, and by chemical description. Following Berner and Berner (1987), a useful breakdown includes:

1. Water
2. Suspended inorganic matter
3. Dissolved major ions (Ca^{2+}, Na^{+}, Mg^{2+}, K^{+}, HCO_3^-, SO_4^{2-}, Cl^-)
4. Dissolved nutrients (N, P, and to some extent Si)
5. Suspended and dissolved organic matter
6. Gases (N_2, CO_2, O_2)
7. Trace metals, both dissolved and suspended

In this chapter we shall concentrate on the major dissolved constituents and the gases. Suspended sediments and their transport were described in Chapter 3. Organic matter and dissolved nutrients are strongly intertwined with biological processes, and are discussed in Chapters 11 and 12 delving into ecosystem dynamics. Readers wishing more detailed discussions of aquatic chemistry and geochemistry should consult Berner and Berner (1987), Stumm and Morgan (1996), or other specialized volumes.

4.1 Dissolved Gases

Oxygen, carbon dioxide (CO_2), and nitrogen (N) occur as dissolved gases in river water in significant amounts. Although N gas can be incorporated into N cycling within stream ecosystems by certain specialized bacteria, the concentration of dissolved N_2 itself is of little biological importance.

Both oxygen and CO_2 occur in the atmosphere and dissolve into water according to partial pressure and temperature (Table 4.1). The solubility of oxygen in freshwater is reduced at high elevations due to lower atmospheric partial pressure. It also decreases with increasing salinity, by about 20% in normal seawater. Air is nearly 21% oxygen by volume and just 0.03% CO_2, but the latter is much more soluble in water. Hence, although saturated freshwater has higher concentrations of oxygen than CO_2, the difference is not nearly as great as is found in air. Groundwater frequently is very low in dissolved oxygen and enriched in CO_2 due to microbial processing of organic matter as water passes through soil. Localities that receive substantial groundwater inputs may reflect this, but equilibration with the atmosphere usually occurs once hyporheic water enters the stream.

In small, turbulent streams that have received only limited pollution, diffusion maintains oxygen and CO_2 near saturation. Should biological or chemical processes create a demand for or an excess of either within the water column, exchange with the atmosphere usually maintains concentrations very near to equilibrium. Concentrations may change seasonally and daily, however, in response to shifts in temperature. Diffusion plays a reduced role in large rivers because of the smaller surface area relative to volume, and in more smoothly flowing rivers because of less turbulence. In these circumstances, high naturally occurring biological activity can alter the concentrations of oxygen and CO_2, organic pollution can greatly increase respiratory demand for oxygen, and acid precipitation can alter the carbonate buffer system, which influences the concentration of free CO_2 in solution.

TABLE 4.1 Concentration of dissolved oxygen and carbon dioxide in saturated pure water for atmospheric partial pressure at sea level.

Temperature (°C)	*O_2 (mg L^{-1})*	*CO_2 (mg L^{-1})*
0	14.2	1.1
15	9.8	0.6
30	7.5	0.4

Respiration and photosynthesis are the two important biological processes that alter the concentration of oxygen and CO_2. Oxygen consumption increases with increased loadings of organic matter due to direct chemical reactions and aerobic respiration. Oxygen demand can be high in certain areas and seasons, for example, within accumulations of fallen leaves in woodland streams in autumn, in backwaters with abundant decaying plant matter, and due to anthropogenic sources. In highly productive waters, whole-system photosynthesis results in elevated concentrations of oxygen during the day, while whole-system respiration causes oxygen to decline at night. These diel (24 h) changes in oxygen concentration provide a means of estimating photosynthesis and respiration of the total ecosystem and are discussed in Chapter 6. First applied to productive, slow-moving rivers and lentic waters where diffusion is relatively low and more easily estimated (Odum 1956, Edwards and Owens 1962), recent improvements in measuring diffusion rates and detecting small changes in oxygen concentrations are extending this approach even to small woodland streams (Young and Huryn 1998).

CO_2 concentrations in streamwater are influenced not only by atmospheric diffusion and instream metabolism but also by groundwater inflows, which commonly are substantially enriched with CO_2 due to soil respiration throughout the catchment. In Walker Branch, Tennessee, streamwater was always supersaturated with respect to the atmosphere and so outgassing occurred at all times (Jones and Mulholland 1998). Free CO_2 exceeded the concentration expected for atmospheric equilibration by a factor >10 at the source of a moorland stream in northeastern Scotland, and decreased to near equilibrium at 2 km downstream, indicating the extent of outgassing of soil-derived CO_2 (Dawson et al. 1995). In highly productive lowland streams that support luxuriant growths of macrophytes and microbenthic algae, diel shifts in dissolved CO_2 can be large (Rebsdorf et al. 1991). Because of the interdependence of CO_2 concentration and pH (a measure of acidity, discussed below), midday pH can increase by as much as 0.5 units. In larger rivers receiving a substantial organic load, outgassing of CO_2 is unable to compensate for excess CO_2 generated by microbial respiration. As a consequence the partial pressure of CO_2 (pCO$_2$) in the water column can exceed that of the atmosphere by as much as 2–5 times, and occasionally by even more (Small and Sutton 1986, Rebsdorf et al. 1991). The CO_2 concentration of the Rhine is a good example. Water leaving the source, Lake Constance, in summer is lower than the atmospheric partial pressure due to the productivity of lake phytoplankton. In winter, however, water leaves the lacustrine source at about twice the atmospheric partial pressure. Because organic pollution increases as one proceeds downriver, the pCO$_2$ increases also. High summer temperatures permit high microbial respiration, with the result that the downstream average pCO$_2$ is about 20 times the atmospheric value (Kempe et al. 1991).

The River Thames is a good example of the effect of organic pollution on dissolved oxygen concentrations (Gameson and Wheeler 1977). Human and animal wastes have been a documented source of foulness since at least 1620, and 1858 was known as the "Year of the Great Stink," but the volume of untreated human sewage reduced water quality to an all-time low in the mid-1950s. Parts of the Thames around London became anaerobic from microbial respiration driven by organic waste, and sparked pollution-control efforts that led to substantial recovery. The impact of high oxygen demand due to pollution can be exacerbated by high summer temperatures, which reduce the solubility of oxygen in water, and by ice cover, which minimizes diffusion.

4.2 Major Dissolved Constituents of River Water

The total dissolved solids (TDS) content of fresh water is the sum of the concentrations of the dissolved major ions. The world average is about 100 mg L^{-1} (Table 4.2). Four major cations, Na^+, K^+, Ca^{2+}, Mg^{2+}, and four major anions, HCO_3^-, CO_3^{2-}, SO_4^{2-}, and Cl^-, make up most of

TABLE 4.2 Chemical compositions of river waters of the world (mg L^{-1}). Cations and anions are in μeq L^{-1}. (From Wetzel (2001) and sources therein.)

	Ca^{2+}	Mg^{2+}	Na^+	K^+	$CO_3^{2-}HCO_3^-$	SO_4^{2-}	Cl^-	NO_3^-	Fe (as Fe_2O_3)	SiO_2	Sum
North America	21.0	5.0	9.0	1.4	68.0	20.0	8.0	1.0	0.16	9.0	142
South America	7.2	1.5	4.0	2.0	31.0	4.8	4.9	0.7	1.4	11.9	65
Europe	31.1	5.6	5.4	1.7	95.0	24.0	6.9	3.7	0.8	7.5	182
Asia	18.4	5.6	5.5	3.8	79.0	8.4	8.7	0.7	0.01	11.7	142
Africa	12.5	3.8	11.0	–	43.0	13.5	12.1	0.8	1.3	23.2	121
Australia	3.9	2.7	2.9	1.4	31.6	2.6	10.0	0.05	0.3	3.9	59
World	15.0	4.1	6.3	2.3	58.4	11.2	7.8	1.0	0.67	13.1	120
Cations	750	342	274	59	–	–	–	–	–	–	1425
Anions	–				958	233	220	17	–	–	1428

the ionic content of fresh water. Other ions, including those of N, phosphorus (P), and iron, are biologically important but make a minor contribution to total ions. Both the total and the concentration of individual constituents vary considerably from place to place, due to variability in natural and anthropogenic inputs. However, the vast majority of the world's rivers have TDS that contain more than 50% HCO_3^-, and from 10% to 30% ($Cl^- + SO_4^{2-}$). This reflects the dominance of sedimentary rock weathering, and especially of carbonate minerals (Berner and Berner 1987). Just under one fourth of the earth's land surface is covered by igneous and metamorphic rocks, versus three fourths covered by sedimentary rocks. Combining this information with the known differences in ionic concentrations associated with different geologies, it is evident that dissolved materials from sedimentary rocks contribute by far the greatest amount (more than 80%, Berner and Berner 1987) of the total dissolved load of rivers, and thus dominate the composition of "average" river water.

Salinity refers to the sum of the concentrations of all dissolved ions, and so is a more inclusive term than TDS, although for all practical purposes it is the same quantity. TDS is measured by evaporation and weighing of the residue. In addition, major ions can be measured directly by a number of ways, including colorimetric methods in which specific ions react with specific chemicals to form colored compounds, ion chromatography, and by means of ion-specific probes. Dissolved constituents are reported as units of mass, milligrams per liter (equal to parts per million [ppm]), or as chemical equivalents. In the latter case, milliequivalents per liter are calculated from milligrams per liter, by dividing by the equivalent weight of the ion (its ionic weight divided by its ionic charge).

Conductivity is a measure of electrical conductance of water, and an approximate measure of total dissolved ions. Distilled water has a very high resistance to electron flow, and the presence of ions in the water reduces that resistance. The relationship between TDS and specific conductance (SC) typically is linear ($TDS = k \times SC$) with a value of k between 0.55 and 0.75. However, the value of the constant varies with location and must be established empirically (Walling 1984). Differences in conductivity result mainly from the concentration of the charged ions in solution, and to a lesser degree from ionic composition and temperature. Values are reported as microSiemens per centimeter ($\mu S\ cm^{-1}$) at 20 or 25°C, and in the older literature as the reciprocal of ohms (μmho cm^{-1}) (Golterman et al. 1978).

The ionic concentration of rainwater (Table 4.3) is much more dilute than most river water, with an average value of a few milligrams per liter (Berner and Berner 1987). Na^+, K^+, Ca^{2+}, Mg^{2+}, and Cl^- are derived primarily from particles in the air, whereas SO_4^{2-}, NH_4^+, and NO_3^- are derived mainly from atmospheric gases. Marine salts (NaCl) are especially important near the oceans, and a transition to $CaSO_4$ or $Ca(HCO_3)_2$ dominated rain occurs as one proceeds inland. The relative importance of these various inputs can vary seasonally and over quite short distances, as Sutcliffe and Carrick (1983) document for streams of the English Lake District.

TABLE 4.3 Concentrations of major ions in continental and marine coastal rainfall (mg L^{-1}). (From Berner and Berner 1987.)

Ion	*Continental rain*	*Marine coastal rain*
Ca^{2+}	0.2–0.4	0.2–1.5
Mg^{2+}	0.05–0.5	0.4–1.5
Na^+	0.2–1	1–5
K^+	0.1–0.5	0.2–0.6
$NH4^+$	0.1–0.5	0.01–0.05
SO_4^{2-}	1–3	1–3
Cl^-	0.2–2	1–10
NO_3^-	0.4–1.3	0.1–0.5
pH	4–6	5–6

Of course, river water will be more concentrated than rainwater simply because of evaporation. Using the world average runoff ratio of 0.35, which means that 35% of precipitation becomes runoff, the concentration of ions in river water should be nearly three times greater than the concentration in rain. Because the true differential is roughly 20-fold, rock weathering, other natural sources, and anthropogenic inputs must account for the majority of dissolved ions in river water (Berner and Berner 1987). Figure 4.1 illustrates this discrepancy for North America. Roughly 10–15% of the calcium, sodium, and chloride in US river water comes from rain, compared to one fourth of the potassium and almost half of the sulfate. In contrast, almost none of the SiO_2 or HCO_3^- comes from rain. This emphasizes the need to examine the origins of each of these major cations and anions in order to understand what influences their concentrations.

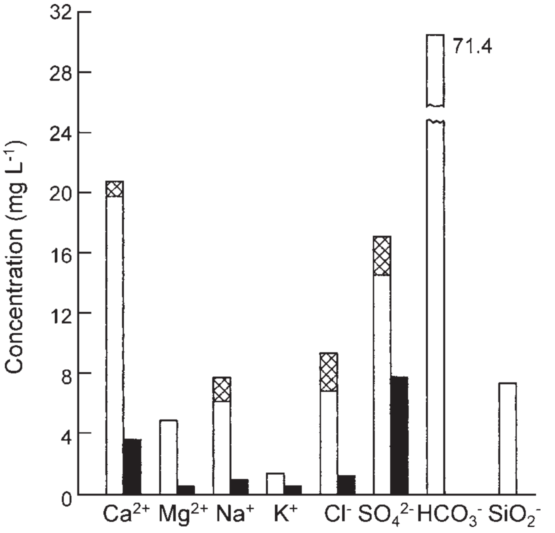

FIGURE 4.1 Dissolved ionic concentrations for river (clear bars) and rain water (shaded bars) from North America. Rainwater concentrations are multiplied by 2.6 to correct for evaporation. Cross-hatching shows anthropogenic contribution to river water values. (Reproduced from Berner and Berner 1987.)

Calcium is the most abundant cation in the world's rivers. It originates almost entirely from the weathering of sedimentary carbonate rocks, although pollution and atmospheric inputs constitute small sources. Its concentration (along with magnesium) is used to characterize "soft" versus "hard" waters, which are discussed fully below. Magnesium likewise originates almost entirely from the weathering of rocks, particularly Mg–silicate minerals and dolomite. Atmospheric inputs are minimal, and pollution contributes only slightly.

Sodium is generally found in association with chloride, indicating their common origin. Weathering of NaCl-containing rocks accounts for most of the Na found in river water. However, rainwater inputs from sea salts can contribute significantly, especially near coasts. Pollution, due to domestic sewage, fertilizers, and road salt, is an especially important factor. Berner and Berner (1987) estimate that, worldwide, ~28% of the sodium in rivers is anthropogenic.

Potassium is the least abundant of the major cations in river water, and the least variable. Roughly, 90% originates from the weathering of silicate materials, especially potassium, feldspar, and mica. Concentrations thus vary with the underlying geology, and also increase substantially from polar latitudes toward the tropics, apparently due to more complete chemical weathering at higher temperatures. Silica is used by diatoms in the formation of their external cell wall and can on occasion limit algal productivity.

Bicarbonate (HCO_3^-) ultimately derives almost entirely from the weathering of carbonate minerals. However, the immediate source of the majority of bicarbonate is CO_2 dissolved in soil and groundwater, which is produced by bacterial decomposition of organic matter, and derives in turn from the photosynthetic fixation of atmospheric CO_2. Bicarbonate is a biologically important anion. High concentrations are reflected in measures of alkalinity and are indicative of fertile waters. The carbonate buffer system, alkalinity, and hardness are interrelated, as will be discussed more fully below. Anthropogenic increases in acidity, caused by acid precipitation or mining, reduce bicarbonate levels through the formation of H_2CO_3.

The origins of chloride are essentially the same as sodium: mostly from weathering of rocks, but inputs of sea salts and pollution including the application of road salts to reduce ice can be important. Chloride is chemically and biologically unreactive, and so is useful as a tracer in nutrient release experiments.

Sulfate has many sources, including the weathering of sedimentary rocks and pollution from fertilizers, wastes, mining activities, and especially the burning of fossil fuels; biogenically derived sulfate in rain and volcanic activity are additional inputs. In areas of sulfuric acid rain, such as Hubbard Brook, New Hampshire, sulfate concentrations are high relative to overall ionic concentrations (Likens and Bormann 1995). Sulfate and bicarbonate concentrations tend to be inversely correlated in streamwater, especially in low alkalinity areas.

The key nutrients N and P are discussed more fully in Chapter 11, where their forms (nitrate, ammonium, phosphate, etc) and influence on ecosystem processes are discussed in detail. Dissolved inorganic P and N are primary nutrients that limit plant and microbial production, and cycle rapidly between their inorganic forms and their incorporation into the food web.

Lastly, the concentration of hydrogen ions is very important both chemically and biologically, because they determine the acidity of water. This is expressed as pH, and is a logarithmic scale in which a tenfold change in hydrogen ion activity corresponds to a change of 1 pH unit. A pH of 7 is neutral, higher values are alkaline, and lower values are acidic.

4.2.1 Variability in ionic concentrations

The chemistry of fresh waters is quite variable, rivers usually more so than lakes. Natural spatial variation is determined mainly by the type of rocks available for weathering, how wet or dry the climate is, and by the composition of rain, which in turn is influenced by proximity to the sea. The ionic concentration of rivers draining igneous and metamorphic terrains is roughly half that of rivers draining sedimentary terrain, because of the differential resistance of rocks to weathering. All of these factors provide the opportunity for substantial local variation in river chemistry. As a consequence the concentration of total dissolved ions can vary considerably amongst the headwater branches of a large drainage. However, these heterogeneities tend to average out, and concentrations tend to increase, as one proceeds downstream (Livingstone 1963).

Although small streams in the same region often are chemically similar, they also can differ markedly. Within a series of small streams in southwest England, Walling and Webb (1975) reported a concentration range of total ions from 25 to 650 mg L^{-1}, resulting from small-scale shifts between igneous and sedimentary rocks. Small streams draining a volcanic landscape in central Costa Rica exhibited pronounced differences in solute concentrations depending on geology, soil types, and elevation (Pringle 1991). Phosphorus, several major cations and anions, and trace elements were high in headwater streams draining younger volcanic landscapes and much lower in streams draining older lava flows. The blackwater Río Negro and whitewater Solimões (the Amazon mainstem) dramatically illustrate the chemical differences between tributaries draining distinctive landscapes. The Río Negro drains well-weathered, crystalline rock and is much lower in ions and much higher in organic acids, whereas the Amazon mainstem drains the comparatively young Andes and has a much higher dissolved load. The unique chemical signatures of these two mighty rivers can be detected as much as 100 km below their confluence.

Climate exerts considerable influence over regional variation in the chemical composition of rivers. Across a gradient from arid to humid conditions, a general inverse relation is seen between annual precipitation and total solute concentration. High concentrations of total dissolved ions are found in rivers draining arid areas due to the small volumes of precipitation and runoff, salt accumulation in the soil, and evaporation (Walling 1984).

River chemistry also varies over time, due to the influence of seasonal changes in discharge regime, precipitation inputs, and biological activity. Flow variation has especially strong effects on ionic concentrations. Rivers are fed by a combination of groundwater and surface water, depending upon local geology and rainfall. Because of its longer association with rocks, the chemistry of groundwater typically is both more concentrated and less variable than surface waters. As a consequence, increases in flow due to rain events typically dilute streamwater, although it is not a simple relationship (Livingstone 1963). Golterman (1975) states that there are two common patterns. TDS may decline with increasing discharge, which is expected when the input of materials is constant. Alternatively, ion concentrations might not change greatly with fluctuations in discharge. This is expected when water chemistry reaches an equilibrium with the soil through which it percolates, or when concentrations approach saturation values. In addition to these two common patterns, however, some ions have been found to increase in concentration with rising discharge. The Orinoco River has very low concentrations of geologically derived nutrients because a large fraction of its catchment is underlain by resistant shield rock and covered with undisturbed forest, and because it has a very high runoff rate (Lewis and Saunders 1990). Seasonal increases in discharge result in a dilution response of major ionic solids, soluble silica and P; however, soluble organic fractions and all particulate fractions showed a purging response in which concentrations increased with increasing discharge.

Long-term studies of streamwater draining a hardwood forest in New Hampshire illustrate how ionic concentrations can change in response to seasonal variation in precipitation inputs, discharge, and the cycle of growth of the terrestrial vegetation (Likens and Bormann 1995). The most significant point is the relative constancy in stream chemistry, which probably is typical of intact, undisturbed ecosystems (Figure 4.2). Most dissolved substances vary within a narrow range (less than twofold), whereas streamflow can vary as much as four orders of magnitude over an annual cycle. In the Hubbard Brook Experimental Forest virtually all drainage water must pass through its mature and highly permeable podzolic soils. This affords considerable buffering capacity, and accounts for the relatively constant chemical composition of streamwater (Likens et al. 1970).

Figure 4.2 illustrates how concentration trends with discharge may differ among cations. Both magnesium and calcium showed no significant correlation with discharge, although the latter was the more variable of the two. Sodium concentrations exhibited a significant inverse relationship with discharge, presumably because of its low availability, and so rising discharge caused dilution. With the exception of some very high values during summer drought, potassium concentrations generally increased with increasing discharge. The explanation for this is complicated, and apparently includes biological activity as well as soil buffering. Stream discharge is low during the summer, higher throughout the winter, and highest at snowmelt. Plant growth during the summer corresponds with low potassium concentrations, and so it appears that seasonal changes in biological demand correlate with seasonal changes in flow conditions.

Although solute concentrations may exhibit only modest variation in response to discharge fluctuations in an intact forest, timber harvest and road building are significant disturbances that are reflected in solute export. Following deforestation and suppression of regrowth by herbicides in a catchment of Hubbard Brook,

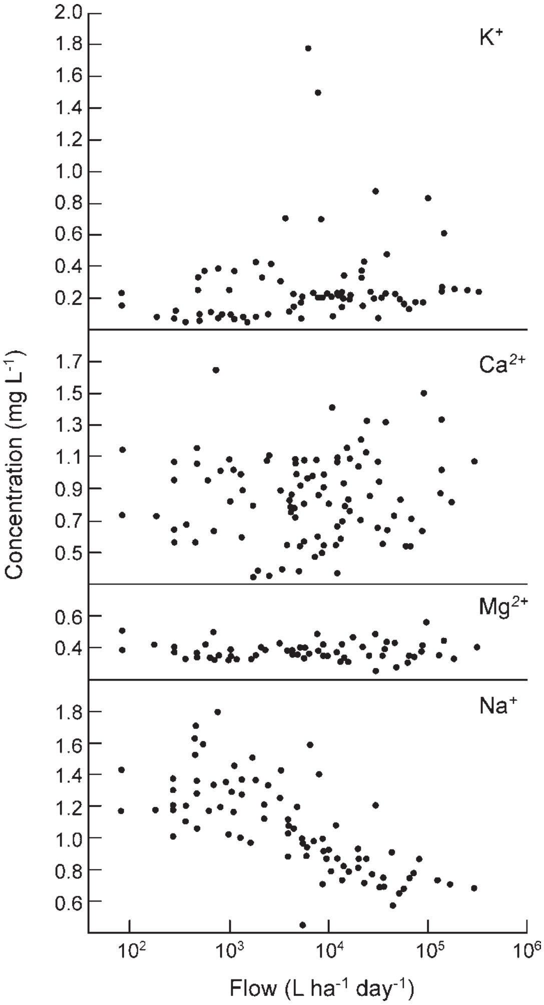

FIGURE 4.2 The concentration of major ions in relation to stream discharge in a small forested catchment in the Hubbard Brook Experimental Forest, New Hampshire, from 1963 to 1965. (Reproduced from Likens et al. 1967.)

most major ions exhibited large increases in streamwater concentration and total output increased sixfold. Only ammonium and carbonate remained low and constant, and sulfate declined because of reductions in sulfate generation by sources internal to the ecosystem. The average values for calcium and magnesium increased by over 400%, sodium by 177%, and potassium over 18-fold. Altered ion concentrations were attributed to increased discharge, changes in the N cycle within the ecosystem, and higher temperatures (Likens and Bormann 1995).

Use of best management practices can moderate the response of streamwater chemistry to the disturbances associated with timber harvest. A long-term study of a well-managed clearcut of a hardwood forested catchment found that almost all solutes and nutrients showed elevated concentrations and exports, but because the forest was harvested using cable logging, which minimizes the need for roads and dragging of felled trees, and other best management practices were employed such as reseeding roads, overall losses were small and judged not detrimental to forest productivity (Swank et al. 2001).

4.2.2 The dissolved load

The dissolved load of a river is the product of concentration and discharge, and usually is expressed as kilograms per day or tons per year. In comparing catchments or river basins it is helpful to present this as a yield per unit area, by dividing by drainage area. Streamflow is more variable than ionic concentration, and so between-year variation in the export of ions depends strongly on interannual variation in discharge (Figure 4.3). Because discharge and ionic concentration often are inversely related, the range of the dissolved load of ions transported by the world's major rivers varies over only two orders of magnitude, from around three to as high as 500 t km^{-2} year^{-1}, with highest values observed in small alpine rivers (Meybeck 1977). It also varies less over time than does the solid load. The greater discharge of rivers in humid areas more than compensates for lower ionic concentrations, and so the dissolved load is less in arid areas and greater in areas of higher runoff.

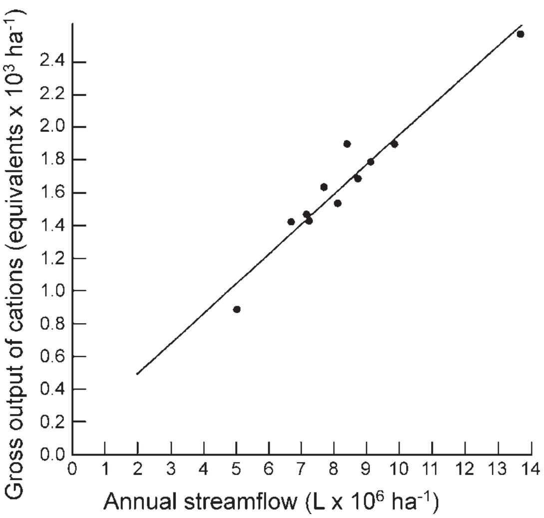

FIGURE 4.3 Between-year variation in the gross output of calcium, sodium, magnesium, and potassium depends mainly on between-year variation in discharge for undisturbed catchments of the Hubbard Brook Experimental Forest. Data span 1963–1974. (Reproduced from Likens and Bormann 1995.)

4.2.3 Chemical classification of river water

If one graphs the relative proportions of principle anions and cations in the world's surface waters against TDS, a curve with two arms emerges (Figure 4.4). Gibbs (1970) interpreted this as evidence that three major mechanisms control surface water chemistry. At the left of the "boomerang" lie systems where the rocks and soils of river basins are the predominant source of their dissolved materials. Relief, climate, and age and hardness of rocks determine the positions of rivers within this grouping. Proceeding along the lower arm to the right of the figure we encounter waters that are lower in ions and whose chemical composition most closely resembles the rain. These are mainly the tropical rivers of Africa and South America with their sources in highly leached areas of low relief. In these humid regions, precipitation with a composition similar to seawater is of major importance as a source of ions. Average river water concentrations are $< 30\,\mathrm{mg\,L^{-1}}$. Proceeding along the upper arm to the right, we encounter systems with high concentrations of dissolved ions and again a relative predominance of Na^+ and Cl^-. These are rivers of hot, arid regions, and the combined influence of evaporation and precipitation of $CaCO_3$ from solution accounts for their chemistry. Total dissolved salts exceed $1{,}000\,\mathrm{mg\,L^{-1}}$, and can be as high as $6\text{–}7\,\mathrm{g\,L^{-1}}$, as in Kazakhstan. Thus three major mechanisms – atmospheric precipitation, dissolution of rocks and the evaporation–crystallization process – are considered to account for the principal trends of dissolved ions in the world's surface waters. Other factors, including relief, vegetation, and the composition of rocks and soils then can be invoked to explain differences within these major groupings.

Critics of this scheme question the interpretation of control at the ends of the boomerang. The Río Negro's chemistry is equally a consequence of its long history of intense weathering and a basin of mainly silicious rocks (Stallard and Edmond 1983). Similarly, saline rivers might be strongly influenced by near-surface halite deposits (Kilham 1990). These arguments downplay the roles of precipitation and evaporation, and suggest that local geology is of primary importance in determining river chemistry over all extremes. Regardless, most of the world's rivers are closer to the middle than the ends of this diagram, are low in $Na^+/(Na^+ + Ca^{2+})$, and are dominated by Ca^{2+} and HCO_3^- from carbonate dissolution. This is in accord with the view that the weathering of sedimentary rocks provides most of the dissolved ions in most of the world's major rivers (Berner and Berner 1987).

4.3 The Bicarbonate Buffer System

Dissolved CO_2 reacts with H_2O to form carbonic acid (H_2CO_3), a weak inorganic acid that occurs at low concentrations relative to unhydrated CO_2 at pH < 8 (Wetzel 2001). H_2CO_3 further

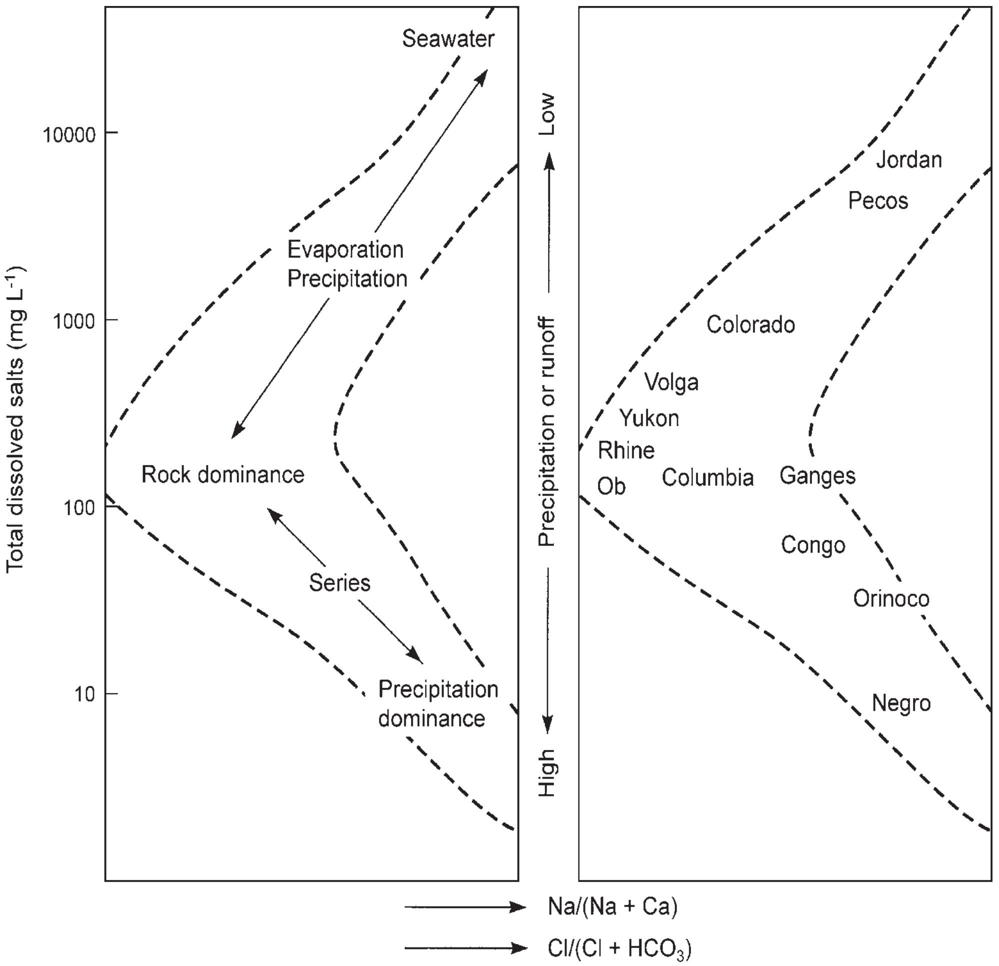

FIGURE 4.4 A classification of surface waters of the world based on ratios of sodium to calcium and chloride to bicarbonate, in relation to total dissolved salts. As one proceeds from left to right along the lower arm, inputs shift from a dominance of rock dissolution to a dominance of precipitation. The majority of large tropical rivers are found to the lower right. As one proceeds from left to right along the upper arm, sodium and chloride increase. These high salinity rivers lie in arid regions where evaporation is great. Note the vertical axis also reflects a gradient from high precipitation and runoff at the base to arid regions at the top. (Modified from Gibbs 1970 and Payne 1986.)

dissociates to form hydrogen (H^+), bicarbonate (HCO_3^-), and carbonate (CO_3^{2-}) ions. The latter in turn react with water to form hydroxyl ions (OH^-). When the natural content of carbonate rocks is high, as is common in the sedimentary rocks that make up most of the earth's surface, these reactions result in sufficient hydroxyl ions to produce alkaline waters. This is known as the $CO_2 - HCO_3^- - CO_3^{2-}$ buffering system, because it resists change in pH. Although addition of hydrogen ions will neutralize hydroxyl ions, more are formed immediately through the reaction of water with carbonate, and so pH resists change. However, once the supply of carbonate is exhausted, which occurs most rapidly in igneous drainages, pH can drop quickly.

The relative proportions of CO_2, HCO_3^-, and CO_3^{2-} are pH-dependent (Figure 4.5). At a pH below 4.5 only CO_2 and H_2CO_3 are present, and almost no bicarbonate or carbonate can be found. Indeed, bicarbonate concentration commonly is measured by titration with a strong acid until reaching a pH of about 4.3. At higher pH values dissociation of carbonic acid occurs, bicarbonate and carbonate are present, and CO_2 and H_2CO_3 are no longer detectable. At intermediate pH values, HCO_3^- predominates. These dissociation dynamics are influenced by both temperature and ionic concentrations, and the relationships shown in Figure 4.5 may not be valid for water of very high ionic concentration.

The inorganic carbon (C) required for photosynthesis is most easily obtained from CO_2, although many photosynthetic organisms can utilize bicarbonate. By influencing the forms of inorganic C available, shifts in pH can influence the efficiency of different primary producers in the ecosystem.

Fresh waters can vary widely in acidity and alkalinity due to natural causes as well as anthropogenic inputs. Very acid and very alkaline waters are harmful to most organisms, and so the buffering capacity of water is critical to the maintenance of life. The pH of water is a measure of the concentration of hydrogen ions, hence the strength and amount of acid present. Because the scale is logarithmic to the base 10, a decline of one pH unit represents a tenfold increase in hydrogen ion concentration.

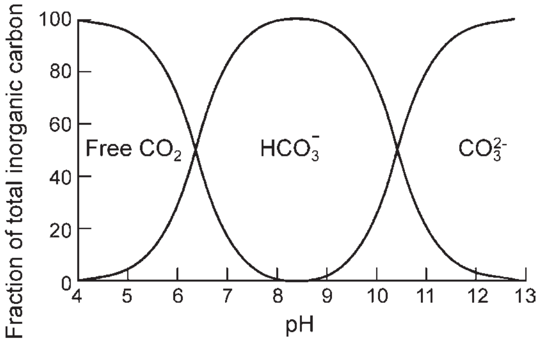

FIGURE 4.5 Influence of pH on the relative proportions of inorganic carbon species, $CO_2(+H_2CO_3)$, $HCO3^-$, and $CO_3{}^{2-}$ in solution. (Reproduced from Wetzel 2001.)

In natural waters, pH is largely governed by H^+ ions from the dissociation of H_2CO_3 and OH^- ions from the hydrolysis of bicarbonate. Rain normally is acid (typically near a pH of 5.7) because of its CO_2 content and also due to naturally occurring sulfate. Normally, these acids are neutralized as rain water passes through the soil. However, in catchments of hard rocks, little buffering capacity, and high surface water (as opposed to groundwater) inputs, streamwater will be acid even if pollution is absent. Organic acids also contribute to low pH values. Where decaying plant matter is abundant, especially in swamps, bogs, and peaty areas, humic acids result in "brown" or "black" waters, and a pH in the range of 4–5. In addition, volcanic fumes and local seepage from sulfurous or soda springs can produce natural extremes of pH.

Over the past several decades, industrial activity has contributed to acid precipitation in many areas. The strong inorganic acids H_2SO_4 and HNO_3, formed in the atmosphere from oxides of sulfur and N released in the burning of fossil fuels, have seriously lowered surface water pH in large areas of Europe and North America, especially in granitic drainages with poor buffering capacity. These anthropogenic inputs initially produce only slow declines in pH, but as the bicarbonate buffering capacity becomes exhausted further acid inputs cause pH to decline rapidly. The biological consequences can be severe, and will be described later in this chapter.

Alkalinity refers to the quantity and kinds of compounds that collectively shift the pH into the alkaline range. The bicarbonate buffering system is mainly responsible for alkalinity. It is a measure of the capacity of the solution to neutralize acid, and is determined by titration with a strong acid and expressed as milliequivalents per liter or milligrams per liter. Often alkalinity is measured as milligrams per liter of $CaCO_3$, which measures the acid-neutralizing capacity due to carbonate and bicarbonate. Because alkalinity is determined from a filtered sample, it measures the capacity of solutes to neutralize acid. Acid neutralizing capacity (ANC) is similar but is determined for an unfiltered sample, and thus measures the capacity of solutes plus particulates to neutralize acid.

Hardness is another commonly used water quality term. It is determined by cations that form insoluble compounds with soap, and so primarily is a measure of the amount of calcium and magnesium salts. Ca and Mg occur mainly in combination with bicarbonate, sulfate, and chloride, and the common co-occurrence of calcium and bicarbonate has led some to equate hardness with alkalinity. However, it is possible to find very high alkalinity with very little calcium or magnesium, and so it can be incorrect to equate these terms.

4.4 Influence of Chemical Factors on the Biota

The biological consequences of variation in the ionic content of fresh waters appear not to be very significant when conditions are reasonably close to the average. However, when one encounters the extremes, due to any of the natural causes already discussed or because of human influence, chemical variation from place to place can significantly affect the distribution of organisms and biological productivity.

4.4.1 Variation in ionic concentration

If one attempts to develop an entirely artificial medium for the culture of freshwater invertebrates, as has been done successfully for planktonic microcrustaceans, a long list of chemicals must be included (D'Agostino and Provasoli 1970). If one holds mayfly larvae in distilled water, 50% mortality is exceeded within a few days (Willoughby and Mappin 1988). Unquestionably, stream-dwelling organisms require water of some minimal ionic concentration. Unfortunately, there has been little effort to establish these requirements experimentally. The majority of the evidence linking the ionic content of water to the stream biota comes from surveys. Often such studies establish that streamwater of very low ionic concentration has a restricted flora and fauna, in both abundance and species richness. Studies may be reported in terms of water hardness, alkalinity, conductivity, or measurements of specific ions. Hynes (1970) describes a number of examples where the species of algae, mosses, and higher plants differ between soft versus hard waters. Among the invertebrates, it appears that mollusks, crustaceans, and leeches are more responsive to the range of ionic concentrations than are aquatic insects. The amphipod *Gammarus* apparently is common in streams of the English Lake District that have at least $3\,\mathrm{mg\,L^{-1}}$ calcium, and rare in streams of lower concentrations. A number of molluscan surveys have described the particular species that occupy soft waters, and reported a positive correlation between hardness and species richness. According to Russell-Hunter et al. (1967), roughly 5% of the molluscan species of a region will occur in extremely soft waters ($<3\,\mathrm{mg\,L^{-1}}$ calcium). Moderately soft waters ($<10\,\mathrm{mg\,L^{-1}}$) will support perhaps 40% of the species of a region, intermediate waters (10–$25\,\mathrm{mg\,L^{-1}}$) will support up to 55%, and hard waters ($>25\,\mathrm{mg\,L^{-1}}$) are needed to include all the molluscan species of an area. Shell growth of juvenile zebra mussels was strongly correlated with water buffer variables of calcium, alkalinity, and hardness, and corroborating field evidence suggests that this invasive species in North America will be unsuccessful at less than $\sim 10\,\mathrm{mg\,L^{-1}}$ calcium and most successful at $>25\,\mathrm{mg\,L^{-1}}$ (Hincks and Mackie 1997). Such a dependence on calcium availability is expected,

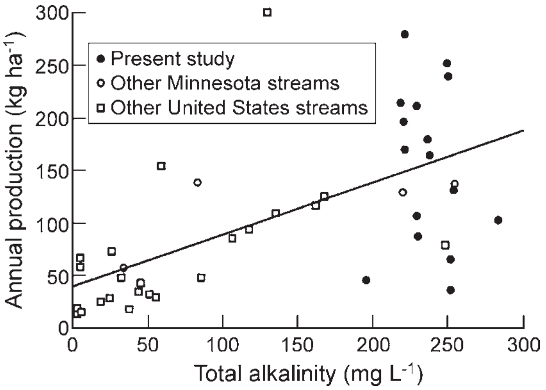

FIGURE 4.6 Relationship between salmonid annual production and alkalinity for streams in southeastern Minnesota (black circles) and other locations throughout the United States. (Reproduced from Kwak and Waters 1997.)

because aquatic mollusks derive a large fraction of their considerable calcium needs by absorption directly from the external medium. $CaCO_3$ is necessary for shell deposition and growth, and calcium is important in general fluid and electrolyte balance.

Alkalinity is widely used as a surrogate for stream fertility and is thought to influence the productivity of fish populations via their food supply (Cooper and Scherer 1967). Compiling data on salmonid production and stream alkalinity from numerous studies in the United States, Kwak and Waters (1997) demonstrated a statistically significant but nonetheless imperfect relationship (Figure 4.6). However, their own data from 13 southeastern Minnesota streams did not show any dependence of salmonid production on stream alkalinity, which the authors suggest may be due to the modest range of alkalinity values among sites as well as the influence of additional variables including temperature and biological interactions.

4.4.2 Salinization

This describes the situation where total dissolved ions, and thus salts, are high, often because of human activities. Salinization refers to either the process or the result of the buildup of dissolved salts in fresh waters. The natural range of salinity in inland waters is considerable, but when referring to the result of human activities, we often are concerned with changes from relatively low background concentrations. Using a world average of 120 mg L^{-1} for reference (Table 4.2), which is thought to be slightly elevated above its natural state due to pollution, a TDS > 250 mg L^{-1} indicates high salinity. From the human perspective, salinities > 250–500 mg L^{-1} are undesirable for drinking water, and detrimental effects on crops and industrial uses occur at levels $> 0.5 - 1$ g L^{-1} (Jackson and Jobbágy 2005, Williams 2001).

Salinization is a particular problem in arid and semiarid areas due to irrigation and dryland farming. Irrigation concentrates salts by evaporation and also because the remaining, more concentrated solution leaches soil salts. Ultimately this more concentrated water returns to the stream, via surface or subsurface flows. In Australia, where salinization is widespread in semiarid agricultural areas, the lower South Australian Murray River averages ~ 0.5 g L^{-1} (Williams and Williams 1991). In North America, the elevated salinity of the Colorado (> 0.8 g L^{-1} at its delta) is the recent consequence of irrigation and impoundments. Although the biological effects of this are not well known, river water in the lowermost sections is unsuitable for agriculture without expensive desalinization facilities.

In urban areas, the runoff of salts and other deicing compounds applied to roads can significantly elevate the salinity of receiving waters and cause large fluctuations at short time scales. In the United States, some 10–15 million tons of road salt are used each year (Benbow and Merritt 2005), primarily in the Northeast and Midwest, and quantities have increased dramatically since 1950 (Jackson and Jobbágy 2005). Kaushal et al. (2005) report chloride concentrations as high as 25% of seawater in some northeastern US streams during winter, and the long-term trend is increasing (Figure 4.7).

Whether the salinities that we would consider high in rivers are harmful to the biota is unclear, although faunal changes unquestionably occur in the brackish waters of estuaries. Acute toxicity levels for stream macroinvertebrates exposed to saline water are relatively high, ranging from 2 to 13 g L^{-1} (Benbow and Merritt 2005), but can decrease with increasing temperature. Road salt runoff had no discernible effect on macroinvertebrates of the Au Sable River, Michigan, which Blasius and Merritt (2002) attributed to dilution from snow melt. In two river systems of Australia, excluding estuarine reaches, Williams et al. (1991) found no relationship between macroinvertebrate assemblages and salinity, which exceeded 2 g L^{-1}. Several fishes of the Murray River survived laboratory exposures to salinities up to 30 g L^{-1}, possibly reflecting a relatively recent marine ancestry for these species (Williams and Williams 1991), and most cyprinids (the minnow family) survive up to 14–20 g L^{-1} (Threader and Houston 1983). Where the salinity range is great, such as the Red River of Texas, a prairie stream where salt concentrations range from ~ 200 mg L^{-1} TDS to approximately full strength seawater, fish assemblages form low-, medium-, and high-salinity groupings and salinity-sensitive species have shown greatest declines in recent years (Higgins and Wilde 2005). In most circumstances, however, although individual freshwater species may be harmed by even moderate salinities, current evidence does not indicate widespread damage to the fauna.

4.4.3 Effects of acidity on stream ecosystems

Fresh waters may be naturally acidic due to the decay of organic matter, and anthropogenically acidified by atmospheric deposition of strong

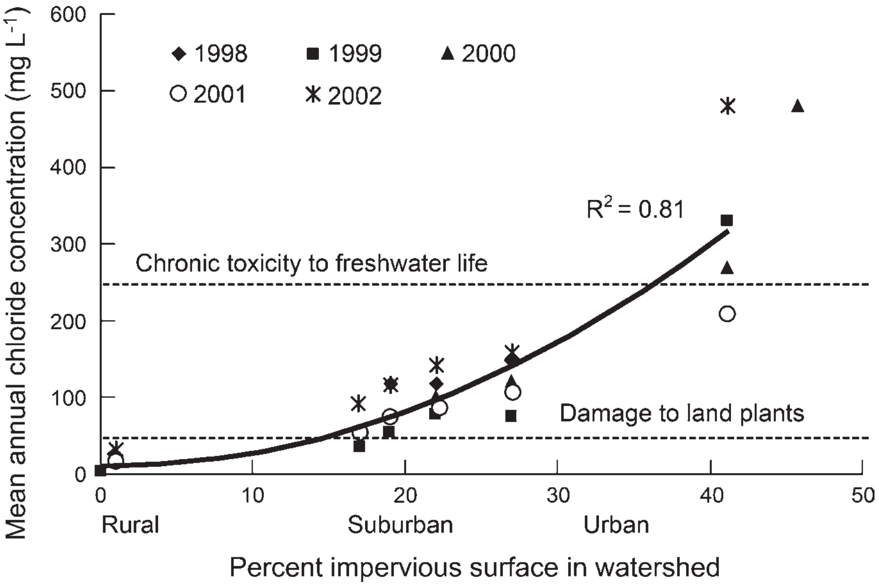

FIGURE 4.7 The mean annual concentration of chloride increases with impervious surfaces area (an indicator of urbanization) for streams along a rural to urban gradient near Baltimore, Maryland. Dashed lines represent thresholds for damage to some land plants and chronic toxicity to sensitive aquatic organisms. (Reproduced from Kaushal et al. 2005.)

inorganic acids formed from sulfate and nitrous oxides released in the burning of fossil fuels, or from acids leached from mining deposits. Naturally acidic waters, tea-colored from the breakdown of organic matter, occur in diverse settings including northern peatlands, tropical regions such as the aptly named Río Negro, and blackwater rivers draining swamp forests such as the Ogeechee River in the southeastern United States. Acid precipitation is a relatively recent phenomenon due to industrialization, and has its greatest influence in regions of poor buffering capacity, especially in granitic catchments. Substantial areas of northern Europe, the northeastern United States and eastern Canada, and the Rocky Mountains have been significantly impacted.

The deleterious effects of acidic streamwater are well established, primarily in terms of reduced numbers of species and individuals (Figure 4.8), but there also is evidence of altered ecosystem processes. The degree of acidification is of course very important, and depends upon both inputs and buffering capacity. Organisms evidently are harmed via diverse pathways, including metal toxicity, and taxa differ in their susceptibility. Consequently, while one can assert that anthropogenic acidification is generally harmful once pH falls much below 5.0, the details depend upon many factors.

The River Duddon in the English Lake District has received acid precipitation from the industrialization of Europe for probably the last 100 years, and prior to this a long and gradual period of postglacial acidification is thought to have occurred (Sutcliffe and Carrick 1973, 1988). The range of pH in this region is approximately 4–7 and varies with geology, upstream–downstream location, and season. Permanently acid (pH < 5.7 at all times) streams have a characteristic and restricted macroinvertebrate fauna, consisting of six plecopterans, four trichopterans, and three

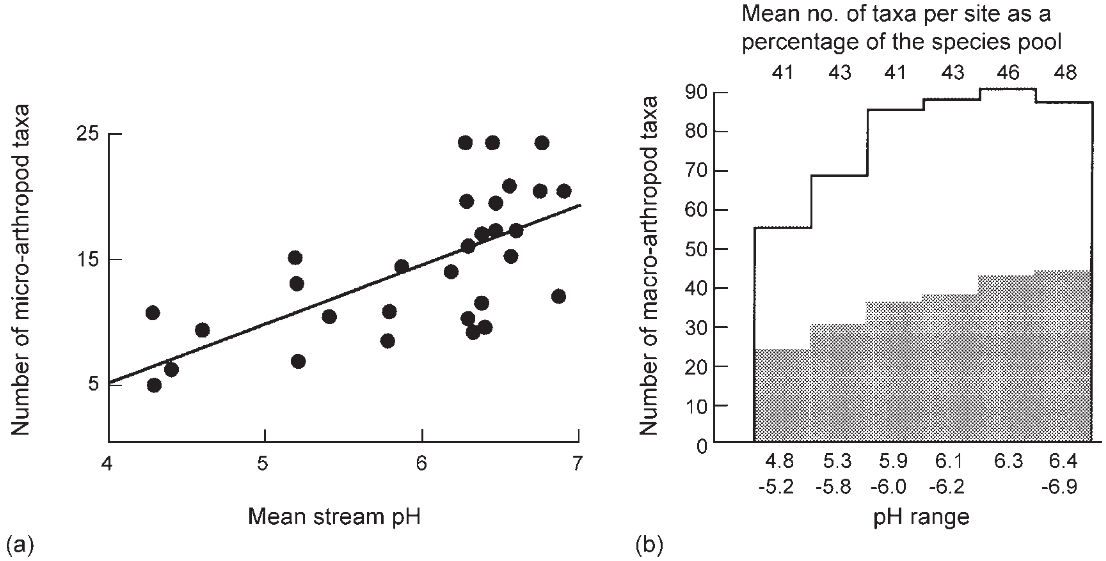

FIGURE 4.8 Influence of pH on the number of species occurring in streams of the Ashdown Forest, southern England. (a) Microarthropods: mainly mites (Hydrachnellae), copepods (Harpacticoida and Cyclopoida), and Cladocera. (b) Macroarthropods: mainly aquatic insects. Note that the number of species of macroarthropods found at a site was a fairly constant 40–50% of the species known to occur under the conditions of water chemistry found at that site. (Reproduced from Rundle and Ormerod 1991 and Townsend et al. 1983.)

dipterans. Such streams occur in areas of relatively hard, slow-weathering rocks, often in the headwaters. Locations with pH permanently >5.7 have additional taxa, including a number of mayflies, two other species of trichopterans, the limpet *Ancylus*, and the amphipod *Gammarus*. They are found in regions of sedimentary slates and exposed veins of calcite. These streams have not changed in acidity since at least the 1950s, evidently because bicarbonate ion availability counters the continued inputs from acid rain.

Naturally acid streams seem less affected than those acidified by atmospheric pollutants. A survey of 34 streams in New Zealand that exhibited a pH range from 4.1 to 8.1 due to variation in natural concentrations of humic substances found no correlation between pH and taxonomic diversity (Winterbourn and Collier 1987). Similar numbers of taxa were obtained from streams with pH ≤5.5, between 5.6 and 6.9, and ≥7.0. Only at a pH below 4.5 was there any evidence of faunal exclusion, in marked contrast to the Duddon example. These contrasting cases suggest that the mechanism must involve more than acidity alone. Indeed, there is growing evidence that lowered pH is accompanied by a number of chemical changes, and also that organism response is due to various physiological, behavioral, and indirect effects.

Leaching of metals from soils is an important consequence of hydrogen ion deposition. Aluminum occurs in elevated concentrations in acidic waters (Figure 4.9), and is known to impair osmoregulatory processes by damaging the ion-regulating organs. Separate and combined additions of aluminum compounds and inorganic acids to stream channels have been used to distinguish the direct influence of hydrogen ion concentration from the effects of elevated aluminum. In a short-term (24 h) manipulation of a soft-water stream in upland Wales, two salmonid species exhibited far greater susceptibility to the combined effects of acid and aluminum versus sulfuric acid alone, apparently because of respiratory inhibition (Ormerod et al. 1987).

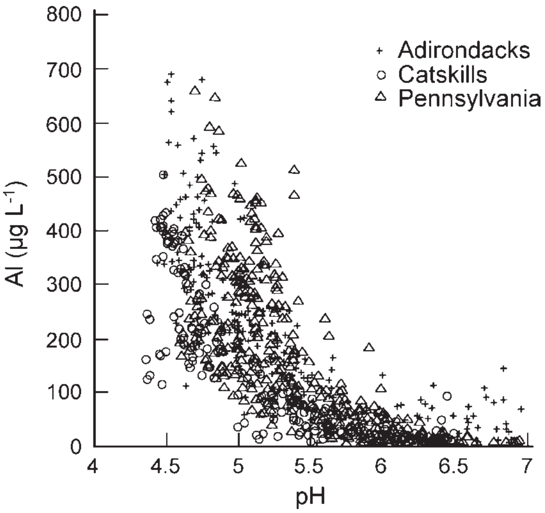

FIGURE 4.9 Relationship between aluminum concentrations (measured as inorganic monomeric Aluminum, AL) and pH for streams of northeastern United States. Note the wide range in AL at low pH values. (Reproduced from Wigington et al. 1996.)

In addition to the mobilization of toxic metals, there are numerous other pathways by which acidity is detrimental to the stream biota. Direct physiological effects of acidity are implicated by field and laboratory demonstration of increased mortality or failure of eggs to develop as pH is reduced (Willoughby and Mappin 1988). Inability to regulate ions apparently is responsible, including loss of body sodium and failure to obtain sufficient calcium from surrounding waters (Økland and Økland 1986). Field collections generally show stoneflies and caddisflies to tolerate waters of lower pH than do mayflies and some dipterans. Hall et al. (1987) speculate that differences in life cycle and respiratory style of these groups account for their differential susceptibility to acid stress.

Episodic pulses of acid water during snowmelt or rainstorms appear to be more influential than stream chemistry during low flow periods. Lepori et al. (2003) were able to differentiate between streams that became acidic during snowmelt (pH reduced to 5) versus well buffered streams (pH remained above 6.6) in an acid-sensitive Alpine area of Switzerland. The streams that were sensitive to acid episodes had different invertebrate assemblages from well-buffered sites and soft-water, stable streams. Episodes of acidification and elevated aluminum concentrations restricted stream fishes from sites in the northeastern United States that had suitable chemical conditions (pH >6 and inorganic Al $< 60\ \mu g\ L^{-1}$) at low flow (Baker et al. 1996). Abundances of the brook trout *Salvelinus fontinalis* were reduced and the blacknose dace (*Rhinichthys atratulus*) and sculpin (*Cottus bairdi* and *C. cognatus*) were eliminated from streams that episodically experienced pH <5 and inorganic Al $>$ 100-200 $\mu g\ L^{-1}$. Behavioral avoidance is one cause of declines, and offers the possibility of subsequent recolonization if alkaline refuge areas are available. Baker et al. suggest that lower mobility in sculpins relative to brook trout may explain why the former were eliminated from acid-pulsed streams. The availability and spatial location of refuge streams of moderate to high alkalinity influenced brook trout population structure in streams of the central Appalachian Mountains of West Virginia. Spawning and recruitment occurred primarily in small tributaries with alkalinity above $10\ mg\ L^{-1}$, whereas large adults apparently dispersed throughout the catchment (Petty et al. 2005).

Ecosystem processes also are affected by stream acidification. Inputs of autumn-shed leaves are an important energy supply to woodland streams, and breakdown rates respond to a number of environmental variables (Chapter 7). Breakdown rates of beech leaves *Fagus sylvatica* varied more than 20-fold between the most acidified and circumneutral sites in 25 woodland headwater streams along an acidification gradient in the Vosges Mountains, France (Dangles et al. 2004a). Microbial factors associated with decaying leaves, particularly microbial respiration, declined with increasing stream acidity, as did the number of taxa. In some instances, however, ecosystem processes may be relatively unaffected due to species substitutions. Here again, evidence indicates that naturally acidic streams differ from anthropogenically acidified systems. Neither the number of taxa nor the rate of leaf breakdown were markedly depressed even at a pH of 4.0 in naturally acidic streams of northern Sweden (Dangles et al. 2004b). Because these naturally acidic Swedish streams contain a unique fauna, they could be adapted to those conditions. In addition, metal toxicity likely is less important in naturally brown- and blackwater streams owing to the chelating abilities of humic acids, which bind metal ions mobilized at low pH (Winterbourn and Collier 1987, Collier et al. 1990).

Addition of lime to neutralize acid conditions is widely practiced. The River Auda in Norway had lost its anadromous salmon and sensitive mayflies due to anthropogenic acidification when liming commenced in 1985. Within 2 years sensitive mayflies had returned, and additional macroinvertebrates appeared over the following 5-plus years. However, in some cases liming has not been sufficient to offset the effects of episodic acidification. In three acidified Welsh streams that were evaluated for 10 years following the liming of their catchments, pH increased to above six and the number of macroinvertebrate species increased, but relatively few acid-sensitive species recovered (Ormerod and Edwards 2002). The occasional appearance but limited persistence of acid-sensitive taxa in limed streams led the authors to suggest that episodes of low pH continued to affect acid-sensitive taxa even after liming. Whether it makes sense to add lime to naturally acidic streams adds a further complication. In Sweden, approximately US \$25 million has been spent since 1991 to lime some 8,000 lakes and 12,000 km of streams to restore their condition, and as Dangles et al. (2004b) point out, expending funds to lime naturally acidic systems may not be wise management.

4.5 Summary

The constituents of river water include suspended inorganic matter, dissolved major ions, dissolved nutrients, suspended and dissolved organic matter, gases, and trace metals. The dissolved gases of importance are oxygen and CO_2. Exchange with the atmosphere maintains the concentrations of both at close to the equilibrium determined by temperature and atmospheric partial pressure, especially in streams that are small and turbulent. Photosynthetic activity in highly productive settings can elevate oxygen to supersaturated levels and result in strong fluctuations between day and night. Respiration has the opposite effect, reducing oxygen and elevating CO_2. High levels of organic waste can reduce oxygen concentrations below life-sustaining levels, and CO_2 can be elevated from groundwater inputs or biological activity.

Many factors influence the composition of river water, and as a consequence it is highly variable in its chemical composition. The concentration of the dissolved major ions (Ca^{2+}, Na^+, Mg^{2+}, K^+, HCO_3^-, SO_4^{2-}, Cl^-) is roughly 120 mg L^{-1} on a world average. However, river water is highly variable, ranging from a few milligrams per liter where rainwater collects in catchments of very hard rocks to some thousands of milligrams per liter in arid areas.

Variation from place to place is determined mainly by the type of rocks available for weathering, by the amount of precipitation, and by the composition of rain, which in turn is influenced by proximity to the sea. The concentration of TDS is roughly twice as great in rivers draining sedimentary terrain compared to igneous and metamorphic terrains, due to differential resistance of rocks to weathering. Areas of high rainfall and surface water runoff usually have less concentrated streamwater chemistry compared to arid areas where evaporation is greater and dilution is less. Precipitation inputs typically are of lesser importance to streamwater chemistry, except in areas of very hard rocks and high surface runoff. Human-generated pollutants enter river water via precipitation and dry deposition, by stormwater transport of fertilizers, road salt, etc., as well as by direct disposal.

River chemistry changes temporally under the multiple influences of seasonal changes in discharge regime, precipitation inputs, and biological activity. Groundwater typically is both more concentrated and less variable than surface waters, because of its longer association with rocks. In undisturbed catchments some ions are remarkably constant across discharge fluctuations spanning several orders of magnitude. However, because rainfall increases the surface water contribution, ion concentrations often are diluted by increases in flow.

Natural waters contain a solution of CO_2, carbonic acid and bicarbonate and carbonate ions in an equilibrium that serves as the major determinant of the acidity–alkalinity balance of fresh waters. Fresh waters can vary widely in acidity and alkalinity, and extreme pH values (much below 5 or above 9) are harmful to most organisms. The bicarbonate buffer system, consisting of the $CO_2{-}HCO_3^-{-}CO_3^{2-}$ equilibrium, provides the buffering capacity that is critical to the health of the freshwater biota.

Although fresh water is highly variable in its chemical composition, and rivers more so than lakes, the biological importance of such variation is mainly evident at the extremes, and where human-generated pollutants are substantial. Water of very low ionic concentration appears to support a reduced fauna, particularly of crustaceans and mollusks. The number of species commonly increases with hardness, and many taxa are distinctly "soft-water" or "hard-water" forms. Anthropogenic additions of strong inorganic acids set off a number of changes in water chemistry, and at a pH much below 5.0, the biological consequences are serious.

Chapter five

The abiotic environment

At all spatial scales in fluvial ecosystems, studies of the stream biota support the expectation that greater physical complexity of the environment promotes increased biological richness. That organisms are adapted to aspects of habitat, such that the traits of organisms reflect features of the environment, is a fundamental idea in ecology referred to as the habitat template concept (Southwood 1988). The key habitat needs of a species are commonly identified from the subset of environmental variables that best correlate with its distribution and abundance. Although additional factors also influence the composition and diversity of biological assemblages, including interactions among species and the taxon richness at the regional scale, the abiotic environment provides an important starting point in investigations of species distributions and abundances. This view has two important corollaries. First, environments that are structurally either simple or extreme tend to support fewer species, whereas more moderate and heterogeneous habitats support more species. Second, a high frequency of disturbance tends to diminish biological richness, although a moderate level of disturbance potentially may enhance diversity by maintaining an ever-changing spatial mosaic of conditions. These principles forecast the consequences of human disturbance: anthropogenic degradation and homogenization of habitat will lead to biodiversity decline with unpredictable consequences for ecosystem function.

Habitat is often described as where a species lives, and so is a subset of a species' niche. The latter term is broader, describing a species' place in a biological community and incorporating all of the physical and biological conditions needed for a species to maintain its population in an area (Begon et al. 2005). The niche concept incorporates species interactions, competition in particular, in distinguishing between the space that a species would occupy in the absence of competitors and the more restricted space, the realized niche, which it actually does occupy owing to the impact of other species. In this chapter we focus on key abiotic aspects of habitat that influence the distribution and abundance of the biota of fluvial ecosystems; later, in Chapter 10, the influence of species interactions will be explored.

Habitat features vary across small to large spatial scales, sometimes referred to as micro-, meso-, and macrohabitat (Vinson and Hawkins 1998), and from very short to long time scales (Figure 1.3). Individual taxa are adapted more or less narrowly to a specific range of habitat conditions, and will be more or less successful depending on the matching of their morphological, behavioral, and physiological traits to environmental conditions. Thus the abiotic environment, acting on species traits, serves as a filter (Figure 1.5) that determines at least the candidate taxa of a locale.

In fluvial ecosystems, key abiotic features of the environment are usually those related to current, substrate, temperature, and sometimes water chemistry variables such as alkalinity and dissolved oxygen. Water chemistry and dissolved oxygen are important under natural conditions only in some unusual environments and under low flows, but both factors can be very influential when human activities result in polluted waters (Section 13.2.3). Current is the defining feature of rivers and streams. It conveys benefits, such as transport of resources to the organism and removal of wastes, and also risks, of which being swept away is the most obvious. The substrate of running waters differs greatly from place to place, and is important to algae and many insects as the surface on which they dwell and to many fishes as the structure near which they find shelter from current or enemies. Temperature affects all life processes, and because most stream-dwelling organisms are ectothermic, growth rates, life cycles, and the productivity of the entire system are strongly under its influence. Thus current, substrate, and temperature are three physical variables that we should understand in order to appreciate the functioning of a lotic ecosystem and the adaptations of its denizens.

To decipher how organisms respond to individual habitat variables is complicated because organisms are subject to the simultaneous and interactive effects of multiple abiotic factors. The relationship of macroinvertebrate abundances to velocity, substrate size, and depth measures (Figure 5.1) illustrates differences in habitat preferences, but because these environmental factors are interrelated, it can be difficult to distinguish causal from correlated variables. Often we focus on the range of average conditions, but the variance in average conditions and the frequency and magnitude of extremes may be equally important. When environmental conditions episodically become unfavorable, such as an area of substrate that receives excessive scour or a stream section that becomes too warm for days or weeks, then patches of remaining suitable habitat provide refuge until the disturbance passes and recolonization can occur.

5.1 The Flow Environment

In fluvial systems the flow of water is a dominant and characterizing variable that influences diverse aspects of the stream environment (Hart and Finelli 1999). It affects channel shape and substrate composition and episodically disturbs both. Flow strongly influences the physical structure and hydraulic forces operating in the benthic and near-bed microhabitats occupied by much of the biota, and is important to ecological interactions, rates of energy transfer, and material cycling (Figure 5.2). Current velocity is a direct physical force that organisms experience within the water column as well as at the substrate surface. Organisms are directly affected when eroded from a substrate or as their energy reserves are depleted by the work of maintaining position. They are indirectly affected when the delivery of food particles, nutrients or dissolved gasses influences their metabolism and growth. Flow conditions are important to ecosystem processes through the delivery of nutrients and gases and removal of wastes, and possibly by influencing which species occur at a site. Definitions and methods of measurement were given in Chapter 2; recall that current is the speed of moving water (usually in cm s^{-1} or m s^{-1}), and flow or discharge is volume per unit time (usually m^3 s^{-1} or cfs).

Current velocity varies enormously, not only along a river's length and with the rise and fall of the hydrograph, but also from place to place within stream channels at meso- and microhabitat scales owing to bed friction, topography, and bed roughness due to large substrate particles and wood. The vertical velocity profile (Figure 2.8) is of fundamental importance to any consideration of the effects of current on organisms, as the flow conditions near the streambed may differ markedly from open-channel flow. When the depth of flow is substantially greater than the height of roughness elements, one expects an outer layer in which velocities vary little with depth and a logarithmic layer of declining velocity near the streambed (Figure 5.3). Under

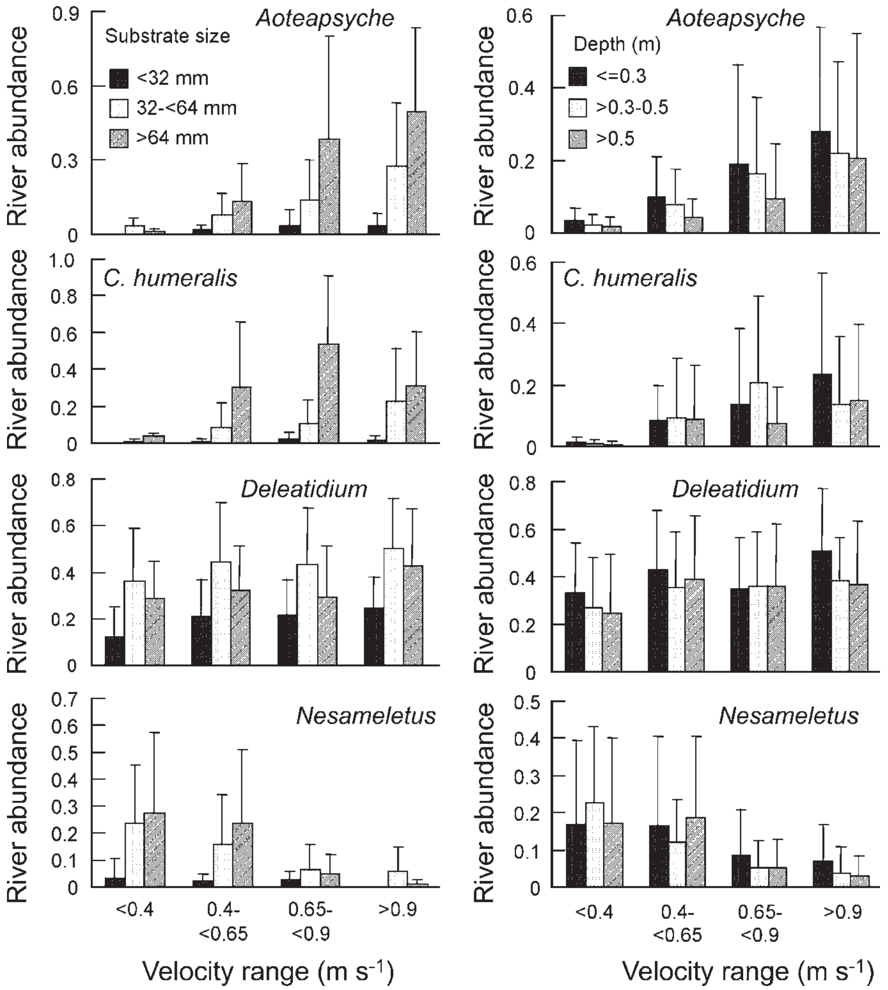

FIGURE 5.1 The relative abundance of some macroinvertebrate taxa in four large New Zealand rivers within substrate size (*left*), depth (*right*), and velocity ranges. *Aoteapsyche* (Trichoptera); *Colobursicus humeralis*, *Deleatidium*, and *Nesameletus* (Ephemeroptera). Error bars are 1 standard deviation. (Reproduced from Jowett 2003.)

smooth, laminar flow conditions, friction with the streambed results in a laminar sublayer of viscous flow very near the channel surface. In most natural circumstances, however, roughness-induced three-dimensional flows and turbulence characterize the near-bed environment where most stream organisms dwell (Hart and Finelli 1999).

Recognition of the complexity of flow conditions near the streambed has led to increasing efforts to measure current and hydraulic forces at scales most appropriate to the organisms. Using methods that allowed quantification of the flow environment of larval black flies at very fine spatial and temporal scales, Hart et al. (1996) established that the spatial distribution of *Simulium vittatum* was better predicted by velocity measured 2 cm above the bed than at 10 cm. When water velocity microhabitats were quantified at the scale of millimeters, rainbow

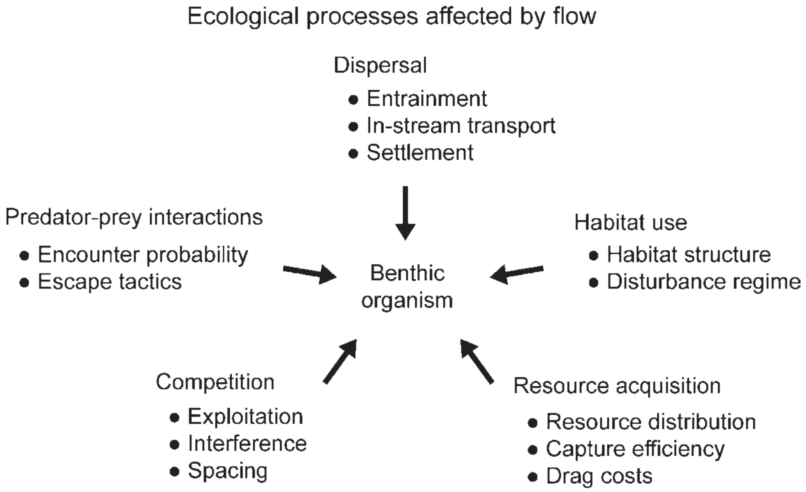

FIGURE 5.2 Multiple causal pathways by which flow can affect organisms. Potential interactions among pathways are not shown. (Reproduced from Hart and Finelli 1999.)

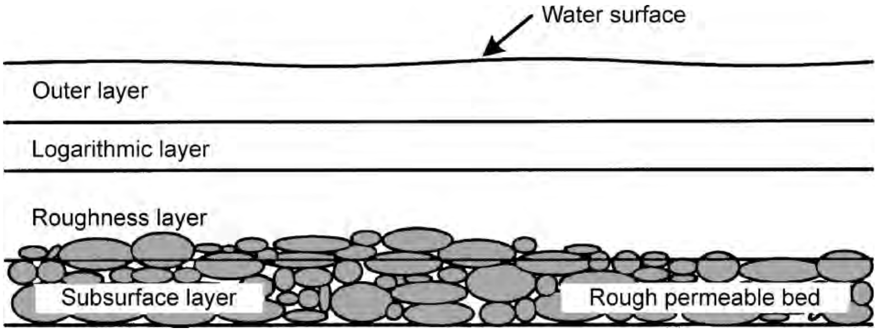

FIGURE 5.3 Subdivision of hydraulically rough open-channel flow into horizontal layers. Flow velocities within the "roughness layer" are unpredictable based solely on knowledge of flow in the logarithmic layer. This figure is not drawn to scale. (Reproduced from Hart and Finelli 1999.)

darters (*Etheostoma caeruleum*) in the Mad River, Ohio, were consistently found in microhabitat shelters where velocities were significantly lower than at adjacent (<5 cm distance) sites (Harding et al. 1998)

Characterizing near-bed flows creates an enormous measurement challenge and has led to a number of imaginative attempts over the past several decades to estimate or directly measure flow microenvironments. Approaches include application of boundary layer theory (Davis 1986, Vogel 1994); classification of flows and depths, and size and spacing of roughness elements (Davis and Barmuta 1989, Young 1992); predictions based on hydraulic engineering models (Statzner et al. 1988); and improvements in direct measurement at fine scales (Hart et al. 1996, Bouckaert and Davis 1998). Despite increasing sophistication these efforts have met with only partial success. Before discussing each in detail it is useful to introduce some language and equations pertaining to the velocity conditions and forces associated with flowing water.

5.1.1 Channel and near-bed flow environments

The biota of running waters dwell in a highly variable environment from the standpoint of current regime. This is apparent to anyone mesmerized by the delicate swirls on the surface of the smallest stream, or the awesome power of a storm-swollen river. Three fundamental types of flow characterize moving fluids: laminar, turbulent, and transitional. In laminar flow, fluid particle movement is regular and smooth, and particles can be thought of as "sliding" in parallel layers with little mixing. Turbulent flow is characterized by irregular movement with considerable mixing. Intermediate conditions are described as transitional. In fact, laminar flow conditions are so rare in aquatic environments that they are relevant primarily as a theoretical reference point. Although laminar flow can occur in pipes, and over smooth mud surfaces, even beds of sand produce complex flow. This complexity increases with increasing roughness of the channel bottom and with mean velocity.

At the interface between a fluid and a solid, the velocity of the two is identical (the "no-slip" condition, Vogel 1994), which means that water in contact with noneroding substrate has zero velocity. Because surface water can move quite rapidly, there must be a gradient in velocity as one approaches the bottom and sides of streams Figure 2.8). This decrease of velocity with depth produces a region of shear, known as the boundary layer. The upper limit of the boundary layer occurs where the speed of the current is no longer influenced by the presence of the stream bottom. The boundary layer may extend to the surface in a shallow stream. Very close to the stream bottom, there may be a viscous sublayer where shear stress is zero and flow is greatly reduced.

The possibility that a thin layer of low flow exists very near the stream bottom, perhaps functioning as a refuge from the turbulence and high velocities of the water column just above, has attracted the attention of stream ecologists since at least the turn of the last century (e.g., Steinmann 1908, Ambühl 1959). This idea gained credibility from the dorsally compressed body shapes exemplified by the water penny *Psephenus* and a number of mayflies, and the expectation that current must be reduced at the water–substrate interface. However, as Vogel (1994) puts it, "most biologists have the fuzzy notion that [the boundary layer] is a discrete region rather than the discrete notion that it's a fuzzy region." Moreover, the terms boundary layer and viscous sublayer should not be used interchangeably. Strictly speaking, the region of greatly reduced flow is the viscous sublayer, which is found very close to the streambed or other surface. It now appears that as flow becomes more turbulent and more typical of natural streams, the viscous layer is thinned to the point that most benthic invertebrates likely experience a turbulent, three-dimensional flow microenvironment (Nowell and Jumars 1984, Hart and Finelli 1999). This shift in perspective heightens the need for a better understanding of the hydrodynamic conditions that organisms actually experience.

5.1.2 Hydraulic variables

Table 5.1 summarizes the simple and complex hydraulic variables in common use. Mean velocity and depth are the same variables described in Chapter 2, although here we use the symbols of hydraulic engineers rather than of hydrologists. Surface roughness can be measured directly from particle dimensions, or by using a bed profiler such as a level plate through which a number of sliding vertical rods are pressed downward to the bed surface to generate a bed topography measure. Mean velocity, depth, and surface roughness are simple hydraulic variables that provide useful information about the flow environment. Using open-channel measurements and certain constants one can estimate hydraulic variables including channel Reynolds number (*Re*) and Froude's number (*Fr*).

TABLE 5.1 Some terms and equations useful in describing streamflow (Adapted from Davis and Barmuta 1989, Carling 1992).

Terms	*Description*	*Units*	*Measurement*	
U	Mean velocity	cm s^{-1}	Measured at 0.4 depth from bottom or from open-channel velocity profile	
*U**	Shear velocity	cm s^{-1}	Estimated from fine-scale velocity plotted against log depth near the streambed	
D	Water depth	cm	Total depth, surface to bed	
k	Substrate roughness	cm	Height of surface roughness elements measured individually or with bed profiler	
D/k	Relative roughness	Dimensionless	Height of roughness elements relative to water depth; influences flow type	
g	Acceleration due to gravity		$9.8\,\mathrm{m\ s^{-2}}$	
v	Kinematic viscosity		$1.004 \times 10^{-6}\ \mathrm{m^2\ s^{-1}}$ at 20°C	
Equations				
Re	Bulk flow Reynolds number	Dimensionless	$Re = \mathrm{U\ D}/v$	$Re < 500 \rightarrow$ laminar flow $500 < Re < 10^3 - 10^4 \rightarrow$ transitional flow $Re > 10^3 - 10^4 \rightarrow$ turbulent flow
Fr	Froude number	Dimensionless	$Fr = U(gD)^{-0.5}$	$Fr < 1 \rightarrow$ subcritical flow $Fr = 1 \rightarrow$ critical flow $Fr > 1 \rightarrow$ super-critical flow
*Re**	Boundary Reynolds number	Dimensionless	$Re^* = U^*k/v$	$Re^* < 5 \rightarrow$ hydraulically smooth flow $5 < Re^* < 70 \rightarrow$ transitional flow $Re^* > 70 \rightarrow$ hydraulically rough flow

It is the convention of this literature to represent velocity with *U*, depth with *D*, and the constant for kinesmatic viscosity of water as *v*

Re quantifies the ratio of inertial forces of the moving fluid to the viscous properties of a fluid that resist mixing (Newbury and Bates 2006). It is a dimensionless number that can be used to distinguish types of flow and the forces experienced by an organism. Depth of flow is used to estimate *Re* for the channel, and the length of a fish or insect can be used to estimate the forces that act directly on an organism.

At low *Re*, flow is laminar and viscous forces predominate, whereas at high *Re* turbulence occurs and inertial forces predominate. Laminar flow usually requires current velocities well below 10 cm s^{-1}, especially if depth exceeds 0.1 m; in short, quite shallow and slow moving water. Hence turbulent flow is the norm in the channels of rivers and streams. *Fr* is a dimensionless velocity to depth ratio, and differentiates tranquil flow from broken and turbulent flow (Davis and Barmuta 1989). Low values of *Fr* are characteristic of pool habitats and higher values of riffle habitats. In some New Zealand streams, *Fr* generally was <0.18 and rarely as high as 0.4 in pools, >0.41, and as high as 1 in riffles, and intermediate in runs (Jowett 1993).

Using an estimate of shear velocity (*U**), which can be derived from the velocity profile near the streambed, and substituting the height of roughness elements for water depth, one can estimate roughness (boundary) Reynolds number (Re^*) (Table 5.1). This variable and the dimensionless shear stress, which is related to the square of shear velocity and inversely related to particle size, describe the conditions under which particle movement is likely (Section 3.3.2). Both near-bed velocity and bed shear stress increase with increasing relative roughness and mean velocity

Physical conditions between the extremes of low and high Re differ greatly (Vogel 1994). At high Re's, pressure drag is the important force and streamlining is an adaptive countermeasure. An airfoil, a trout, and a *Baetis*, each with blunt front and tapered rear, are ideal shapes to minimize turbulent drag that results from the rejoining of flow streams downstream of the object. By minimizing wake turbulence, streamlined shapes reduce the pressure differential between front and rear, which creates the drag we experience on our legs as we wade through a swift stream. At low Re, water is more viscous, flow is much more laminar, and the force exerted as layers of water slide over one another is greater. This last force, due to the no-slip condition, results in skin friction. It is minimized by reduction in surface area, and so stubby or rotund shapes might be advantageous. Streamlining will be of little benefit due to the reduced role of pressure drag and the increased surface area that streamlining entails. These are only generalizations, however; at Re between 10^2 and 10^4, the best shapes to minimize total drag are not known.

Lastly, it should be noted that these equations characterize the flow environment based on average or mean conditions. In the complex, three-dimensional flow environment of turbulent streams, velocity measured at a point fluctuates markedly, and it is this temporal variance that defines turbulence. How organisms and substrate particles respond to the forces of moving water may be influenced more by spikes than by the mean condition.

5.1.3 Quantification of flow conditions

Recent years have seen the development of a number of applications of fluid dynamics and hydraulic principles in stream ecology. Recent books by Gordon et al. (2004) and Vogel (1994) provide excellent treatments of fluid mechanics for biologists. Reviews by Davis and Barmuta (1989), Carling (1992), and Hart and Finelli (1999) are especially useful from the perspective of life on the streambed. Webb (1994) reviews the biomechanics of fish swimming movements. Application of these ideas often requires measurements of current velocity at finer spatial and temporal scales than was previously the norm, resulting in various efforts to better characterize the flow conditions experienced by organisms. This continues to be a challenge, as many methods are too expensive or delicate for easy field use, and some obtain measurements at a coarser scale than is desirable, or are invasive, potentially disturbing the flow microenvironment they intend to measure. While perhaps none is perfect, several approaches in wide use are worthy of description.

The FST-hemisphere method (Statnzer and Müller 1989) consists of 24 hemispheres of identical size (7.8 cm) and surface texture but different densities exposed sequentially to current on a weighted Plexiglas plate. The heaviest hemisphere that the current is able to displace is an indication of near-bed hydraulic forces, and calibrations to near-bed velocity and shear stress are obtained from near-bed velocity profiles or hydraulic simulations. The plate is placed at locations of interest on the streambed, such as where benthic invertebrates have been collected. It is not a direct measurement, introduction of the apparatus may distort local flow, and the scale is large relative to the organism. Methods allowing direct measurement in some field settings at scales approaching that of benthic macroinvertebrates include hot film anemometers (HFA) and acoustic Doppler velocimeters (ADV). However, HFA is both expensive and fragile, limiting its usefulness in the field. ADVs are gaining interest because they allow three-dimensional, fine-scale velocity measurements in field settings and thus estimation of shear stress and turbulence. The Doppler shift between transmitted and received signals from suspended particles is used to calculate velocity. Nikora et al. (1998) used an ADV to examine how the presence of the aquatic moss *Fissidens rigidulus* on cobbles influenced near-bed flow environment in a stream flume by measuring flow around cobbles with moss, and then repeated the measurements after removing the moss without disturbing the cobbles' position. Velocities in the upper layer followed the standard logarithmic profile, but within the lower sublayer the interaction of flow with roughness due to moss had a marked effect, with reductions in velocity, stress measures, and turbulence (Figure 5.4). Another approach that appears to hold promise for fieldwork uses tubes of very small diameter (syringe needles) to measure pressure differences in the boundary layer (Ackerman and Hoover 2001).

5.1.4 Influence of flow on the biota

Field studies that compare the abundances of macroinvertebrates to hydraulic variables measured at the typical sampling scale of 0.1 m^2 or less provide strong support for the influence of the flow environment on benthic organisms. In the Ardèche River, a tributary of the River Rhône in southern France, Mérigoux and Dolédec (2004) collected invertebrates from microhabitats and estimated hydraulic conditions at sampling locations using FST hemispheres. Some dependence of distribution on hydraulic parameters was found in nearly 70% of the taxa analyzed (54 in spring, 31 in autumn), whereas others (the mayfly *Epeorus* in spring, the stonefly *Leuctra* in autumn) appeared indifferent to the range of hydraulic conditions. The ordination of the spring assemblage against shear stress (Figure 5.5) illustrates the influence of hydraulic variables; of these, shear stress and *Fr* were better predictors than substrate size. In riffle microhabitats (0.07 m^2) of the Kangaroo River of southeastern Australia, the majority of the macroinvertebrate community was associated with riffle areas of lowest near-bed turbulence (Brooks et al. 2005). Macroinvertebrate abundance and number of taxa were negatively related to roughness *Re*, shear velocity, velocity, and *Fr*. In particular, some mayflies of the families Leptophlebiidae and Baetidae, and the water penny Psephenidae, were associated with

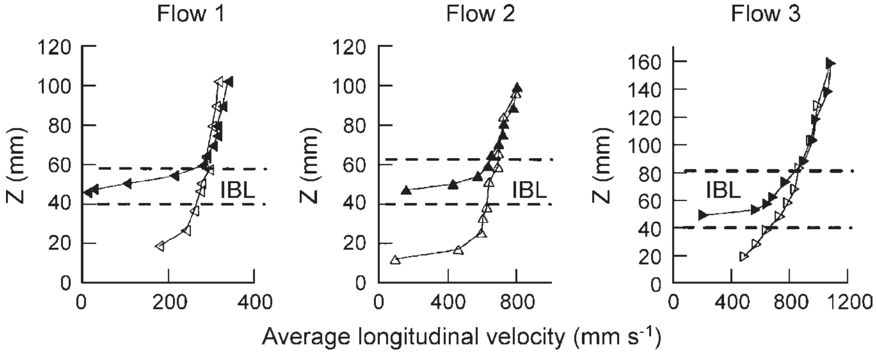

FIGURE 5.4 Average longitudinal velocity over cobbles with (open triangles) and without (closed triangles) the moss *Frissidens rigidulus* in a laboratory flume at three flow levels (1 is lowest, 3 is highest). The vertical axis is distance above the streambed. The existence of the internal boundary layer (IBL) and influence of the moss are clearly evident. (Reproduced from Nikora et al. 1998.)

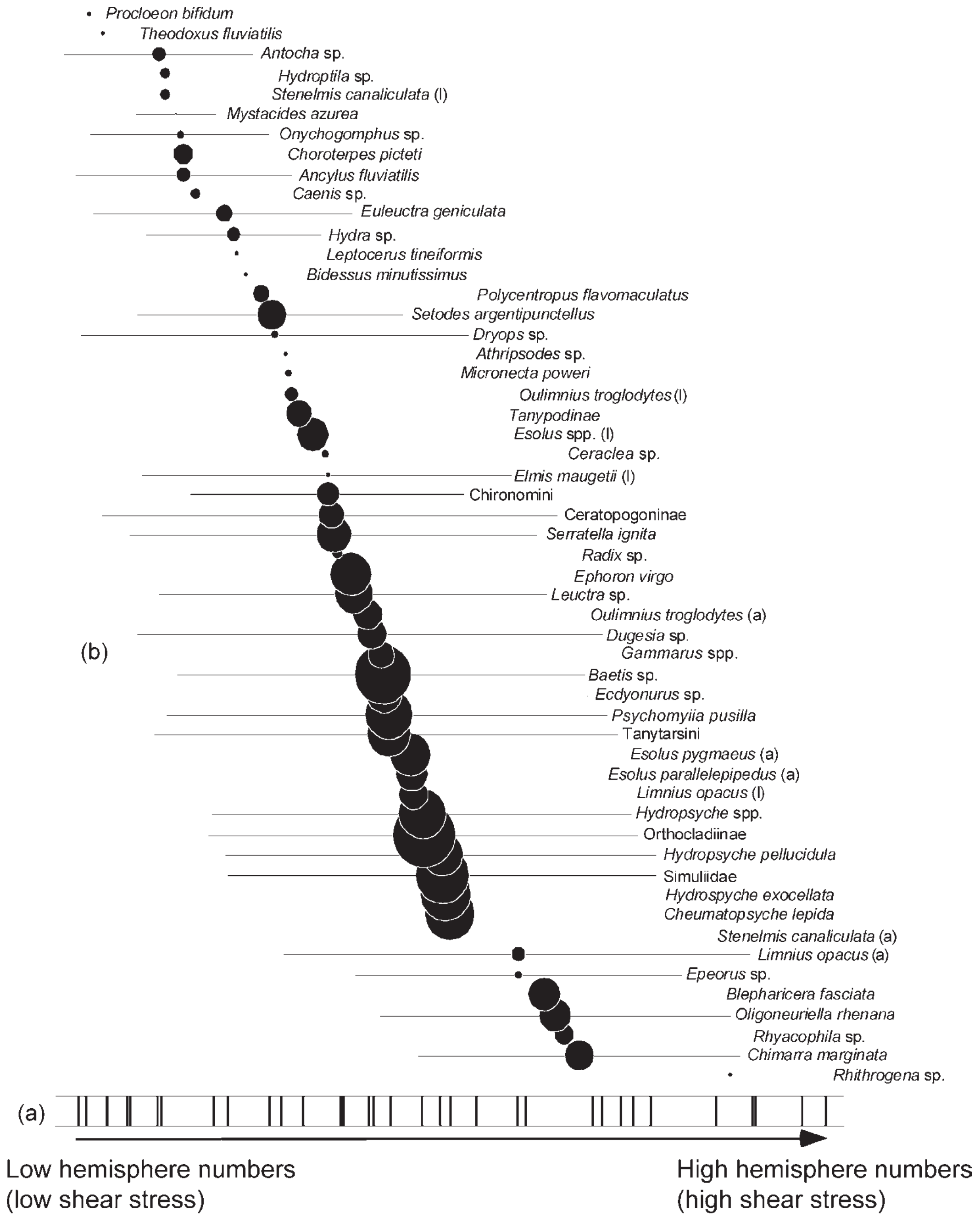

FIGURE 5.5 Ordination of the fauna collected from the Ardèche River, France, during spring sampling versus a hydraulic axis constructed from hydraulic parameters including shear stress estimated using the FST-hemisphere method, Froude number, and depth and substrate measures. The bottom axis (a) denotes the hydraulic axis. (b) Taxa are positioned according to their locations along the axis, and the area of each circle is proportional to taxon abundance. Horizontal lines represent the standard deviation of the hydraulic score. (Reproduced from Mérigoux and Dolédec 2004.)

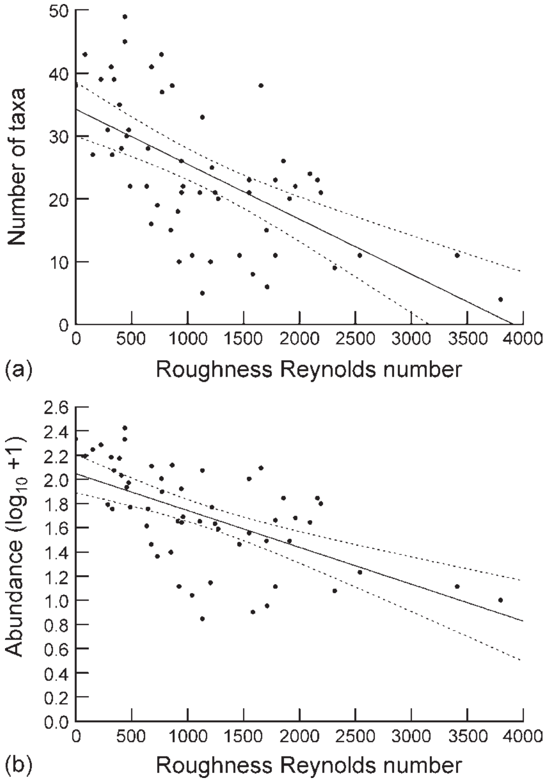

FIGURE 5.6 Relationship between roughness Reynolds number and (a) number of invertebrate taxa and (b) macroinvertebrate abundance in sampled areas of 0.07 m^2 within three riffles in the Kangaroo River, New South Wales, Australia. Dotted lines indicate 95% confidence intervals. (Reproduced from Brooks et al. 2005.)

low Re (Figure 5.6). Although each of these studies makes a strong argument for the utility of characterizing the flow microenvironment using both simple and complex hydraulic variables, at this time it is not obvious which variables might be more important, nor their mode of action.

A conceptual model (Biggs et al. 2005) outlines the mechanisms by which current and its associated forces will commonly have offsetting influences on the biota of running waters. Current exerts a drag force on individual organisms and, due to episodic fluctuations and substrate dislodgement, can be a powerful disturbance force as well. However, current benefits the biota through mass-transfer processes, transporting dissolved nutrients and gases to plants and food resources to animals. Biggs et al. (2005) further contend that large-scale temporal events predominantly affect lotic ecosystems through physical drag processes (drag-disturbance), whereas small-scale flow variations affect ecosystems through mass-transfer processes (including invertebrate and fish food-uptake). Drag-disturbance and mass-transfer related processes are viewed as the opposite ends of a continuum of the influence of flow variability, with moderate temporal-scale flow variability affecting ecosystems through both processes. Thus the location where organisms are found at steady state is a reflection of their ability to hold position and acquire resources, and, if a recent disturbance has been sufficiently extreme, their ability to survive and recolonize. Traits associated with avoiding or resisting the forces of flow, acquiring resources under particular flow conditions, and with movement and dispersal should therefore be expected to match certain taxa to particular flow environments.

The growth rates and distribution of periphyton illustrate the beneficial effects of small-scale fluctuations in flow (see also Section 6.1.1). Mixing of nutrients in the water column and reduction of the thickness of the viscous sublayer of the boundary layer surrounding microorganisms are expected to enhance rates of molecular diffusion across external membranes and thus the biological uptake of inorganic nutrients (Larned et al. 2004). Indeed, velocity variation over small spatial scales generates gradients in the biomass and growth form of periphyton patches, in which the biomass of dense, mucilaginous diatom mats increases with increasing near-bed velocities while the biomass of loosely aggregated filamentous green algal mats declines (Biggs and Hickey 1994, Biggs et al. 1998). In accord with the expectation that filter-feeding invertebrates will occupy regions of high near-bed current and collector-gatherers locations where particles are deposited, Mérigoux and Dolédec (2004) found that filter feeders displayed a positive relationship with shear stress and collector-gatherers a negative relationship. By holding low-velocity positions behind current obstructions, stream-dwelling salmonids optimize the tradeoff between the energy supply from drifting invertebrates and the energy cost of swimming (Fausch 1984). Position choice in drift-feeding Arctic grayling (*Thymallus arcticus*) was estimated well by a model in which net energy intake depended on capture rate, which was a function of visual reaction distance, depth, and velocity; and on swimming cost, which depended on velocity (Hughes and Dill 1990). Because a fish must intercept prey entering its field of view before the prey is swept downstream, velocity increases the encounter rate but decreases the proportion captured.

Microhabitat preferences can be strongly influenced by competitive dominance hierarchies and predation risk, especially in young individuals, and so habitat structure and overhead cover provide visual isolation from competitors and predators. Offered a choice among artificial structures placed in a natural stream, young steelhead trout (*Oncorhynchus mykiss*) were most influenced by overhead cover and favored a combination of cover, visual isolation, and velocity refuge, whereas young coho salmon (*O. kisutch*) showed strongest preference for velocity refuges and thus appeared to emphasize net energy gain (Fausch 1993).

Current acts as a negative environmental factor when floods cause dislodgment due to shear forces acting directly on the individual or indirectly through erosion of substrate particles, and when organisms must expend energy to maintain position. Organism distributions are influenced by disturbance events ranging from those of high frequency and low magnitude that result from turbulence and modest rainfall, to low frequency and high magnitude floods. The severity of the impact of any such event is further determined by the presence of flow refuges and the ability of organisms to seek out refuges and recolonize following disturbance. A survey of the snail *Potamopyrgus antipodarum* from 48 streams across New Zealand showed that local densities were inversely related to flood frequency, and populations were more abundant in low-gradient streams of foothill regions that tended to have fewer, less severe floods (Holomuzki and Biggs 1999). In flume studies, snails and the mayfly *Deleatidium* moved into low-velocity crevices on all substrates as current velocities increased, evidently because they were able to "feel" the increase in skin friction, and caddis larvae *Pycnocentrodes* unreeled their silken drag-lines to reach more sheltered locations (Holomuzki and Biggs 2000). There is much still to be learned about the possible ability of stream organisms to sense and respond behaviorally to changes in their flow environment, but some clearly do (Lytle and Poff 2004). Others, however, may simply accumulate and persist in areas that are sheltered most or all of the time. Because mussels occur within the surface substrate of the streambed and are long-lived, one might expect their distribution to be related to hydraulic variables. Strayer (1999b) indeed found that mussel beds occurred in flow-protected locations of two rivers in New York.

Locations that act as refuges from high-flow episodes can be identified at multiple scales, and their utility is a function of many factors. The size of the organism, its position within the water column or the streambed, how the hydraulic environment changes as flows increase to flood stage, and any behaviors such as seeking shelter or modifying body shape and position in response to increasing hydraulic forces will influence the effectiveness of flow refuges. At a large spatial scale, tributaries in a river network and side channels in a river may maintain favorable environmental conditions, such as alkaline tributaries that resist episodic pulses of acidification (Section 4.4.3) or locations in the streambed that are below the depth of substrate scour during a spate. At an intermediate scale, floodplains, stream margins, depositional areas, and debris dams may serve as refuges (Lancaster and Hildrew 1993, Palmer et al. 1995, Francouer et al. 1998). At the finest scale, heterogeneity of the substrate including crevices and surface roughness may provide refuge for small organisms (Dudley and D'Antonio 1991, Bergey 2005).

Although there is ample evidence that some areas experience comparatively less hydrologic disturbance and maintain greater invertebrate abundances following a spate, it can be difficult to establish that specific habitats truly act as refuges. Colonization of artificial refuges (wire cages) placed in streams in the United Kingdom found differential accumulation of organisms in cages with finer mesh (and therefore reduced flow) compared to coarser mesh cages, and this occurred differentially at high flow (Winterbottom et al. 1997). A similar study reported accumulations of certain taxa in cages protected by baffles versus exposed cages following high-flow events in an upland Scottish stream, whereas no differences were seen at low flows (Lancaster 2000). However, whether colonization is by active or passive means is not known. In a sand-bed river in Virginia, the hyporheic zone within the streambed failed to act as a refuge because floods scoured to bedrock, a depth of roughly 20 cm; however, invertebrates associated with woody debris dams were more resistant to displacement than those in the channel (Palmer et al. 1996).

A true refuge effect requires that organisms are able to move actively or passively among habitat patches in response to a disturbance, have a greater likelihood of persistence due to reduced exposure to extreme currents and hydraulic forces, and have sufficient numbers and mobility to subsequently recolonize highly disturbed habitats (Lancaster and Belyea 1997). The flume studies of Holomuzki and Biggs (2000) provide evidence of such movements in response to increasing flows, and Lancaster (1999) reported that the dytiscid beetle *Oreodytes sanmarkii* and the mayfly *Ephemerella ignita* accumulated in low flow areas of a laboratory flume by combination of crawling and drifting behaviors in response to a simulated spate. Invertebrates declined on unstable stones but exhibited no change on stable stones in a gravel-bed stream of the South Island of New Zealand, suggesting that organisms on unstable stones detected vibrations that stimulated their departure (Matthaei et al. 2000).

In comparison with invertebrates, stream fishes can more readily shift location in response to high-flow events and seek flow refuges associated with physical habitat complexity. Side-channels, wood, and large roughness elements may be especially important in high-gradient streams, and access to floodplains may be important in low-gradient streams. Schwartz and Herricks (2005) used prepositioned electrofishing devices to show that the fish assemblage of small, low-gradient Illinois streams occupied different habitats depending on flood stage. At near-bankfull flows fish were associated with vegetated point bars and concave-bank benches, at half-bankfull conditions fish abundance and biomass were greatest in low-velocity eddies, and at base flow the main channel habitat of pools, riffles, and glides contained higher numbers and greater biomass than did lateral habitat units.

The size and longitudinal spacing of roughness elements along the streambed influences the complexity of flow in the near-bed environment, as shown hypothetically in Figure 5.7. When channel depth is shallow relative to substrate roughness, such as in riffles and broken water, flow will be very complex. At depths greater than three times the height of roughness elements, Davis and Barmuta (1989) recognize three additional categories based on longitudinal spacing. When substrate elements are separated by sufficient distance, the wake behind each element dissipates before the next element is encountered. This is called isolated roughness flow.

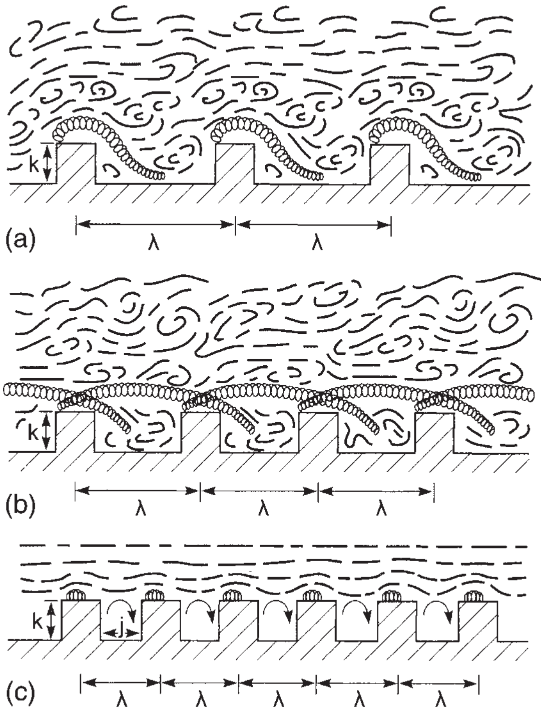

FIGURE 5.7 Conceptualization of three types of flow occurring over a rough surface, depending upon differences in relative roughness and longitudinal spacing between roughness elements. (a) Isolated roughness flow, (b) wake interference flow, (c) quasi-smooth flow. (Reproduced from Davis and Barmuta 1989, after Chow 1981.)

When spacing between roughness elements is less, their wakes interfere with one another, producing high local velocities and turbulence, termed wake interference flow. Lastly, skimming flow describes the circumstance when roughness elements are very closely spaced, which allows flow to skim across the tops of elements and produces a relatively smooth flow environment and slow eddies in the intervening spaces.

Bed surface roughness is not only due to stones of various sizes, but also wood and vegetation. Flow measured in and around a common lotic macrophyte, *Ranunculus penicillatus*, showed that velocities dropped to a low and constant value within 5 cm into the plant bed, forcing most of the flow over and around it. A dead-water zone formed immediately downstream, and then a region of high turbulence (Green 2005). Quinn et al. (1996) added artificial roughness elements (half-pipes of various diameters attached to a plywood base) to a section of a New Zealand gravel-bed river of uniform current and depth. Near-bed velocities declined and turbulence increased with increasing roughness, as expected. All invertebrates and especially filter feeders declined with increasing upstream roughness, whereas the periphyton apparently was affected by both microhabitat conditions and the differential response of grazers. Velocities at the front and in the wake of selected boulders in a western Australian stream, measured with a field-portable ADV, were greatly reduced at 5 mm and 2.5 cm above the bed relative to velocities at channel mid-depth (Bouckaert and Davis 1998). Turbulence and shear stress were greater in the wake than the front area, although not significantly so due to high variability, and both total abundance and species richness were greater in the wake locations (Figure 5.8), suggesting that turbulence resulted in more favorable conditions.

Although a great deal of effort has gone into the characterization of near-bed flow environments, progress has been modest. In a review of studies attempting to relate organism distributions to hydraulic variables, Jowett (2003) concluded that complex hydraulic variables had not yet been shown to be superior to simple measures of velocity, depth, and substrate roughness. Although the many studies reviewed above establish convincingly that organism abundances and ecosystem processes vary with the flow environment, the mechanism of action often is uncertain. Even in the most carefully controlled experimental studies it is difficult to ascertain whether organisms are responding to mean velocity or to the intensity of turbulence, meaning the variance and extremes of velocity. To identify the flow conditions likely to cause an organism to be eroded is difficult because

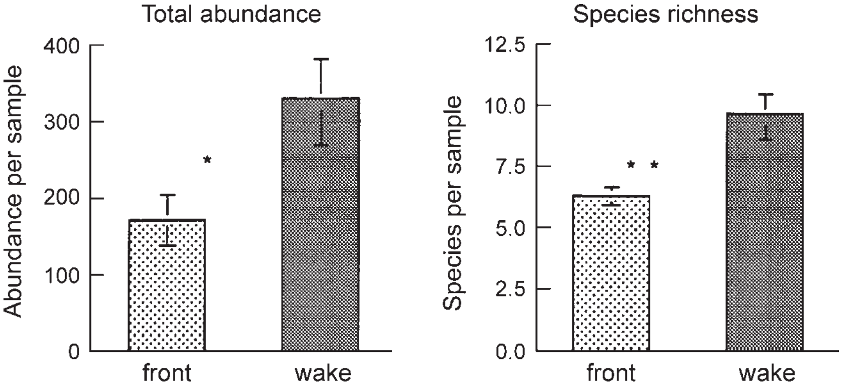

FIGURE 5.8 Mean invertebrate abundance and species richness (±1SE, n = 10) in front (dotted bars) and wake (shaded bars) of boulders in a western Australian stream. * = significant at 0.05, ** = significant at 0.01. (Reproduced from Bouckaert and Davis 1998.)

dislodgement may result from infrequent, high-velocity turbulence rather than average flow fields, and organisms may modify their posture and location as forces change. Nonetheless, it is apparent that current, interacting with substrate, profoundly influences life in running waters, and we turn next to an examination of these issues from the perspective of substrate.

5.2 Substrate

Substrate is a complex variable of the physical environment. Often we think of substrate in terms of the material of the streambed, including the cobbles and boulders of a mountain stream, and the mud and sands that are more typical of lowland rivers. Current, together with available parent material, determines mineral substrate composition (Chapter 3). There are, additionally, many kinds of organic substrates in running waters, from minute organic fragments up to fallen trees in size, along with rooted plants, filamentous algae, even other animals. In essence, the substrate includes everything on the bottom or sides of streams or projecting out into the stream, not excluding a variety of human artifacts and debris, on which organisms reside (Minshall, 1984). There are instances where substrate is relatively uniform, as in sandy bottoms of low-gradient rivers, but usually it is very heterogeneous.

For benthic organisms dwelling on the surfaces and within the crevices and interstices of the streambed, substrate provides the platform and living space where they attach, forage, and complete most or all of their life cycles, as well as find refuge from current and enemies. Periphyton and biofilms usually are more productive on stable substrates (Section 6.1.1) and invertebrates achieve greater biomass and diversity on some substrates compared to others. Substrate is a critical component of fish habitat for foraging, sheltering from current, and spawning. However, it often is difficult to identify just how substrate affects organisms because it interacts with so many other variables, especially current. In Figure 5.1, for example, the habitat preferences of several benthic invertebrates are shown as a function of current velocity, but substrate preferences also are evident, and in some instances appear to vary with current.

The size of inorganic particles is easily measured and can be summarized with a single term such as median size, but one cannot easily average observations of, for example, moss, rocks, and submerged wood. As a consequence, substrate typically is described by the relative amount of various categories. Even when quantification seems straightforward, such as estimating median particle size or the volume of wood per linear stream distance, there may be uncertainty concerning what feature of the substrate is important to the biota. Is it the size of a stone that matters, its surface area and texture, or the interstitial spaces and how tightly stones are packed together? Quantification of substrate is further complicated by its spatial heterogeneity, both vertically and horizontally within the streambed, and because substrate can change over time in response to fluctuations in flow.

5.2.1 Inorganic substrates

Many of the important features of inorganic substrate were described previously from the perspective of fluvial geomorphology (Section 3.3.1), where the emphasis was on the interaction of sediment supply and flow on particle transport and channel form. Relevant tools and concepts include the size categories of inorganic particles (Table 3.1) and their quantification using pebble counts to determine the median (D_{50}) and range (D_{16} and D_{84}); the relationship between particle size eroded and current velocity (Figure 3.8); and the development of channel features including riffles, pools, point bars, and undercut banks, which strictly speaking are not substrate types but mesoscale physical features often referred to as habitat units. Surface substrate usually is coarser than subsurface substrate and at least partially protects this finer material from transport, resulting in vertical heterogeneity. The stability of the substrate depends on the magnitude and frequency of hydrological events and particle size.

Although ecologists borrow freely from the geomorphologist's tool kit, the ecologist's focus is on characteristics of mineral substrates that may influence their suitability as biological habitat. A greater range of particle sizes, and thus substrate heterogeneity, benefits many taxa (Minshall 1984), and the permeability of the subsurface region (known as the hyporheos) adds a vertical dimension to available habitat by allowing water to circulate and transport gases, nutrients, and fine organic material. Texture and the availability of crevices also can influence a particle's suitability as habitat. Low levels of siltation may be beneficial, particularly for species adapted to consuming silt for its organic content, but high silt levels usually have a negative influence on habitat for surface-dwelling organisms by reducing habitat heterogeneity, filling interstitial spaces, and coating consumers and their food resources. In the upper River Rhône, for example, the amount of interstitial space (defined by porosity) in the subsurface zone was negatively related to percentage of fine sediment (Gayraud and Philippe 2001). Invertebrate density was significantly and positively related to the amount of interstitial space, particularly for taxa of intermediate body size (5–10 mm), intermediate body flexibility, and flattened or streamlined shape.

Streambeds of gravel, cobble, and boulders occur in a great many areas around the world, harboring a diverse fauna of lithophilous taxa that Hynes (1970) remarks is broadly similar almost everywhere. Many species are equally common on stones of all sizes, but others are demonstrably more likely to be found associated with a particular size class (Cummins and Lauff 1969). Sand generally is considered to be a poor substrate, especially for macroinvertebrates, due to its instability and because tight packing of sand grains reduces the trapping of detritus and can limit the availability of oxygen. Nevertheless, a variety of taxa, termed psammophilous, are specialists of this habitat. The meiofauna, defined as invertebrates passing a 0.5 mm sieve, can be very abundant, dwelling interstitially to considerable depth. In Goose Creek, a sandy-bottom stream in Virginia, Palmer (1990) reported meiofaunal densities (rotifers, oligochaetes, early instar chironomids, nematodes, and copepods) that averaged $> 2000/10\,\text{cm}^2$

and at times reached nearly 6000/10 cm^2. The psammophilous fauna includes some macroinvertebrates as well, and can exhibit distinctive adaptations, often associated with respiration. The dragonfly nymph *Lestinogomphus africanus*, found burrowing deep in sandy-bottom pools in India, has elongated respiratory siphons that reach above the sand surface (Hora 1928). Several mayflies, including *Dolania* in the southeastern United States, have dense hairs that apparently serve to keep their bodies free of sand (Hynes 1970). Burrowing taxa can be quite specific in the particle size of substrate they inhabit. The mayflies *Ephemera danica* and *E. simulans* burrow effectively in gravel. *Hexagenia limbata* cannot, but does well in fine sediments. Substrates composed of finer sediments generally are low in oxygen, and *H. limbata* meets this challenge by beating its gills to create a current through its U-shaped burrows (Eriksen 1964).

5.2.2 Organic substrates

Organic substrates including algae, moss, macrophytes, dead leaves, and wood vary greatly in size, the conditions where they occur (depth, current, stream size) and in their temporal persistence. Small organic particles <1 mm usually serve as food rather than as substrate, except perhaps for the smallest invertebrates and microorganisms. Macroinvertebrates generally are more abundant where greater amounts of fine organic matter occur on the surfaces of mineral substrates, within their interstices, and in depositional zones behind obstructions. Autumn-shed leaves and the fungi and bacteria they support are a major energy source, especially in woodland streams (Chapter 7), and often are most abundant in depositional zones where fine particles are trapped as well. Thus aggregations of leaves on the streambed provide both food and habitat and typically support a high abundance and diversity of invertebrates (Mackay and Kalff 1969). On the other hand, higher plants and submerged wood are consumed by only a few specialists, and support high animal abundances because these large organic substrates serve as perches from which to capture food items transported in the water column, as sites where fine detrital material accumulates, and as surfaces for algal and biofilm growth. The presence of wood in streams also adds substantially to mesoscale habitat complexity, acting both as a geomorphic agent influencing channel shape and pool formation (Chapter 3), and directly as habitat.

The invertebrate taxa that live in association with aquatic plants are referred to as phytophilous. A number of species are found primarily on moss, including the free-living caddis larva *Rhyacophila verrula* and a number of mayflies with backward-directed dorsal spines that are thought to minimize entanglement (Hynes 1970). Most commonly, mosses and filamentous algae provide habitat, serving as a refuge and a trap for silt and organic matter, rather than a direct food source (e.g., Steinman and Boston 1993, Downes et al. 1998). Submerged macrophytes add to the physical complexity of the environment, creating habitat that algae and invertebrates may colonize (Tokeshi and Pinder 1985) and providing refuge for fishes from high flows and predators (Grenouillet et al. 2000, Harrison et al. 2005). These effects can operate at very fine scales associated with leaf surfaces and plant architecture up to the coarser scale of a macrophyte patch. Using both natural and artificial macrophytes, Taniguchi et al. (2003) showed that greater architectural complexity of habitat led to a higher number of macroinvertebrate taxa. The mechanisms may include greater living space, detritus trapping, and altered microhabitat conditions.

Xylophilous or wood-dwelling taxa attest that wood constitutes yet another substrate category of lotic environments. In the headwater streams of forested areas, as much as one quarter to one half of the streambed can be wood and wood-created habitat (Anderson and Sedell 1979).

Dudley and Anderson (1982) considered 52 taxa in the northwestern United States to be closely associated with wood, and another 129 to be facultatively associated. Even in agricultural streams in the midwestern United States where wood was not abundant, the majority of the recorded taxa (~90%) used wood as habitat, and the presence of wood substantially increased the number of taxa at a site (Johnson et al. 2003). Wood appears to be substrate more often than it is food, although some taxa, such as the beetle *Lara avara*, feed mainly on wood. However, this beetle has the slowest growth rate and longest life cycle of all stream insects (Huryn and Wallace 2000). Many wood-associated taxa obtain their nourishment from biofilms occurring on wood surfaces (Hax and Golliday 1993).

In lowland rivers where the substrate is largely sand, fallen trees (snags) are especially important as a substrate. In the Satilla River, Georgia, Benke et al. (1985) estimated that snag, mud, and sand substrates occurred in the ratio 1:1.4:14 at an upriver site, and 1:3.6:18 at a downriver site. However, snags supported more taxa and a far higher biomass of invertebrates than did mud, where values were higher than in sand (Table 5.2). Interestingly, total numbers per unit area did not differ markedly between snags and sand. However, the invertebrates in the sand substrate were mostly oligochaetes and psammophilous midges of very small size, and so their biomass was modest. Integrating among all habitats in the river channel, snag surfaces accounted for over half of the invertebrate biomass. Because sand made up 70–80% of the substrate, it was responsible for most of the remaining biomass despite a low biomass per unit area.

A number of species of fishes and other vertebrates of rivers tend to occur on or near particular substrates, and some fishes are quite specialized in their affinities. For example, the mud darter *Etheostoma asprigene* is restricted primarily to the backwaters of larger tributaries of the Mississippi River, the southern sand darter *Ammocrypta meridiana* to clean, sandy substrates of the Mobile River basin, and the Blenny darter *E. blennius* to the gravel and rubble bottom of fast riffles in Tennessee River tributaries (Lee et al. 1980). Bottom substrate is important to many freshwater fishes when spawning because eggs require an adequate supply of oxygen and protection from predators, for which gravel is well suited. The majority of freshwater fish select stony substrates for reproduction, from individual large stones to some mix of gravel (Balon 1981). An advantage of coarse mineral substrates is that they can be sculpted into nests where eggs and sperm can mix without being swept away by the current. In addition, because water flows into the interstices of coarse substrates, ample oxygen is transported to buried eggs. Mineral substrates also allow behavioral elaboration. A number of species move rocks or pebbles with their mouths: the North American chub *Nocomis* erect structures as much as 30 cm in height and 1 m in diameter to attract mates. In addition to lithophilous fishes, a number of freshwater species are psammophilous or phytophilous. A few species such as the log perch *Percina caprodes* spawn in sand, depositing sticky eggs that become camouflaged with a sandy coating. Among the species-diverse darters, examples also exist of species that spawn on such specialized surfaces as rotting vegetation (*E. exile*), the macroalga *Cladophora* (*E. blennioides*), and other rooted plants (*E. lepidum*, *E. punctulatum*) (Hynes 1970).

Aquatic insects also select particular substrates for oviposition. Egg masses of the mayfly *Baetis* were highly aggregated under protruding stones with specific characteristics associated with lower probabilities of desiccation in a Rocky Mountain stream (Encalada and Peckarsky 2006). Similarly, hydrobiosid caddis flies were observed to lay their eggs in single masses beneath emergent rocks in an upland Australian stream, and "landing pad size" was thought to influence oviposition choice (Reich and Downes 2003).

TABLE 5.2 The number of taxa and standing crop biomass of invertebrates found in snag, sand and mud habitats in the Satilla River, Georgia. Wood was a small percentage of habitat but contributed over half of the total biomass to the river reach. (From Benke et al. 1985.)

	Wood substrates			*Sand*			*Mud*		
		Biomass (mg m^{-2})			*Biomass (mg m^{-2})*			*Biomass (mg m^{-2})*	
	No. of genera	*Lower site*	*Upper site*	*No. of genera*	*Lower site*	*Upper site*	*No. of genera*	*Lower site*	*Upper site*
Diptera	17	243	696	15	64	124	11	148	309
Trichoptera	9	4222	1581	0	–	–	3	24	30
Ephemeroptera	5	97	56	0	–	–	0	–	–
Plecoptera	2	137	109	0	–	–	0	–	–
Coleoptera	3	218	117	1	8	11	0	–	–
Megaloptera	1	379	259	0	–	–	0	–	–
Odonata	3	529	578	1	–	–	0	–	–
Oligochaeta	0	–	–	3	22	22	0	420	290
Total	40	5825	3396	20	94	157	17	592	629

5.2.3 The influence of substrate on stream assemblages

Because the flora and fauna of fluvial ecosystems are so intimately associated with the substrate, a great deal of research has been directed toward unraveling how substrate acting as habitat influences biological assemblages. In gravel-bed rivers, a diverse macroinvertebrate fauna exhibits a patchy spatial distribution that surely is determined at least in part by the heterogeneity of the substrate. In fact, abundance and taxa richness typically are low in fine substrates and increase with substrate size at least up to gravel and cobble (Minshall 1984, Mackay 1992). The density and richness of invertebrates have been shown to correlate with amount of detritus, algal biomass, substrate stability and complexity, depth, and velocity (Rabeni and Minshall 1977, Barmuta 1989, Quinn and Hickey 1994); and strength of correlation has been found to depend upon spatial scale at which substrate-related variables are measured (Downes et al. 1995, Beisel et al. 2000). Substrate size tends to decline downstream, for reasons discussed in Chapter 3, but tributaries can interrupt the longitudinal fining of substrate with inputs of coarse material. In gravel-bed rivers of western Canada, Rice et al. (2001) found an increased abundance of taxa that prefer coarse substrate at these points of sediment recruitment, as well as an overall increase in diversity.

A series of studies of substrate-induced habitat complexity conducted in Steavenson River, a stony upland stream in southeastern Australia, found that stone surface area accounted for some 70–80% of variation in species richness, small stones had fewer species because they had less surface roughness, and the filamentous red alga *Audouinella hermannii* enhanced roughness and the presence of macroinvertebrates (Douglas and Lake 1994, Downes et al. 1995). Using clay bricks as experimental substrate, Downes et al. (1998) manipulated three aspects of habitat structure: large surface pits and cracks, surface texture (small pits), and abundance of macroalgae. Sampled after 14 and 28 days of macroinvertebrate colonization, the majority of common species reached higher abundances on rough substrates, there was a disproportionate accumulation of small individuals, and each of the three manipulated elements of habitat structure had separate, additive effects on taxa richness (Figure 5.9). By employing a statistical procedure known as rarefaction to compare number of species (S) standardized for overall abundance (n), Downes et al. concluded that S increased disproportionately to n, indicating that species richness was augmented by habitat complexity. Although this study provided strong evidence for the importance of substrate roughness, the mechanisms by which crevices and surface roughness affected the biota were unclear. In particular, because *A. hermannii* responded strongly to surface texture, it was not possible to separate the effects on the fauna of increased algal cover alone from that of increased algae in combination with a rough surface.

Crevices and surface roughness evidently protect both microorganisms and invertebrates from disturbance associated with high flows, sediment scour, and tumbling of substrates. Using a range of substrates from beer bottles to smooth and rough stone types, Bergey (2005) showed that algal biomass remaining after an artificial disturbance (scrubbing with a toothbrush) was enhanced by crevice quantity and surface roughness. On rough stones, some 60–80% of the algae remained, indicating the effects of increased surface area and greater protection. In laboratory flumes, nymphs of *Baetis rhodani* were able to maintain position in fast velocities that are typical of their preferred microhabitat only on the roughest substrates (Lancaster and Mole 1999). The presence of certain organisms may add a biological dimension to substrate texture and stability. Cardinale et al. (2002a) showed that the presence of net-spinning caddis larvae of the family Hydropsychidae increased the velocity at which particle movement was initiated in a laboratory flume, presumably due to their silk secretions, and stabilized smaller particles to a greater extent than larger particles. Thus the abundance of caddis larvae may influence the ability of other taxa to retain position when current increases.

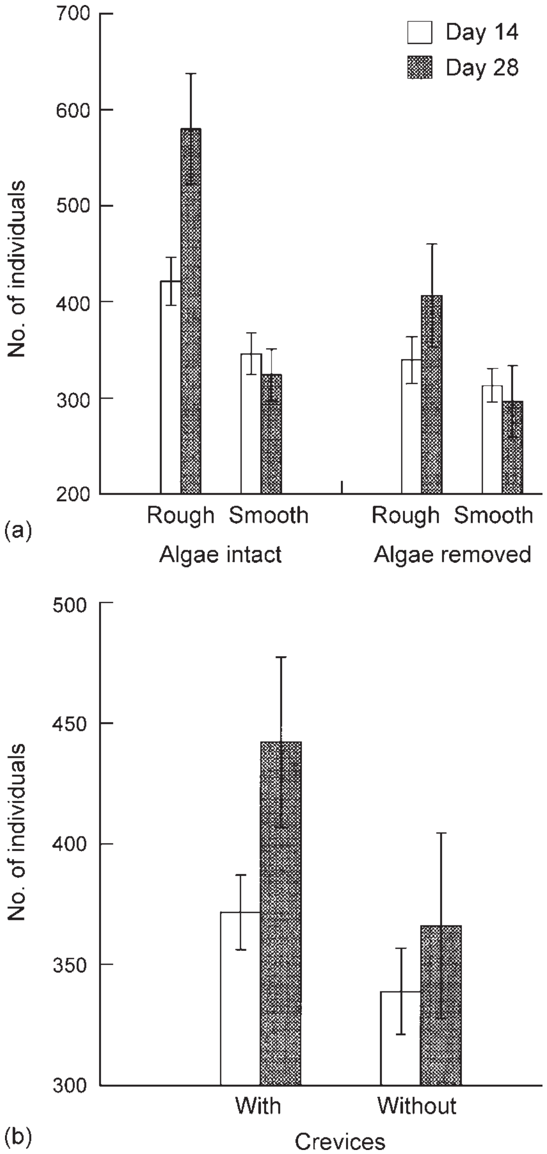

FIGURE 5.9 Mean number of species (±1 SE) colonizing rough and smooth stones from which microalgae were either (a) removed or left intact and (b) with or without crevices. Values are adjusted for area of stone. (Reproduced from Downes et al. 1998.)

Streambed regions of saltating bed load likely provide unstable habitat and fewer food resources for benthic invertebrates, and thus may explain why invertebrate abundance generally increases with increasing substrate size, because larger stones are more stable than smaller ones (Death 2000). By monitoring individual marked stones that experienced high flows in a gravel-bed stream on the South Island of New Zealand, Matthaei et al. (2000) observed strong invertebrate declines on unstable stones but no change on stable stones. This finding raises the possibility that the influence of various measures of current and hydraulic forces on organisms discussed earlier in this chapter may be useful because they are predictors of bed stability, rather than as measurements of forces acting directly on individuals.

To conclude this topic it is apparent that the interaction between current and substrate provides considerable insight into the local-scale distribution and abundance of the stream biota. They remain inextricably interwoven, however, and this is unsurprising when one considers that the flow variables used by stream ecologists have their origins in the efforts of fluvial geomorphologists to understand particle transport, and bed instability is a key element of habitat unsuitability.

5.3 Temperature

Temperature is a critical environmental variable determining the metabolic rates of organisms, their distribution along a river's length and over geographic regions, and quite possibly their success in interacting with other species. Because species composition and biological rates are temperature dependent, ecosystem processes including leaf breakdown, nutrient uptake, and biological production are affected as well. Stream temperature changes in response to a variety of human actions, and so management intervention may be required to maintain a natural range of stream temperatures.

The temperature of running waters usually varies on seasonal and daily time scales and among locations due to climate, extent of streamside vegetation, and the relative importance of groundwater inputs. Stream temperatures can be quite constant wherever groundwater inputs are important, as in springs and some headwater streams. Even medium-sized rivers that are fed by large groundwater aquifers, such as the Metolius in Oregon and the Manistee in Michigan, will show significantly less seasonal warming and cooling than rivers in the same climate that are fed by shallow subsurface flowpaths. Very constant river temperatures are also found in tropical locations owing to the constancy of solar radiation throughout the year and, in the case of large rivers, their thermal inertia. The Amazon River at Manaus, Brazil, at $29 \pm 1^\circ$C, is one of most thermally stable water masses in the world (Sioli 1984). In most temperate rivers, the annual temperature range is between 0°C and 25°C, but desert streams can reach nearly 40°C, which is near the thermal tolerance even of fishes adapted to these extreme environments (Matthews and Zimmerman 1990). At high latitudes and elevations, maximum temperatures rarely exceed 15°C, and they can be cooler yet in very cold climates where ice-cover can extend for over half the year.

Seasonal changes in water temperature in rivers closely follow seasonal trends in mean monthly air temperature, except that in winter the water temperature does not fall below 0°C, and rivers warm more slowly in spring than does the atmosphere. For temperatures above freezing, Crisp and Howson (1982) found that mean weekly water temperatures (and the growth rate of brown trout) could be predicted from air temperatures using a 5- to 7-day lag. Some 60% of their estimates were within $\pm 1^\circ$C, and 80% within $\pm 1.5^\circ$C, of the measured stream temperatures. Despite the frequent use of correlations between air and water temperatures, however, solar radiation, not convective warming of water by the air, is the main heat input to streams, and so air temperature is better viewed as a surrogate rather than a causal variable (Johnson 2003).

Because temperature varies through the seasons as well as with location, the number of degree-days, calculated by summing daily mean temperatures above 0°C, provides a useful measure of the cumulative temperature that an organism experiences. This approach shows that even when sites experience similar maximum summer temperatures, degree-days can be very different. For example, three sites in a Rocky Mountain stream all experienced similar maximum summer temperatures near 16°C, but the annual degree-days were estimated to be 800 at 3,350 m, 1,000 at 3,050 m, and 1,500 at 2,740 m (Allan 1985). As Figure 5.10 illustrates, the same number of degree-days can result from very different seasonal temperature patterns (Vannote and Sweeney 1980). Six locations along a stream in Pennsylvania each accumulated about 4,200 degree-days annually, but temperature variation throughout the year was much more pronounced at downstream sites. Organisms living in the headwaters would experience cool, constant temperatures year-round, and presumably be physiologically adapted to such conditions, whereas the relatively short but very warm summer season at downstream locations would favor those organisms best adapted to grow quickly at higher temperatures. As can be seen in Figure 5.11, annual degree-days decrease with increasing latitude. Values in the range of 3,000–5,000 degree-days are typical of temperate, low elevation sites. At subtropical Silver Springs, Florida, annual degree-days were in excess of 8,000 (Odum 1956), which is an order of magnitude greater than at the highest elevation Rocky Mountain stream studied by Allan.

Large-scale temperature variation associated with upstream–downstream position, elevation,

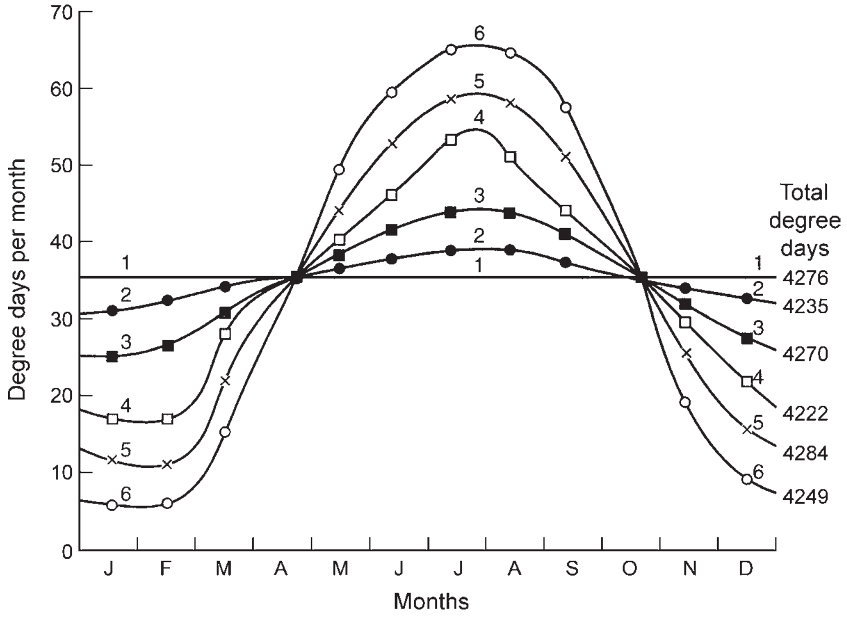

FIGURE 5.10 Degree-day accumulations and annual totals at six sites along White Clay Creek, Pennsylvania: (1) groundwater, (2) spring seeps, (3) first-order spring–brooks, (4) second-order streams, (5) upstream segment of third-order stream, (6) downstream segment of third-order stream. (Reproduced from Vannote and Sweeney 1980.)

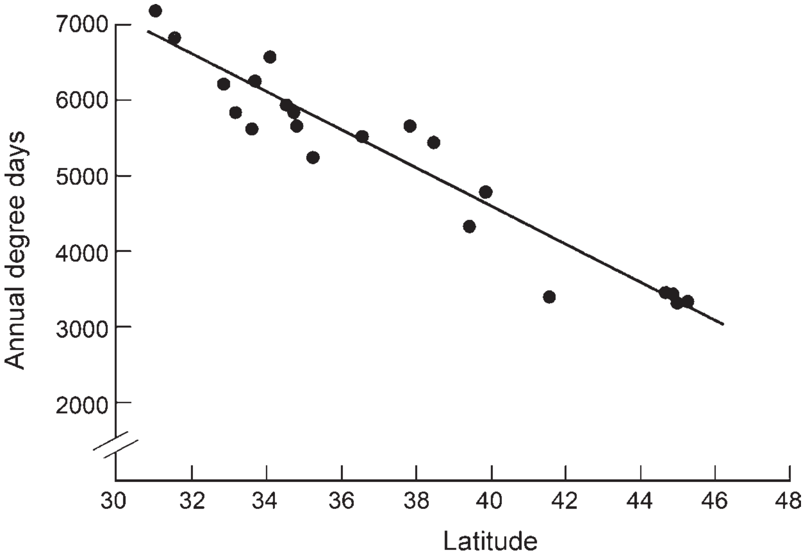

FIGURE 5.11 Total annual degree-day accumulation (>0°C) as a function of latitude for various rivers of the eastern United States. (Reproduced from Vannote and Sweeney 1980.)

and latitude is influenced primarily by solar radiation. Considerable thermal heterogeneity also occurs at meso- and microhabitat scales in response to local air temperature and wind speed, which influence evaporative cooling; temperature of the source water, which is strongly dependent on the relative amounts of groundwater versus surface runoff; and the extent of topographic and riparian shade (Poole and Berman 2001). Lakes, impoundments, beaver ponds, and even the frequency of pools along the channel tend to increase stream temperatures because they increase the residence time of water and the surface area exposed to solar radiation, and thus allow for more warming (McRae and Edwards 1994, Hawkins et al. 1997).

In geologically complex regions, the source water of the tributaries of a single river system can be very different, resulting in a wide range of thermal habitats among headwaters that in turn may favor greater biodiversity as well as provide unique thermal niches for endemic taxa (Milner et al. 2001). In alpine streams of the French Pyrenees where source waters include glaciers, snowpack, karst groundwater, and hillslope aquifers, karstic groundwater streams are coolest and most stable, hillslope groundwater streams are warmest and most variable, and glacial streams warm and become more variable downstream (Brown et al. 2005). Temperature variation due to source water and flow paths can be observed at much finer scales as well. In floodplain sections of the Tagliamento, a large, braided river of the Swiss Alps, cool-water habitats governed by groundwater inputs differ by as much as 15°C from warm-water habitats of semi-isolated backwaters (Arscott et al. 2001). Microhabitat-scale temperature variation is also observed when streamwater is forced into or drawn out from the streambed due to topographic undulations, meanders, bars, or other channel obstructions (White et al. 1987).

The temperature of large rivers is unlikely to be affected much by shading, as their size conveys considerable thermal inertia and virtually ensures that they are highly exposed to the sun. In small streams, however, riparian forest moderates stream temperature by reducing the amount of solar radiation reaching the water surface, which also reduces the extent of temperature change between day and night (Beschta et al. 1986). An extensive literature documents the influence of the presence or absence of shade on water temperature, particularly in the context of logging practices and the impact of stream warming on salmonid fishes. Forest harvest usually results in substantial warming of stream temperatures, by as much as 13°C, and daily ranges have increased by as much as 7–8°C (Moore et al. 2005). Riparian buffers can substantially ameliorate these effects, supporting the management recommendation that a riparian width equal to one tree height be retained. As vegetation and shade recover in logged riparian zones, temperatures return to their prior state, often within 5–10 years.

Small streams that flow through alternating pasture and woodland provide further evidence of shade effects, showing temperature differences of several degrees (Sweeney 1993). The influence of riparian shade diminishes with increasing stream channel width due to the natural gap in forest canopy in wider streams, and so riparian thinning may be of minor importance at stream widths >10 m (Davies-Colley and Quinn 1998). This influence of stream size on direct warming due to solar radiation is evident in the relationship between maximum daily temperature range and stream order (Figure 5.12). Small headwater streams are thermally stable due to groundwater influence and the additional effects of riparian and topographic shading, whereas large rivers are thermally stable due to their large water mass. Streams of intermediate size are large enough to be minimally influenced by riparian shade and of small enough volume to warm and cool between day and night.

Human actions influence stream temperatures in a number of ways. By reducing river volume, water withdrawals reduce the temperature buffering capacity of the river; furthermore, reduced flows may result in longer residence times and thus greater heat absorption. In urban areas with substantial areas of impervious surface, water passing over roads and other built structure can be heated well above the natural range (Paul and Meyer 2001). Models developed specifically for streams subject to urbanization indicate that shade, groundwater inputs, and stream width have the greatest influence over stream temperature, thus suggesting management options likely to be most effective in ameliorating human impacts (LeBlanc et al. 1997).

The impoundments created by dams can greatly affect stream temperatures, and although dams create other problems as well (Section 13.2.1.1), their temperature effects can be significant. The majority of impoundments are the result of small, surface-release dams, and they are most likely to raise downstream temperatures during summer. These impoundments act like small lakes and beaver ponds that tend to increase stream temperatures because they

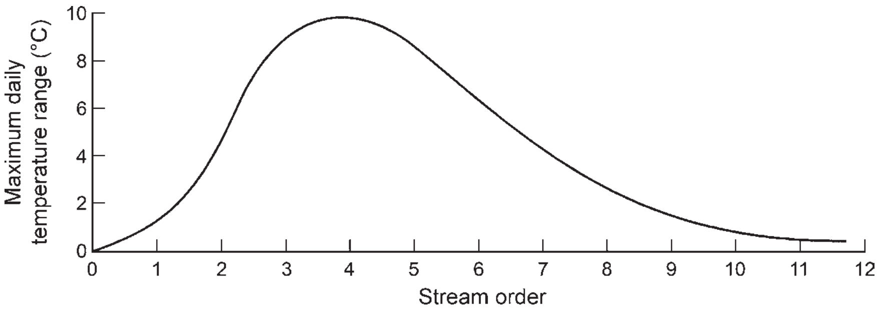

FIGURE 5.12 Maximum daily temperature ranges in relation to stream order in temperate streams. (Reproduced from Vannote and Sweeney 1980.)

increase the residence time of water and the surface area exposed to solar radiation (McRae and Edwards 1994). A study of small dams on rivers in Michigan found a modest warming (up to 5°C) during summer to be common. Cold-water fish species generally were less abundant below than above dams, but overall fish diversity increased below dams due to the influx of warm-water species (Lessard and Hayes 2003). Large, deep impoundments that release water from the bottom of the dam have a very different effect. Because the hypolimnion of reservoirs is relatively cool throughout the year, deep-release dams result in downstream temperatures that are cooler in summer and warmer in winter than the norm (Stanford and Ward 1979). Temperatures in the lower Colorado River below Glen Canyon Dam are 9–12°C year-round, compared to the historic temperature range of 2–26°C (Petersen and Paukert 2005). Restoration of warmer summer temperatures via surface releases would likely result in higher growth rates of the federally endangered humpbacked chub *Gila cypha* and reduce the “window of vulnerability” of young chub to predators. By reengineering the dam release, so that water can be drawn from warmer or cooler depths, it may be possible to manage the temperature of released water to recreate pre-dam conditions (Figure 5.13).

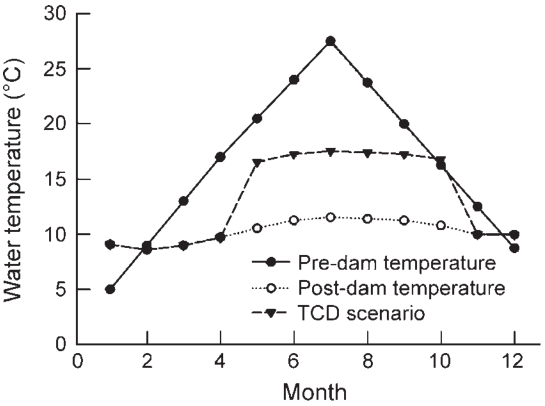

FIGURE 5.13 Average monthly water temperatures in the Grand Canyon of the lower Colorado River before and after the construction of Glen Canyon Dam, and for a potential temperature management scenario using a temperature control device (TCD). Temperature data are from the US Geological Survey at river mile 61 near the confluence with the Little Colorado River. (Reproduced from Petersen and Paukert 2005.)

Future climate change presents additional scenarios for altered streamwater temperatures (see also Section 13.2.5). Using present-day latitudinal distributions as a guide, a warming of 4°C is predicted to result in approximately a 600 km poleward shift in the distribution of macroinvertebrates (Sweeney et al. 1992). It is worth noting, however, that temperature changes of a similar or greater magnitude occur in forested headwater streams due to riparian clearing.

5.3.1 Influence of thermal regime on the biota

Every species is restricted to some temperature range that also limits its geographic distribution to a certain range of latitude and elevation. Species that occupy a narrow temperature range are referred to as stenothermal, while those that thrive over a wide range are called eurythermal. In addition, a species may be considered adapted to cold-, cool-, or warm-water thermal environments. Few taxa are able to cope with very high temperatures, however. Cold-water fishes cannot survive water above 25°C for long, and most warm-water fishes including the pike family (Esocidae) and many minnows (Cyprinidae) have upper limits near 30°C. Some fishes of desert streams can tolerate nearly 40°C, a few invertebrates live at up to 50°C, and specialized Cyanobacteria of hot springs survive 75°C (Hynes 1970).

There are a number of reasons for the specific temperature requirements of a particular species. The taxonomic lineage to which it belongs may have originated and diversified in cool waters at high latitudes (e.g., Plecoptera, Hynes 1988), or in warmer water at low latitudes (e.g., Odonata, Corbet 1980). The timing of an insect’s life cycle, which often is both cued and regulated by temperature, determines the seasons when it most actively grows, consumes resources, and is exposed to predators. Thus resource availability and predation risk, two topics that will reappear in later chapters, can be important evolutionary pressures that are responsible for a particular life cycle and suite of temperature adaptations. A number of studies document how closely related species hatch, grow, and emerge in such a neatly staggered sequence that their life cycle separation appears to ameliorate competition (Sweeney and Vannote 1981, Elliott 1987a) (Figure 5.14). By determining when an insect hatches and grows, temperature synchronizes the life cycle to changing seasonal conditions, coordinating growth with resource availability and ensuring the availability of mates. When the growing season is very short, a common life cycle is to alternate short periods of rapid growth separated by long periods of dormancy or diapause (Danks 1992). Such life cycles are often seen at high latitudes and may require exposure to near-freezing temperatures followed by a rapid temperature rise in order to break egg diapause. When a deep-release dam was built on the Saskatchewan River, winter temperatures were maintained near 4°C, and so the cue to ending egg diapause was eliminated. Virtually all taxa disappeared from the stretch of river with modified temperatures. A fauna that previously included 12 orders, 30 families, and 75 species was reduced to only the midge family Chironomidae (Lehmkuhl 1974).

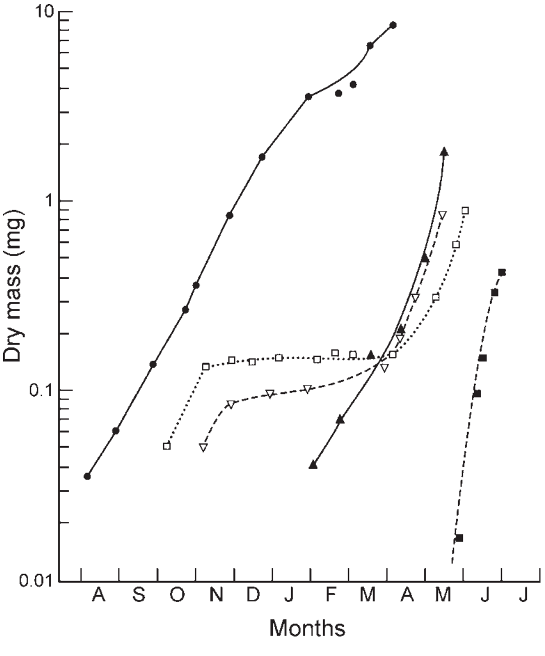

FIGURE 5.14 Larval growth period for five species of riffle-inhabiting ephemerellid mayflies in White Clay Creek, Pennsylvania. (●) *Ephemerella subvaria*; (▲) *E. dorothea*; (□) *Seratella deficiens*; (■) *S. serrata*; (inverted open triangle) *Euryophella verisimilis*. (Reproduced from Sweeney and Vannote 1981.)

Differences in thermal regimes, whether natural or anthropogenic, can have complicated effects on the life cycles of aquatic insects. As with all ectotherms, their growth rates increase with increasing temperature provided sufficient food is available. Often, but not invariably, insects that complete their life cycles more rapidly due to warmer temperatures mature at a smaller final size. Thus thermal regime can alter the timing of adult emergence and adult size, and because the number of eggs produced by a female usually is a logarithmic function of her mass, fecundity is also affected. *Ephemerella dorothea* individuals emerging from cool tributaries of White Clay Creek were nearly twice the mass of those emerging from a warm tributary (Vannote and Sweeney 1980). There is also evidence that species have an optimal temperature range where both body size and fecundity are maximized. Rearing studies with the mayfly *Centroptilium rufostrigatum* showed adult body size to be reduced at both high and low temperatures, suggesting that intermediate values were optimal (Sweeney and Vannote 1978).

The influence of temperature on stream biota has been demonstrated in the laboratory, from life cycle studies, and from their distributions. Quinn et al. (1994) determined lethal temperatures based on 50% mortality after up to 4 days of exposure. For 12 invertebrate taxa from

New Zealand, the temperature that killed half of the individuals in 96 h (the LT_{50}) ranged from 22.6°C to 32.6°C; the highest tolerance was for an elmid beetle and the lowest was for the mayfly *Deleatidium*. Based on temperature records for over 100 New Zealand rivers, maximum temperatures exceed the thermal tolerance for *Deleatidium* at over one third of sites, and high temperature was more likely to be a limiting factor in streams of the North Island than at South Island sites. Laboratory results on thermal tolerances were also consistent with field observations (Quinn and Hickey 1990) that Plecoptera and Ephemeroptera were much less abundant in rivers where typical summer temperatures exceeded 19°C and 21°C, respectively.

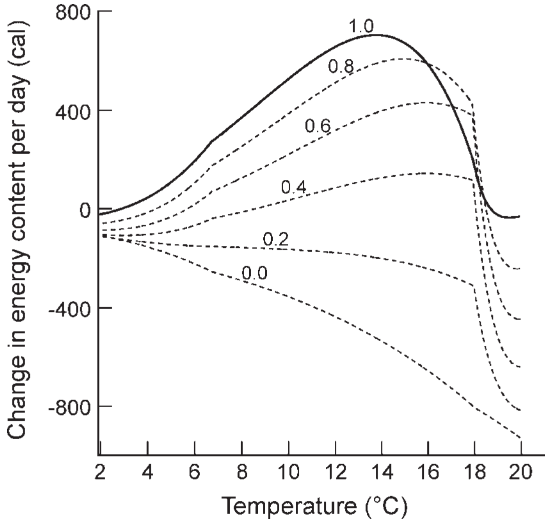

FIGURE 5.15 Relationship between the mean daily change in the total energy content of a 50 g brown trout and water temperature. The solid curve shows the values for fish on maximum rations and the dotted lines for proportions of the maximum energy intake. (Reproduced from Elliott and Hurley 2000.)

The influence of temperature on growth and its interaction with food supply has been well studied in trout (Elliott 1994). In brown trout, growth rate increases with temperature over the range from a few degrees to approximately 15°C, and then declines dramatically with further temperature increase. Although warmer temperatures increase feeding activity and digestion rate, they also raise respiratory rates, and for brown trout the energetic costs of high metabolic rates significantly curtail growth when reared at constant temperatures much above 15°C. As can be seen in Figure 5.15, food availability is critical. At maximum rations, warmer temperatures promote faster growth, but as food ration declines the energy budget turns negative because the fish's metabolic rate is controlled by temperature. This is the typical response of all ectotherms approaching their upper temperature limit for growth, which may be several degrees lower than the thermal tolerance revealed in a short-term mortality trial.

The importance of temperature to large-scale distribution patterns in river assemblages can be seen in the longitudinal zonation of invertebrates and fishes along a river's length. A downstream increase in macroinvertebrate diversity is especially apparent in alpine streams (Allan 1975, Ward 1994). Typically, dipteran larvae (midges and black flies) dominate at the coldest temperatures, and the nymphs of a number of mayflies (Baetidae) and stoneflies (Nemouridae, Chloroperlidae) are added to the assemblage as one proceeds downstream and waters warm above 4°C. At still warmer temperatures, caddisfly larvae and additional families of aquatic insects appear. Milner et al. (2001) used maximum summer water temperatures and channel stability to construct predictive models of macroinvertebrate diversity across seven glacial rivers in Europe. A combination of zonation and downstream addition of fish species was evident along an elevational gradient from 2,200 to 1,200 m in a Rocky Mountain stream (Rahel and Hubert 1991). Salmonids dominated headwater reaches but were replaced by a warmwater minnow–sucker (Cyprinidae–Catostomidae) assemblage below 2,000 m. Such longitudinal replacements may involve a combination of competitive effects and the influence of temperature on feeding and physiological performance. The longitudinal replacement of trout at high elevations in Rocky Mountain streams by the creek chub *Semotilus atromaculatus* at low elevations was attributed to both appetite loss and behavioral interactions and so was not solely a function of physiological performance (Taniguchi et al. 1998).

Fishery scientists have long been aware that fish assemblages vary along latitudinal gradients and can be classified according to their position and the maximum summer temperatures (Lyons 1996). In the heterogeneous glaciated landscape of Michigan, streams exhibit substantial regional variation in weekly mean temperature and in temperature fluctuation during warm seasons, allowing Wehrly et al. (2003) to determine the realized thermal niche of stream fishes based on three temperature categories (cold, <19°C; cool, 19–22°C; and warm, ≥22°C) and three temperature fluctuation categories (stable, <5°C; moderate, 5–10°C; and extreme, >10°C). The brook trout *Salvelinus fontinalis* and smallmouth bass *Micropterus dololieu* are good examples of cold-water and warm-water species, respectively (Figure 5.16). Overall fish diversity increased with mean water temperature across some 300 Michigan sites (Figure 5.17), documenting the well-established higher diversity of warm-water streams over cold-water streams. This pattern has often been reported as a longitudinal gradient in which temperature increase is accompanied by an increase in river size and change in many other variables (e.g., Huet 1949), but because the Michigan study provided a wide range of temperature regimes within a relatively modest range of stream sizes, these results strongly implicate temperature as the causal variable.

Local-scale thermal heterogeneity may explain apparent exceptions when cold- and cool-water fishes occur in warm-water streams. In the Grande Ronde basin in northeastern Oregon, cold-water patches (at least 3°C colder than ambient) were found associated with side channels, lateral seeps, and floodplain spring–brooks, and riparian shading could effect further cooling, indicating that these could be thermal refuges for salmonids (Ebersole et al. 2003). Chinook salmon *Oncorhynchus tshawytscha* persist in streams in the John Day River basin in northeastern Oregon where water temperatures

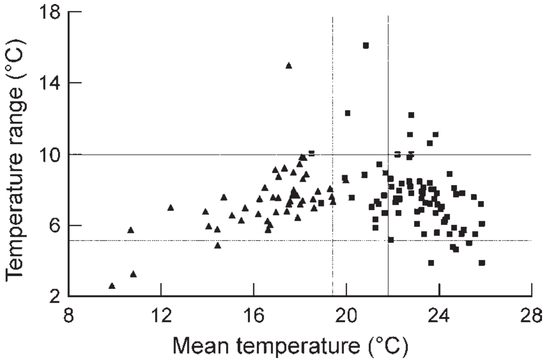

FIGURE 5.16 Thermal niches of two stream fishes in Michigan, based on field distributions and thermal regimes defined by three categories of mean temperature (vertical lines) and three categories of temperature variation (horizontal lines). Brook trout (▲), smallmouth bass (■). (Reproduced from Wehrly et al. 2003.)

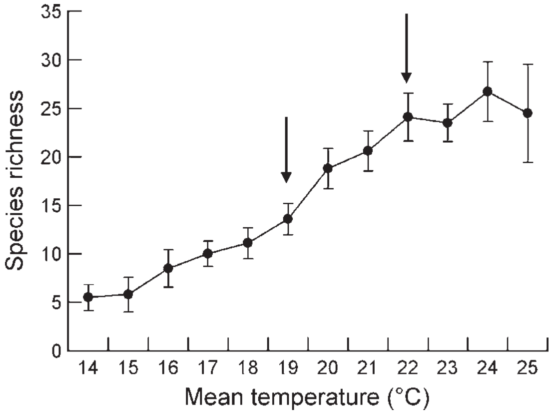

FIGURE 5.17 Relationship between species richness (±2 standard errors) and mean temperature developed from approximately 300 sites in Michigan's Lower Peninsula. Arrows denote breakpoints between cold-, cool-, and warm-water streams. (Reproduced from Wehrly et al. 2003.)

frequently exceed their upper tolerance levels (25°C) during spawning migration. Salmon distribution and cool-water temperature patterns were strongly correlated in a warm stream but only weakly in a cold stream, further evidence that local-scale thermal patchiness provided needed habitat (Torgersen et al. 1999).

Finally, temperature controls the metabolism of all producers and ectothermic consumers in fluvial ecosystems, so it will strongly affect numerous ecosystem functions. Rates of photosynthesis and microbial activity are strongly temperature dependent (Sections 12.3.1), as are the metabolism and growth of macroinvertebrates and fish. Secondary production, which is the amount of new consumer biomass added per unit time, is estimated from the product of species-specific growth rates and standing crop biomass. As Figure 5.18 illustrates, daily growth rate of aquatic insects increases markedly with temperature, and so warmer ecosystems are more productive overall (Benke 1993).

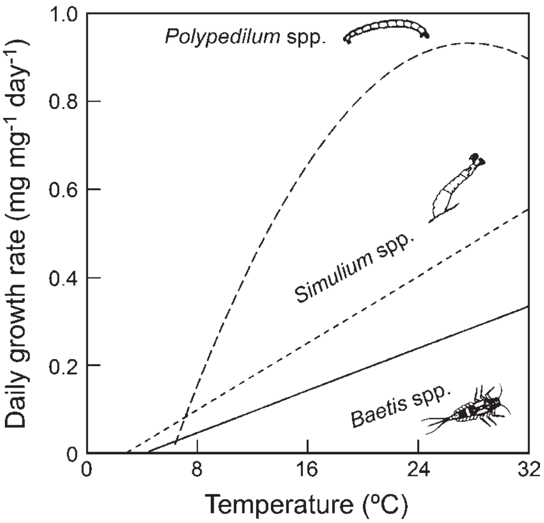

FIGURE 5.18 Daily growth rates (mg mg^{-1} day^{-1}) as a function of temperature for three aquatic insects found on snag habitat in the Ogeechee River, Georgia, and reared in stream-side artificial channels. Insects include the midge *Polypedilum*, the black fly *Simulium*, and the mayfly *Baetis*. (Reproduced from Benke 1993.)

5.4 Summary

Abiotic factors include all physical and chemical variables that influence the distribution and abundance of organisms. Current, substrate, and temperature often are the most important variables in fluvial environments, and all organisms show adaptations that limit them to a subset of conditions. Species differ in the specific conditions under which they thrive, and whether those conditions are narrow or comparatively broad. Habitat preferences can be inferred from the subset of environmental variables that best correlate with a species' distribution and abundance, with the important caveat that interactions with other species may further restrict the habitat occupied. Environments that are structurally either simple or extreme tend to support fewer species, and habitats that are more complex tend to support more species. How patterns in the abiotic environment are manifested across spatial scale, and the persistence of suitable conditions over temporal scale, add challenge to the task of deciphering organism–habitat relationships.

Current and related hydraulic forces affect diverse aspects of the stream environment including channel shape and substrate composition, the physical structure and hydraulic forces operating in the benthic and near-bed microhabitats, and the balance between physical drag processes and the benefits due to the delivery of food, nutrients, and gasses and the removal of wastes. Most organisms live attached to, within, or associated with the streambed, where flows are turbulent and difficult to measure, especially at relevant scales. Considerable effort has gone into theoretical approaches and methods of measurement that can better characterize the flow environment experienced by organisms. Both simple and complex hydraulic variables can be effective predictors of the distribution of individual species and the overall abundance and richness of the invertebrate fauna.

Even under "normal" flows many organisms will experience drag and lift forces, the short-term variability of which is called turbulence. At intervals, flows increase creating disturbance events on a longer temporal scale, redistribution, and possibly death. Thus the association of organisms with particular currents and substrates can reflect the ability of particular habitats to serve as refuges. Some invertebrates and fishes have been shown to move quickly into more sheltered habitats as flows increase, but in other cases it may be happenstance whether an organism is protected from flow during a spate.

Substrate is a complex physical variable that includes inorganic and organic substrate types. It interacts strongly with current, which both influences substrate stability and is in turn influenced by bed friction; and with roughness, which creates complex, near-bed flow environments. The quantification of substrate requires multiple approaches, including size analyses for inorganic substrates, counts of wood, and descriptive categories such as leaf accumulations and debris dams. At the mesohabitat scale, channel units such as riffles and pools, and channel depth, while not strictly substrate categories, are analogous habitat categories for larger organisms, especially fish. Among inorganic substrates, gravel of intermediate size supports a diverse, lithophilous flora and fauna that have received a great deal of study by lotic ecologists. Terrestrial leaves that accumulate in streams and wood that modifies habitat and channel shape are important and well-studied organic substrates.

Studies of the importance of substrate frequently are simultaneously studies of current, as these two abiotic factors are linked. Substrate size and heterogeneity appear to promote species richness, at least to a degree, and surface texture and roughness additionally promote abundance and diversity. The stability of the substrate and the protection it affords from the forces of current clearly are critical aspects as well.

Temperature is a key environmental variable determining the metabolic rates of organisms, their distributions, and quite possibly their success in interacting with other species. Stream temperature usually varies on seasonal and daily timescales and among locations due to climate, extent of streamside vegetation, and the relative importance of groundwater inputs. For these reasons, thermal regimes are highly diverse and can vary on all spatial scales from microscale patches to the longitudinal gradient from headwaters to river mouth. Human activities can alter the natural temperature regime in many ways, including removal of shade-enhancing vegetation, changes to flow paths such as increased impervious surface, construction of impoundments, and of course by influencing the climate.

Freshwater organisms exhibit a wide range of thermal tolerances that correspond to the thermal environment they inhabit, which may be cool or warm, constant or fluctuating. With few exceptions the organisms of running waters are ectotherms, and so external temperature governs their metabolism and growth. Although warmer temperatures generally allow greater activity, they also impose greater metabolic costs. A cold-blooded organism in warm water, with an inadequate food supply, quickly loses mass. Whether the evidence is based on lethal temperatures in the laboratory, detailed analysis of energy budgets, or field surveys, it is evident that temperature strongly affects distributions and abundances. The thermal tolerances of fish have received a great deal of study, and it is common in the temperate zone to speak of cold-water and warm-water fishes, which are typically arrayed along latitudinal and elevational gradients. The extreme sensitivity of cold-water fishes to micropatch differences in temperature is evident in their ability to at least temporarily reside in cool- and warm-water systems by using locations where groundwater inputs and shade provide suitable thermal conditions.

Chapter six

Primary producers

In this and the following chapter we examine the sources of energy to lotic food webs. Autotrophs or primary producers are organisms that acquire their energy from sunlight and materials from nonliving sources. Algae, higher plants, and some bacteria and protists are important autotrophs in running waters. Heterotrophs obtain energy and materials by consuming living or dead organic matter. All animals of course are heterotrophic, but so also are fungi and many protists and bacteria that gain nourishment through the processing of dead organic matter and often make that organic matter more nutrient rich and more accessible to other consumers. Together, these autotrophs and microbial heterotrophs constitute the basal energy resources that support higher trophic levels in lotic food webs. The major autotrophs of running waters include large plants, referred to as macrophytes, and various small producers including individual cells, colonies, and filamentous growth forms. Algae suspended in the water column are referred to as phytoplankton; those attached to substrates are referred to as benthic algae or periphyton.

Macrophytes include aquatic angiosperms, bryophytes (mosses and liverworts), and some members of the benthic algae when they become large (filaments of the green alga *Cladophora* have been estimated to reach 6 m). Angiosperms generally require moderate depths and slow currents, and so are most common in springs, rivers of intermediate size, and along the margins and in backwaters of larger rivers. Bryophytes are restricted in distribution, but can be abundant in cool climates and in shaded headwater streams. Benthic algae occur on virtually all surfaces within rivers, typically in intimate association with heterotrophic microbes and an extracellular matrix, to which the all-inclusive terms periphyton, biofilm, or *Aufwuchs* apply. Phytoplankton are unable to maintain populations in fast-flowing streams, but can become abundant in slowly moving rivers and backwaters where their doubling rates exceed downstream losses due to current. Thus, according to a somewhat idealized view of the longitudinal profile of a river system, benthic algae and occasional bryophytes predominate in headwater and upper stream sections, and benthic algae become more abundant farther downstream where the river widens and hence is less shaded by streamside vegetation. Macrophytes occur mainly in midsized rivers and along the margins of larger rivers, and substantial phytoplankton populations develop only in large, lowland rivers (Figure 1.7). Because benthic algae are found in nearly all running waters and often are important in fluvial food webs, they have been the main focus of study.

6.1 Benthic Algae

Virtually all substrates that receive light, whether in small streams or large rivers, sustain a benthic algal community. Benthic algae support fluvial food webs, remove nutrients from the water column, and can attenuate the current and stabilize sediments, thereby modifying the aquatic habitat (Stevenson 1996, Dodds and Biggs 2002).

Benthic algae can be further categorized by their size. Macroalgae are benthic forms having a mature thallus visible to the naked eye, in comparison with smaller microalgae that cannot be distinguished without a microscope. Algae also can be categorized by whether they grow on stones (epilithon), sediments (epipelon), sand (epipsammon), wood (epixylon), or other plants (epiphyton). Epipelic and epipsammic taxa form films or mats on silt and mud bottoms, and typically are motile and easily swept away by an increase in current. Because of their motility, filter paper and glass slides placed on the sediment surface are readily colonized, thus serving as one sampling technique. Epiphytic taxa occur on macrophytes, particularly angiosperms, where epiphytic coating can be detrimental to the host plant. Unlike epipelic species, epiphytic and epilithic taxa usually are firmly attached by mucilaginous secretions or via a basal cell and stalk, and thus are less likely to be dislodged by the current.

Some algal species are in contact with the substrate along the entire cell wall, colony, or filamentous system. This growth form is termed adpressed, and contrasts with erect forms in which only a basal cell or basal mucilage contacts the substrate. As a consequence of this variety in growth form and lifestyle, a close look at a benthic algal community reveals much structural diversity (Figure 6.1).

Diatoms, green algae, and cyanobacteria typically contribute the majority of species found within the periphyton, although red algae, chrysophyceans, and tribophyceans may also occur

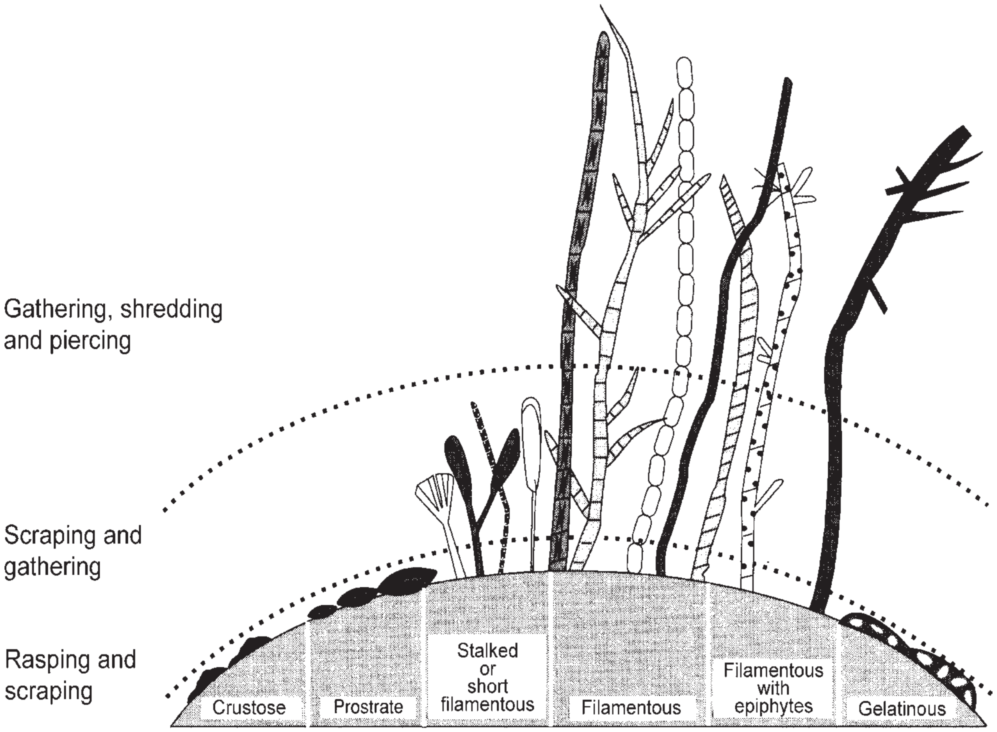

FIGURE 6.1 Hypothetical representations of major growth forms of periphyton assemblages. Different modes of herbivory are expected to be most effective with particular growth forms. (Reproduced from Steinman 1996.)

(Graham and Wilcox 2000). The prevalence of diatoms is apparent from Patrick's (1961) cell counts from glass slides placed in three US rivers, Moore's (1972) study of the epipelon of a southern Ontario stream, and Chudyba's (1965) study of epiphytes of *Cladophora glomerata* in the Skawa River, Poland (Table 6.1). In an extensive survey of the macroalgae of 1,000 stream reaches in North America, Sheath and Cole (1992) recorded 259 taxa of macroalgae, of which 35% were green algae, 24% were cyanobacteria, 21% were diatoms and other chrysophytes, and 20% were red algae. Many diatoms do not form mats, gelatinous colonies, or filaments, and so would be underrepresented in a survey of visible macroalgae.

6.1.1 Benthic algal distribution and abundance

Proximate factors that may influence benthic algae include light, temperature, current, substrate, scouring by floods, water chemistry, and grazing. Biggs (1996) proposed that regional and catchment features such as topography, geology, land use, vegetation, and climate affect these proximate variables, which directly regulate the accrual and loss of benthic algal biomass. Light and nutrients, interacting with temperature, influence biomass accrual while disturbance (substrate turnover and transport, high current velocities) and grazing lead to the dislodgement of algae and biomass loss (Figure 6.2).

The abundance or biomass of benthic algae can be measured in several ways (Stevenson and Smol 2003, Steinman et al. 2006). Typically a known area of substrate is sampled using a brush to dislodge algae. Some researchers favor a suction device constructed by fitting a brush inside a cylinder to which a side port is added to withdraw the slurry by suction. The resultant slurry can then be filtered onto a filter paper and the cells counted, the biomass determined, or the chlorophyll pigment extracted and assayed using a spectrophotometer. Artificial

TABLE 6.1 Representation of major periphyton taxa in collections where all habitats were sampled, and from studies emphasizing epipelic and epiphytic assemblages. Patrick's (1961) data are from one time of year and include only those species represented by a minimum of six specimens in a very large sample (a count of 8,000 individuals). Inclusion of rarer species would at least double the species list. The studies of Moore (1972) and Chudyba (1965, 1968) probably represent close to the entire flora for the site.

	Number of taxa				
	All habitats			*Epipelon*	*Epiphyton*
Diatoms	81[a]	80[b]	59[c]	321[d]	176[e]
Chlorophyta (green algae)	12	12	7	32	27
Cyanobacteria (blue-green algae)	9	9	6	14	19
Euglenophyta (phytoflagellates)	17	15	7	29	—[f]
Chrysophyta (yellow-brown algae)	0	1	1	1	2
Rhodophyta (red algae)	1	3	0	0	1
Total	120	120	80	388	225

[a] Potomac River, Maryland
[b] Savannah River, Georgia
[c] White Clay Creek, Pennsylvania (Patrick 1961)
[d] Clay and detritus bottom stream, southern Ontario (Moore 1972)
[e] Epiphytes on *Cladophora glomerata* in the Skawa River, Poland (Chudyba 1965)
[f] Flagellates present but not identified to species

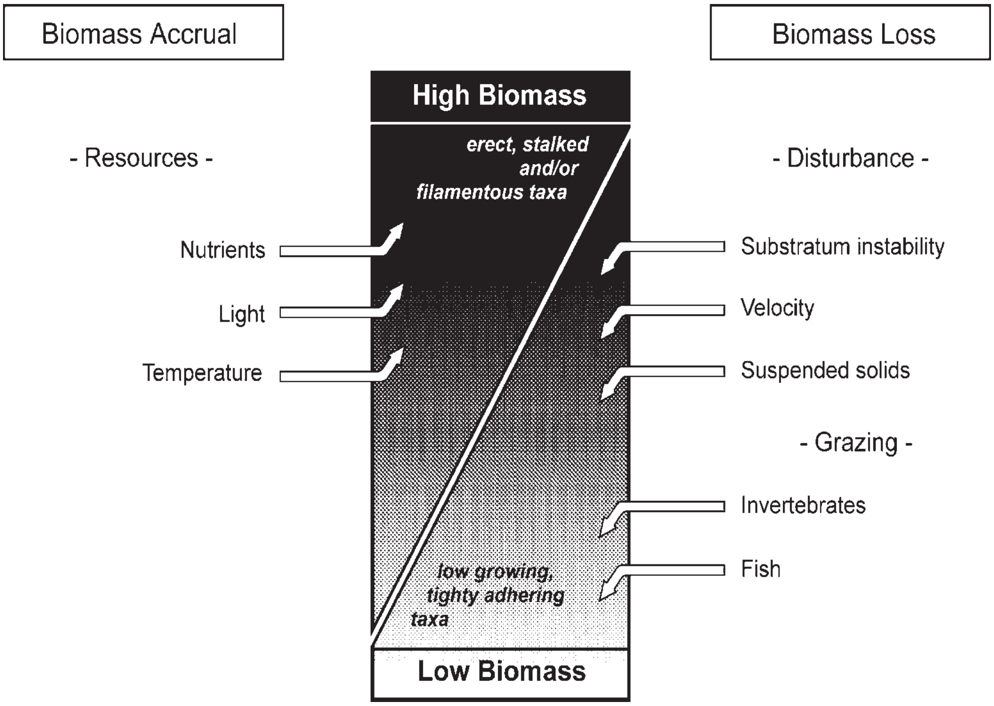

FIGURE 6.2 Factors controlling the biomass and physical structure of periphyton in streams. (Reproduced from Biggs 1996.)

substrates including clay tiles and glass slides can also be allowed to become colonized, and soft sediments can be collected by inserting the top of a petri dish into the sediment, and then sliding a glass plate underneath to sample a known area and depth. Cell counts usually are reported as numbers per square centimeter, or if cell volume also is estimated, as biovolume per square centimeter. To estimate the algal biomass it is usual to weigh a dried sample, then weigh a second time after combusting all organic matter at ~500°C. The loss of mass represents the organic material present (all of which was converted to CO_2 by combustion), and is referred to as ash-free dry mass (AFDM). Because chlorophyll *a* is the most abundant pigment in plants, its absorbance is measured most frequently. These are all static measures, often referred to as standing crop. Measurement of primary production, or the rate of formation of new biomass, also is important. Methods based on the release of O_2, either within an enclosed chamber or for the entire stream, are described later in this chapter.

The simplest framework for discussing limiting factors is to take them one at a time, although in reality these factors interact in complex ways. This is because the importance of any one factor in limiting plant growth depends upon whether some other factor is in even shorter supply. Thus, light might be limiting if nutrients are plentiful, and their importance can alternate seasonally or from place to place. In addition, it is possible that two or more factors simultaneously limit growth. For these reasons it is difficult to address any one factor without specifying the context of other environmental variables. Before considering singly and in detail the factors that potentially limit benthic algae, it may help to present a brief overview of the role played by each.

Light can be a limiting factor in small streams under dense forest cover, where benthic algae populations tend to reach maxima just prior to canopy development and then decline through the summer. However, other factors often override light. Nutrients, particularly phosphorus (P) and nitrogen (N), might be expected to exert a critical influence over autotrophs in rivers just as they do in standing freshwaters, but this turns out to be rather complicated. Flow provides continual delivery of water, thus minimizing the depletion of nutrients, and thermal stratification does not occur to restrict mixing of nutrients throughout the water column, so nutrient exhaustion should be less likely to occur in rivers than in lakes, where its importance is well established. In some studies, enrichment of stream water with N and P has had no effect on benthic algal development, and in others it has. Phosphorus and N have been found to be limiting, sometimes in combination, depending on location. Other nutrients, trace metals, and bicarbonate probably are of some importance, temperature increases rates of metabolism, and grazing can limit algae populations, sometimes severely. Fast currents restrict the establishment of macrophytes and influence the distribution of benthic algae in terms of both taxa and growth forms. Where discharge is variable, flood events and scour by suspended sediments can cause major reductions in algal standing crops. As a consequence, in very rainy climates the growing season is restricted to the time between the last spring flood and the first autumn flood, and summer standing crops depend upon the number of consecutive flood-free days. However, in running waters where extremes of discharge are minimal, direct effects of current may be less important to the benthic algae. Overall, it appears that the effects of light, nutrients, and scour are of greatest importance, and each can be strongly limiting at a particular location or time. Now, what is the evidence for this scenario?

6.1.1.1 Light

Available light can influence the community composition as well as the biomass and productivity of benthic algae. Most evidence suggests that there are differences in the responses of the major groups of algae to irradiance. Green algae usually are associated with high light levels, and diatoms and cyanobacteria appear to require lower light intensities than do green algae (Hill 1996). Motile algae are able to avoid extremes by movement along the light gradient, while nonmotile, prostrate taxa that grow near the substrate may decrease in abundance when light levels decline as a result of shading by overgrowth of the algal community. Becoming dormant or heterotrophic may allow some nonmotile species to persist during conditions of very low light.

Seasonal changes in periphyton in the Metolius River, Oregon, can reasonably be attributed to variation in light intensity and photoperiod because other environmental variables including temperature, current velocity, dissolved substances, and turbidity are essentially constant throughout the year in this spring-fed system (Sherman and Phinney 1971). Benthic algal abundance declined during winter, presumably because of reduced light, and some diatoms such as *Diatoma hiemale* were restricted to the spring–summer time period. However, of the 60 species sufficiently common for detailed study, only nine were seasonal while the rest occurred throughout the year, suggesting only minimal influence of changing light regime on taxonomic composition.

Light can be a limiting factor in small streams under dense forest cover, as evidenced by a number of studies that have observed enhanced periphyton growth after forest harvest permitted more light to reach the streambed (Murphy and Hall 1981, Keithan and Lowe 1985, Lowe et al.

1986). In tropical streams of Hawaii, chlorophyll was significantly higher in partially shaded than in heavily shaded pools. When P was added to test nutrient limitation, chlorophyll increased in partially shaded pools, but not in heavily shaded pools, indicating that benthic algae usually were light limited in heavily shaded areas (Larned and Santos 2000). When photosynthetically active radiation (PAR) was reduced by 60%, 90%, and 98% using shade cloth in experimental channels set up alongside a New Zealand pasture stream, algal production decreased consistently under the highest shade treatments and frequently under 60% shade, whereas algal blooms were common in unshaded troughs (Quinn et al. 1997). The tree canopy can block more than 95% of PAR, and so shaded streams commonly experience irradiances below the level at which photosynthesis is maximal (Hill 1996). A comparison of light reaching two headwater streams in deciduous forest versus an open site for reference documents the rapid diminishment of light following leaf emergence (Figure 6.3) resulting in a rapid decrease of primary production by periphyton (Figure 6.4), which in turn may reduce nutrient uptake and the food available to herbivores. Although some physiological acclimation by algae is possible, it is insufficient to compensate for light scarcity (Steinman 1992, Hill et al. 1995).

In contrast, some studies have found no difference between shaded and unshaded sites, suggesting that other factors can override light limitation of benthic algae. Primary production was only marginally enhanced by greater light penetration after forest clear-cutting in nutrient-poor streams of coastal British Columbia (Stockner and Shortreed 1978). Only if streams experienced nutrient enrichment or if light declined to very low levels did those authors find evidence that available light was limiting to benthic algae. In a subtropical stream in Queensland, Australia, no differences in chlorophyll were observed among three shade treatments (0%, 50%, and 90%) but addition of N resulted in an increase in chlorophyll, suggesting nutrient rather than light limitation of periphyton (Figure 6.5). Strong herbivory also might account for a limited response of benthic algal biomass to increased light levels. When Steinman (1992) substantially increased irradiance in a heavily shaded stream using halide lamps, the

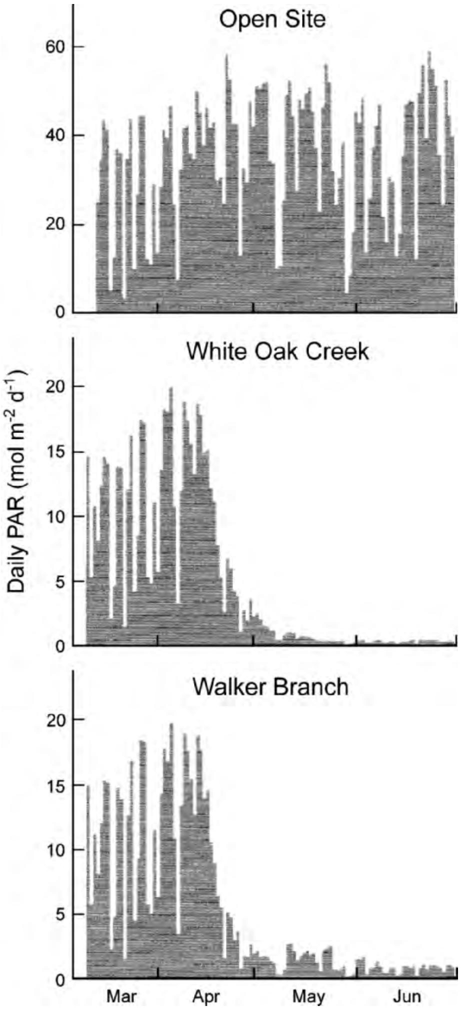

FIGURE 6.3 Daily photosynthetically active radiation (PAR) at three sites in eastern Tennessee. The open site is for reference. White Oak Creek and Walker Branch are small headwater streams in deciduous forest. (Reproduced from Hill et al. 2001.)

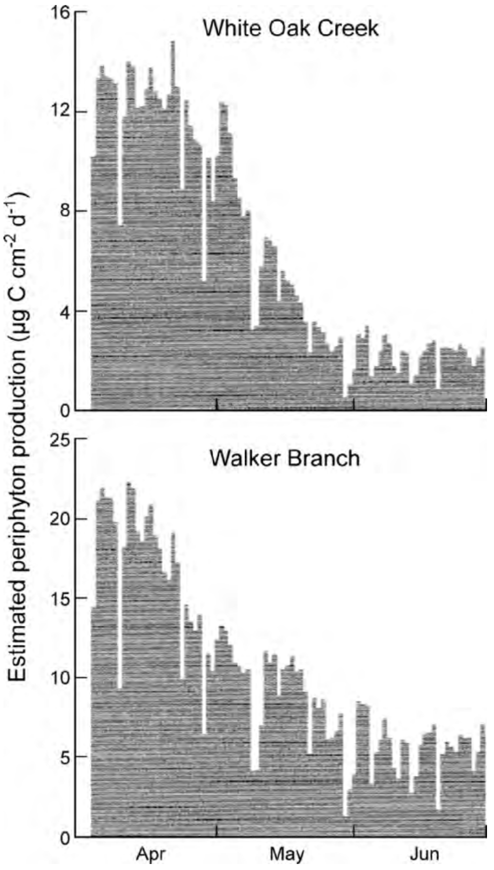

FIGURE 6.4 Daily primary production by periphyton for two small forested streams over the period of spring leaf-out. Primary production was estimated from equations relating production to incident light based on experiments in which stones with periphyton were incubated in chambers placed in the stream and differentially shaded. (Reproduced from Hill et al. 2001.)

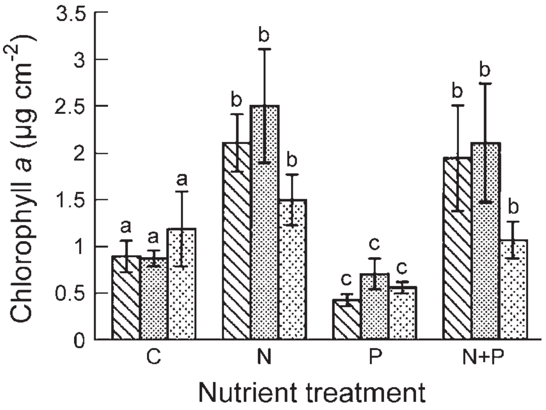

FIGURE 6.5 Chlorophyll *a* values of periphyton in experiments testing the influence of shade and nutrients on periphyton growth. Bars represent the mean of five replicates and error bars correspond to one standard deviation. Letters over bars indicate significant differences among means. Treatments: ▧, no shade; ▩, 50% shade; ░, 90% shade. (Reproduced from Mosisch et al. 1999.)

biomass-specific carbon (C) fixation rates of periphyton increased significantly, indicating higher rates of primary production. However, an increase in periphyton biomass was observed only when snail populations were drastically reduced. At least in this system, intense herbivory prevented the positive influence of light on periphyton production from being translated into a greater biomass of autotrophs. In a meta-analysis of the effects of light and grazers on benthic algae, Hillebrand (2005) found that a decrease in grazers or an increase in light each had positive effects on algal biomass, and the enhanced effect of light was generally observed in the absence of grazers.

Studies of the potentially negative effects of increased ultraviolet (UV) radiation on benthic algae have resulted in mixed outcomes. In a Tennessee stream, Hill et al. (1997) observed no significant effects on periphyton biomass and photosynthesis when ambient UV levels were reduced by placing UV-opaque Plexiglas over a stream section. In a laboratory experiment that varied UV irradiance from zero to four times ambient, rates of photosynthesis and photosynthetic pigments of periphyton communities were reduced by UV irradiance greater than ambient levels (McNamara and Hill 2000). Mean diatom cell size also was reduced under the higher UV levels, but cell N and P content did not change, suggesting that increased UV irradiance had no effect on periphyton food quality. The outcome of PAR and UV manipulations over 91 days in a coastal stream in British

Columbia differed with canopy cover (Kelly et al. 2003). The reach with full canopy showed no response to UV reduction and had higher invertebrate biomass and lower algal biomass compared to other reaches. At sites with less canopy cover, algal biomass declined in response to higher UV-A, whereas invertebrate biomass declined in response to both UV-A and UV-B. This negative effect of UV radiation on invertebrate biomass, including grazers, likely resulted in higher algal biomass in the reduced canopy sites. Experiments conducted to study the effects of UV radiation on diatoms found that responses were highly species-specific (Hodoki and Ohbayashi 2005). Greater growth inhibition in response to UV radiation was observed in species adapted to low light versus high light-adapted species. In addition, higher tolerance has been recorded in algae with dense growth forms.

6.1.1.2 Nutrients

Dissolved inorganic P, N as nitrate and ammonia, and silica are generally considered the most critical nutrients for algal production, although other chemical constituents also can limit growth under some circumstances. Limitation of benthic algae by nutrients is primarily by N or P. The supply of silica also might be expected to become limiting, because the frustules of diatoms are composed of silicious material and diatoms are a major component of the periphyton of cool, shaded streams. Although the dynamics of lake diatom populations have been shown to depend upon silica concentrations (Wetzel 2001), silica in rivers rarely is in short supply (Chapter 4) and consequently it may seldom limit diatom growth. However, few studies have assessed its importance as a limiting factor in running waters (Borchardt 1996).

Nutrient enrichment studies provide ample evidence that nutrient supply can indeed limit benthic algal growth in nature. Studies of periphyton dynamics in small streams of the west coast of Vancouver Island, a temperate rain forest setting, have demonstrated strong P limitation (Stockner and Shortreed 1978). Nitrate enrichment produced little response, but periphyton accumulated rapidly when dissolved inorganic P was added, exhibiting roughly a fivefold increase in response to P enrichment alone, and an even greater increase when both nutrients were added (Figure 6.6). Filamentous green algae responded dramatically to P enrichment. Cyanobacteria, which can fix atmospheric N and thus should have a competitive advantage under low N conditions, did not flourish under the nitrate treatment, despite the fact that N fell to low levels. However, the frequency of the diatom *Achnanthes minutissima* decreased in the nitrate-only treatment while it increased in the other troughs, and this may be an indication that changes in the N/P ratio can adversely affect particular taxa. Subsequently, this catchment was logged, allowing a direct test of the effect of increased light on periphyton biomass. Essentially no change occurred, and the case seems clear that low P concentration is the primary limiting factor in this environment.

Sixteen years of summer P additions to the Kuparuk River on the North Slope of Alaska (Slavik et al. 2004) resulted in a change in community composition in which bryophytes replaced epilithic diatoms as the dominant primary producers. Positive responses to fertilization were observed at all trophic levels including increases in epilithic algal stocks, some insect densities, and fish growth rates. However, this open tundra stream receives ample light. A 2-year nutrient enrichment with both N and P in a forested stream in Georgia had little detectable effect on benthic algal composition or periphyton biomass, again showing that heavy shade can suppress response to nutrients (Greenwood and Rosemond 2005). In a forested Mediterranean stream with modest light levels, nutrient addition increased chlorophyll concentration and algal density, but no changes in community composition were observed (Sabater et al. 2005).

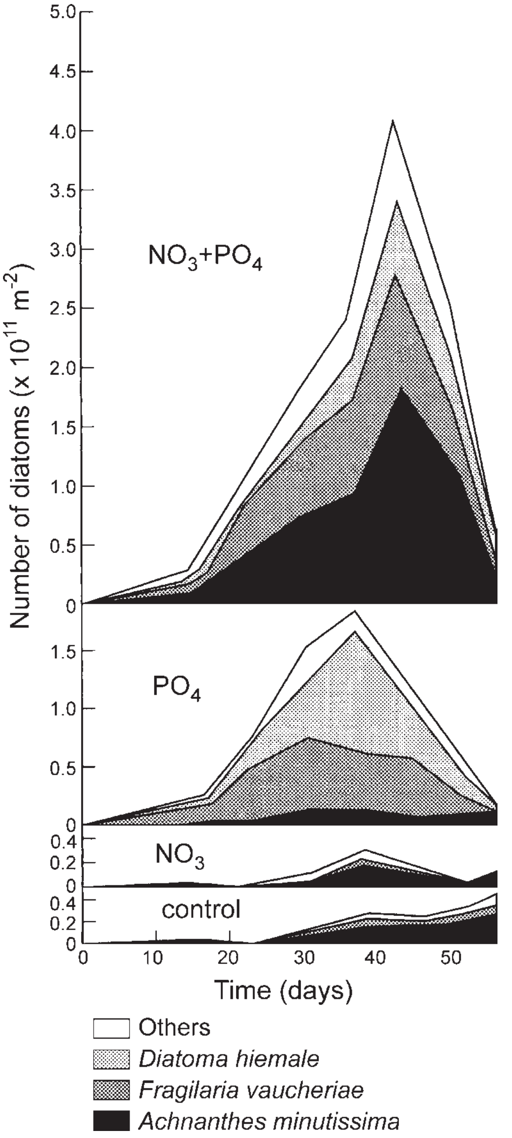

FIGURE 6.6 Changes in the numbers of the dominant diatom species in troughs enriched with NO_3-N, PO_4-P, or both in combination. Troughs were placed in Carnation Creek, Vancouver Island, allowed 4 weeks to colonize, and then fertilized for 52 days. Note that periphyton populations peaked after 30–40 days, and then declined sharply prior to termination of the fertilization experiment. (Reproduced from Stockner and Shortreed 1978.)

Additional evidence of nutrient limitation of benthic algae has been obtained through the use of nutrient-diffusing substrates. In this approach, clay pots are filled with an agar solution containing the desired mix of nutrients and capped with a plastic petri dish (Fairchild and Lowe 1984). Nutrients leach through the pot, although rates can be somewhat variable depending on thickness and consistency of the clay walls. Pringle and Bowers (1984) used sterilized sand from the streambed consolidated with agar and nutrients in petri dishes, thus achieving very consistent release rates. Studies in Carp Creek, a small, nutrient-poor stream in northern Michigan, demonstrated that P was limiting to periphyton, and additions into the water column and from diffusing substrates each could enhance periphyton abundance (Pringle and Bowers 1984).

Nitrogen has been shown to be the primary factor limiting benthic algae in a number of cases. Additions of nitrate to a tropical stream in the foothills of the Venezuelan Andes during the dry season resulted in major increases in algal biomass, whereas P additions did not (Figure 6.7) (Flecker et al. 2002). In addition, nutrient uptake rates were significantly higher for nitrate-N and ammonium-N than for phosphate-P. Grazing fish

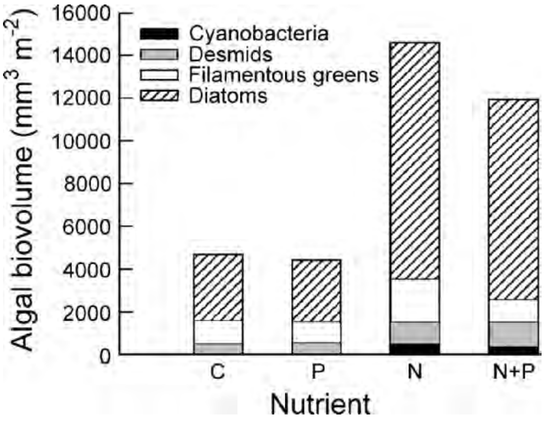

FIGURE 6.7 Algal community responses after 8 days of nutrient additions into flow-through channels placed in Río las Marías, Venezuela. (Reproduced from Flecker et al. 2002.)

are abundant in this system, and simultaneous manipulation of both fish and nutrients revealed a stronger effect of consumers than of nutrients on benthic algae. Interestingly, the N addition produced a greater response where fish were present, suggesting that fish had the dual effect of consuming algae and regenerating nutrients. Nitrogen limitation was demonstrated in Sycamore Creek, a desert stream in Arizona, by adding nitrate-N to agar within clay saucers placed on the streambed (Peterson and Grimm 1992). Unenriched substrates were dominated by an N-fixing diatom, whereas enriched substrates had a higher diversity of non-N-fixing diatoms and a delayed transition to an N-fixing cyanobacterium that typically became abundant later in algal succession. In a subtropical river in Queensland, Australia, chlorophyll increased on N-enriched substrates in comparison with the controls and P-enriched treatments (Figure 6.5).

Whether N or P is limiting to algal cells often is assessed from their ratio in the environment. Based on the finding that for marine phytoplankton, the ratio of C/N/P in algal cells is remarkably constant at 106:16:1 (Redfield 1958), it is generally held that P is limiting when environmental concentrations of N/P exceed 16:1, and N is limiting when the ratio is <16:1. This should be viewed with some caution, however, as recent evidence suggests that the Redfield ratio is an average of ratios for phytoplankton species in the ocean, and N/P ratios for individual species can vary widely (Klausmeier et al. 2004). For several reasons the use of nutrient ratios as an indicator of N or P limitation should be viewed with caution (Dodds 2003). Internal cell concentrations should be considered when assessing nutrient limitation because cell nutrient content may differ from ambient levels due to P storage within cells and differences among nutrients in uptake rates (Borchardt 1996, Dodds and Welch 2000). In addition, streamwater concentrations may not reflect rate of supply, and the substitution of nitrate and phosphate for total N and total P may underestimate what is actually available. Nonetheless, interpreted cautiously, N/P ratios provide helpful insight into which nutrient is more likely to be limiting.

Most streams of the eastern United States have quite high (~70:1) ratios of N/P, suggesting that P limitation is common. Nitrate levels and N/P ratios are low in some mountainous regions, especially in the Pacific Northwest and in desert streams of the southwestern United States where N limitation has been reported (Fisher et al. 1982, Tank and Dodds 2003). In some cases, however, N/P ratios have been found to be poor predictors of nutrient limitation. Although N/P < 10 for periphyton in tributaries of Lake Superior suggested N limitation, Wold and Hershey (1999) found that colimitation by N and P was the most common condition. When Stelzer and Lamberti (2002) manipulated N/P ratios (65:1, 17:1, 4:1) and total nutrient concentration (low and high) in a factorial experiment using once-through streamside flumes, chlorophyll concentration and algal biovolume responded to N addition, but not to changes in N/P ratios. Because the N/P ratio in the source water was high, this outcome was unexpected. In addition, algal composition exhibited more response to treatments than did overall periphyton abundance, measured as chlorophyll *a* concentration. Despite very low concentrations of P and N/P ratios between 20 and 36, P limitation was not observed in ten North American streams located over a wide range of latitudes from 18° N (Puerto Rico) to 68° N (Alaska) (Tank and Dodds 2003). Thus, although the concentrations of nutrients and N/P ratios might suggest potential nutrient limitation, it is difficult to generalize about geographical or temporal patterns based only on these values and without confirming experimental evidence.

Field studies provide evidence of N, P, and colimitation, and it is difficult to generalize about the frequency of each. When Tank and Dodds (2003) compared algal development on filter papers that capped nutrient-diffusing containers filled with agar and nutrients and placed in ten rivers across the United States, results were variable (Figure 6.8). There was evidence for N limitation alone, N with P as a secondary limiting element, and N and P colimitation depending on location. Positive responses were mainly to N enrichment, and in fact no responses to P alone were observed. Although all the streams of Figure 6.8 had relatively low nutrient levels, only half seemed to be primarily nutrient limited; the others probably were limited by other factors such as light or grazing. In a review of 158 studies to assess the extent of nutrient limitation of periphyton, Dodds and Welch (2000) found that 13% showed stimulation by N, 18% by P, 44% by both, and 26% did not respond to nutrient additions. A similar but independent analysis by Francoeur (2001) of 237 experiments conducted in the United States, Australia, New Zealand, and India found N limitation in 17%, P limitation in 19%, and colimitation in 23% of the cases. A few studies reported inhibition by N or P, and 43% of the studies found neither stimulation nor inhibition of periphyton by either nutrient.

Colimitation by N and P may be a common finding because the periphyton includes multiple species that have different nutrient requirements (Tank and Dodds 2003). In addition, in systems where N and P concentrations are low the simultaneous addition of both nutrients may result in rapid uptake of the secondary limiting element and therefore elicit a response to both (Wold and Hershey 1999). As more such studies are completed, we may be able to generalize concerning the geographical and temporal patterns of nutrient limitation. Most studies have been conducted in the temperate zone, particularly in North America, and less is known about other regions, particularly the tropics and high latitude regions (Borchardt 1996).

6.1.1.3 Current

Stream current has opposing effects on the accrual of benthic algae, best described as a "subsidy-stress" response owing to both beneficial and detrimental effects of flow (Biggs et al. 1998). The flow of water brings continual renewal of gases and nutrients, and so current benefits algal growth by enhancing nutrient uptake. However, current also exerts a shear stress on benthic algae, which can cause cell sloughing, and high flows disturb and scour the substrate. The growth form and architecture of benthic algal assemblages influences their responses to these two factors. Adherent forms are less vulnerable to sloughing than filamentous forms, and may be especially dependent upon diffusion to supply needed materials. Thus, they would benefit most from increased current velocity. Filamentous forms, on the other hand, are exposed to higher rates of diffusion and are more vulnerable to shear.

Many species have been found to occupy specific flow regimes. Under high current velocities, unicellular algae usually are represented by small, adherent diatoms that are attached to the substrate along their length (Stevenson 1996). In Carnation Creek, British Columbia, *Achnanthes minutissima* was abundant everywhere except in riffles, where *Hannaea arcus* was the dominant species (Stockner and Shortreed 1976). Keithan and Lowe (1985) found different algal taxa associated with particular regions in small Tennessee streams, and their description of individual growth forms is consistent with a direct effect of current speed. In slower currents they found diatoms to be more densely packed, with a higher proportion growing in an erect position and a greater abundance of large colonial forms. Many of the same species also were found at faster currents, but in the prostrate position. At the highest velocities most of the diatoms were prostrate, many were in crevices, and tightly adherent species were prevalent. In a diatom community dominated by *Cymbella kappi* and *Gomphoneis herculeana*, the accumulation of mucilage was greater at higher current velocities, which may be a response by the algae to reduce turbulence, and suggests that these

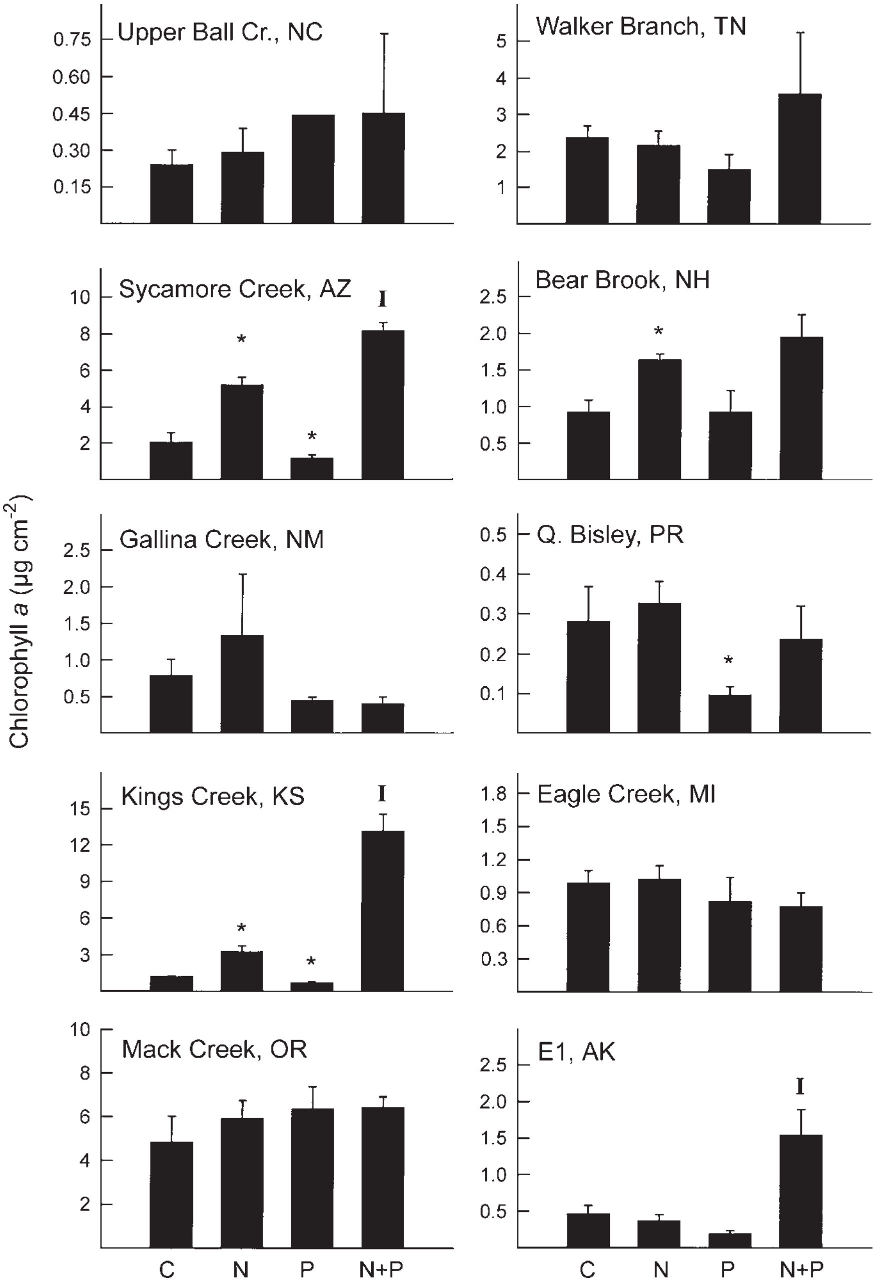

FIGURE 6.8 Chlorophyll *a* values of periphyton growing on diffusing agar substrata capped with filter paper and representing four nutrient treatments: C, control; N, nitrogen (nitrate) alone; P, phosphorus (phosphate) alone; N + P, nitrogen and phosphorus. The mean responses plus one standard deviation are shown. Asterisks indicate significant effects of N or P alone and I indicates a significant interaction between the two nutrients. (Reproduced from Tank and Dodds 2003.)

diatoms have more ability to respond to shear than is commonly thought (Biggs and Hickey 1994).

Current velocity can influence the arrival rate of algal cells and therefore the process of colonization. Algal community development proceeds more slowly at high velocities, evidently because algal cells are less able to become established, but higher biomass accumulation occurs under intermediate velocities rather than in low velocities due to the positive effect of current on nutrient uptake (DeNicola and McIntire 1990, Poff et al. 1990). Small species appear to be most effective at colonizing fast current sites, whereas both large and small species were present at sites with slower current velocities (Stevenson 1996). Diatom immigration rates (Stevenson 1983) and emigration rates (Stevenson and Peterson 1991) have been found to vary with current velocity.

The continual renewal of nutrients provided by flowing water, along with turbulence and mixing that favor the diffusion of nutrients, can stimulate algal growth, respiration, and reproduction (Borchardt 1996, Stevenson 1996). Whitford and Schumacher (1964) conducted one of the first studies of such physiological enrichment, showing that rates of ^{32}P uptake and CO_2 liberation in *Spirogyra* and *Oedogonium* increased with current up to $40\,cm\ s^{-1}$, the highest velocity tested. When algae colonized laboratory streams that were similar except for current velocities (9 versus $38\,cm\ s^{-1}$) and received the same propagules from common source water, different assemblages developed (McIntire 1968). At the higher current, initial colonization was slower but biomass eventually exceeded that of the slower channel, chlorophyll *a* content was higher, and more biomass was exported. Filamentous chlorophytes and chrysophytes became abundant in the slow stream, whereas diatoms, especially *Synedra*, dominated under faster current. Stevenson (1990) attributed stimulation of diatom growth following a 24 h storm in a gravel bed stream to an increased nutrient supply, caused either by greater flow through mats or increased delivery of nutrients from the catchment.

Current velocity may also influence the stable isotopic signature of algae (Trudeau and Rasmussen 2003). In diatom assemblages growing on glass and filamentous algae growing on rocks, the fractionation of N and C stable isotopes was greater as water velocity increased, probably because of the effects of current on boundary layer thickness and the diffusion of nutrients.

Extreme discharge can have a strongly negative impact on lotic algal populations. Scouring of cells from surfaces can result simply from increases in current velocity, from overturning substrates (Robinson and Rushforth 1987), and from abrasion due to tumbling (Power and Stewart 1987) and perhaps by suspended sediments as well. In streams on the west coast of Vancouver Island, winters are very rainy and limit the growing season to the period between the last spring flood and the first autumn flood. Periphyton accumulation demonstrated a clear inverse relationship with a flow index that gave greater weight to more recent as well as more severe events (Shortreed and Stockner 1983). Tett et al. (1978) reached similar conclusions from their study of the Mechums River in Virginia. During a study that extended from 15 May until the following 31 January there were 11 flood-free periods of 7 days or longer, the median duration of low stable flows was 12 days, and the longest was 33 days. The mean density of chlorophyll *a* increased during low flows and decreased abruptly following floods, indicating that chance rainfall events were the main factor controlling algal populations.

The effects of extreme high discharges on benthic algae depend on growth form, the senescence of the mat, and substrate. Thus “dense and coherent” communities such as mucilaginous diatom–cyanobacterial mats tend to increase their biomass as current increases within the interflood period, while stalked–short filamentous diatom communities show a unimodal relationship with current, and communities dominated by long filamentous green algae exhibit a negative response to increases in current (Biggs et al. 1998). Benthic algae can also influence water velocity depending on its growth form. Dodds and Biggs (2002) found that dense diatom assemblages attenuate water velocity more than do filamentous green algae or red algae.

Experiments and field surveys of periphyton communities in New Zealand provide reasonable support for the above generalizations. The biomass of one mucilaginous diatom–cyanobacterial assemblage increased with increasing current velocity as expected, presumably because of greater nutrient availability at higher velocities (Figure 6.9). However, a second assemblage did not, possibly because it was less nutrient limited. The response for the stalked–short diatom community was unimodal (Figure 6.10), as expected, suggesting that the mat received a nutrient subsidy as velocities increased, until higher velocities resulted in a decrease in biomass. Evidently the stalked–short diatom community experiences greater drag and cell dislodgment than the mucilaginous mat. The filamentous green algae community showed a steady decrease in biomass as current velocity increased, also as expected (Figure 6.11), due to the greater drag experienced by this growth form even at moderate velocities.

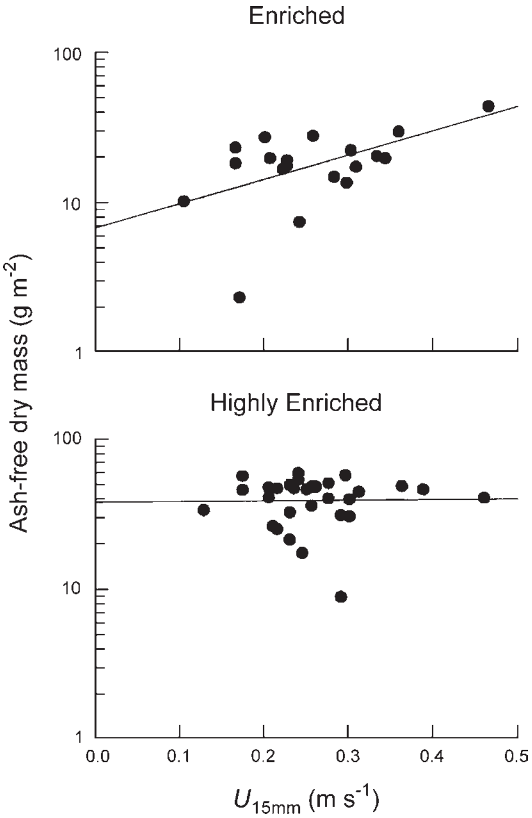

FIGURE 6.9 Responses of periphyton biomass (AFDM) to variation in near-bed velocities ($U_{15\,\mathrm{mm}}$) in mucilaginous diatom communities from enriched and highly enriched reaches in the Mataura River, New Zealand. (Reproduced from Biggs et al. 1998.)

Thick periphyton mats are particularly vulnerable to dislodgement due to senescence of the bottommost layers, which weakens their attachment to the substrate and renders the entire mat vulnerable to sloughing. Shading, the buildup of metabolites, and reduced rates of exchange of gasses and nutrients all can contribute to the lowermost layer being unable to support the weight of the overlying mat. In experimental channels with constant discharge, periphyton biomass commonly goes through a rapid increase followed by a precipitous decline over a time span of ~3–6 weeks (e.g., Stockner and Shortreed 1978, Triska et al. 1983). In Sycamore Creek, Arizona, a substantial periphyton mat was observed to increase steadily in biomass and chlorophyll *a* for ~60 days following a flood event, until a second flash flood virtually eliminated periphyton and the process recommenced (Fisher et al. 1982).

Storm events, in addition to dislodging and burying benthic algae, can shift the substrate to which they are attached. This will of course depend upon the surface occupied and how increases in current are experienced at that location. In a Montana mountain stream where winter anchor ice and spring floods are the principal

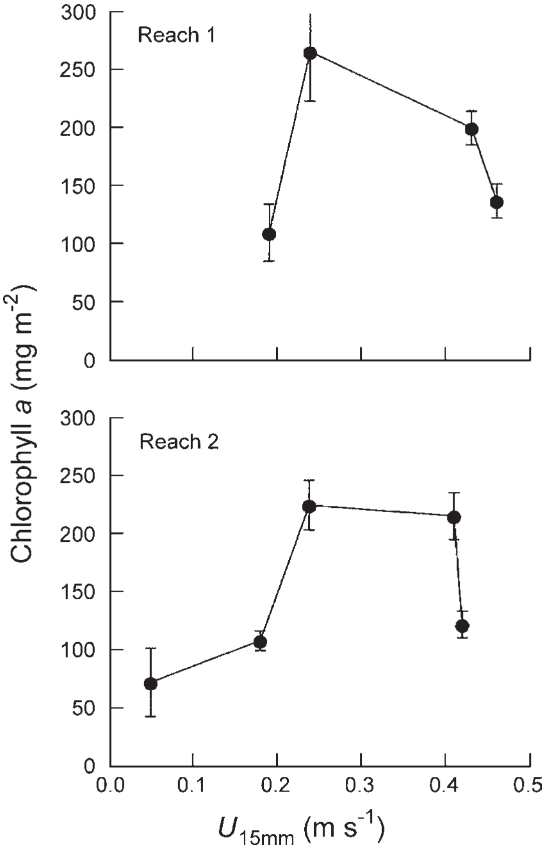

FIGURE 6.10 Chlorophyll *a* responses to variation in mean near-bed velocities ($U_{15\,\mathrm{mm}}$) in stalked-short filamentous diatom communities in the Cust River, New Zealand. (Reproduced from Biggs et al. 1998.)

scouring agents, a moss was found to cover a high percentage of surface only for stones larger than ~ 400 cm^2 (Figure 6.12). Evidently, smaller stones in this system are too unstable for extensive moss cover to accumulate (McAuliffe 1983). Bryophyte abundance also was associated with stable substrates in a Tennessee woodland stream (Steinman and Boston 1993). Benthic algal species richness declined following flooding in New Zealand streams that received high sediment inputs and had mobile beds, but floods had no effect in streams with an armored substrate (Biggs and Smith 2002). Algal taxon richness did not correlate with time post disturbance in streams that experienced frequent, bed-moving flood events, whereas a positive relationship was observed in streams where such floods were less frequent. Biggs and Smith (2002) proposed that initial recovery of benthic algae proceeds rapidly (within 1 week) and

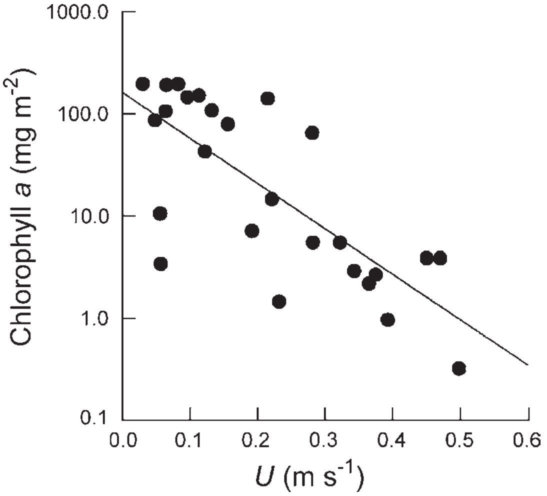

FIGURE 6.11 Chlorophyll *a* responses to variation in water column velocities (U) in long filamentous green algal communities in the Waiau River, New Zealand. (Reproduced from Biggs et al. 1998.)

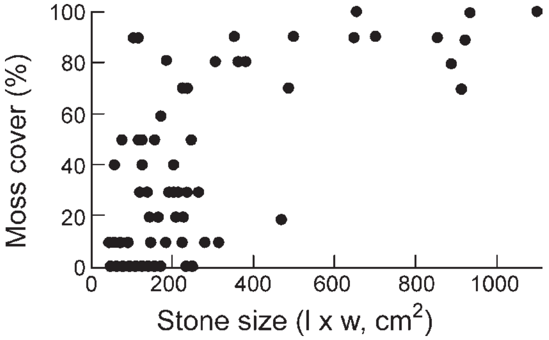

FIGURE 6.12 Amount of stone surface covered by the moss *Hygrohypnum* as a function of stone size in a mountain stream. (Reproduced from McAuliffe 1983.)

involves taxa with high tolerance to disturbance as well as taxa with high reproduction and immigration rates. Subsequently, taxa appear that are less resistant to flood disturbance and have lower rates of immigration and growth. The duration of this second phase (one to several months) is more variable among streams because it is more susceptible to resource supply, which likely varies among streams.

6.1.1.4 Substrate

Substrate, either living or nonliving, provides a surface for benthic algal growth where physical and chemical conditions differ from the surrounding water (Burkholder 1996). The physical structure and the stability of the substrate may influence algal colonization. Algae that grow into large mats are usually found on larger stones, while small, motile algae colonize sediments and small particles (Burkholder 1996). In streams of Eastern Ontario and Western Quebec, Canada, finer substrates were dominated by motile diatoms and cyanobacteria, whereas prostrate and filamentous algae occurred on larger substrata (Cattaneo et al. 1997).

Microbial conditioning of substrates can influence algae colonization, resulting in higher algal colonization when biofilm development or bacterial abundance is greater (Hodoki 2005). Peterson and Stevenson (1989) found that diatom colonization was enhanced by conditioning of the substrata with a nonalgal biofilm, although the result was observed only in fast currents, and reversed in slow currents. Steinman and Parker (1990) suggest that substrate conditioning has a short-term influence on benthic algal growth and probably is more important in streams with high frequency of disturbances. Nutrients and other aspects of the chemical environment may vary with substrate conditions, particularly for epipelic and epiphytic populations, but perhaps also for epilithic taxa on occasion, depending on the chemical characteristics of the stone (Burkholder 1996).

6.1.1.5 Temperature

By influencing algal growth rates, temperature affects the biomass and production of benthic algae, and because species may differ in their responses, temperature also can alter assemblage composition. Major divisions of algae show a trend to dominate in different temperature ranges: diatoms between 5°C and 20°C, green and yellow-brown algae between 15°C and 30°C, and cyanobacteria above 30°C, although this is by no means a universal pattern (DeNicola 1996). Seasonal changes in the taxonomic composition of benthic algal assemblages are observed in temperate rivers, and warmer temperatures probably are partly responsible for the greater representation of green algae and cyanobacteria during summer months. By assembling data on primary productivity for stream periphyton as well as lake and ocean phytoplankton, Morin et al. (1999) developed empirical models to predict primary production from chlorophyll *a* and water temperature. Although production was lower in stream periphyton than in lake or marine phytoplankton, presumably because of reduced nutrient diffusion into algal mats, production was more strongly related to water temperature in stream periphyton than for phytoplankton of either lakes or oceans.

6.1.1.6 Grazers

Numerous studies provide strong evidence of the important influence of grazers on benthic algae in fluvial ecosystems (Feminella and Hawkins 1995). Grazers can reduce algal biomass and influence community composition by selectively eliminating certain species and growth forms (Steinman 1996, Rosemond et al. 2000), and also can affect nutrient content and diversity (Poff and Ward 1995, Hillebrand et al. 2004). Regulation of algal biomass by grazing invertebrates and fishes has been reported in a number of instances, often with evidence of an interaction between the effects of grazers and nutrients (Hillebrand 2002). From a literature survey of 85 experiments that examined herbivore presence and nutrient supply, Hillebrand (2002) found that both had strong influence, and grazer effects were greater than nutrient effects. Manipulation of nutrients and grazing snails (*Elimia clavaeformis*) in Walker Branch, Tennessee, showed that algal species most reduced by herbivores were those that increased most in response to nutrient addition, and vice versa, suggesting a trade-off between resistance to herbivory and nutrient-saturated growth rates (Rosemond et al. 1993). Grazed communities were dominated by chlorophytes and cyanobacteria, which were overgrown by diatoms when herbivores were removed. Flecker et al. (2002) observed strong effects of both N addition and herbivorous fishes on algal standing crop in a tropical river, but consumer limitation was found to be considerably stronger than resource limitation in influencing algal biomass and composition. Hydrologic variability is an important mediator of grazer–algal–nutrient interactions. Algal biomass is more responsive to nutrients in frequently scoured streams, whereas in more stable streams grazers can suppress algae regardless of nutrient concentration (Riseng et al. 2004). This growing body of experimental evidence that argues convincingly for strong interactions between herbivores and algal communities in lotic ecosystems will be described in greater detail in Chapter 9.

6.1.2 Temporal and spatial variation in benthic algae

The interaction of the multiple environmental factors just discussed is responsible for the diverse temporal and spatial patterns observed in algal composition and biomass. Temporal patterns fall into three categories (Biggs 1996): (1) relatively low but constant biomass when disturbance is frequent; (2) cycles of accumulation and loss when disturbances are less frequent; and (3) seasonal cycles owing to seasonal change in the environmental factors discussed above. Spatial variation is likewise associated with locational differences in controlling variables, for example, between riffles and pools and among streams differing in size and landscape position.

Seasonal abundance data from the tropics are few, but numerous studies of stony streams from Europe, Japan, and North America suggest a fairly regular seasonal pattern in temperate streams. Diatoms dominate during winter and continue to be a major component of the flora in spring and early summer, although the species composition changes. Other groups can become abundant during summer, particularly green algae and cyanobacteria.

In temperate rivers, total abundance and biomass generally is greatest in the spring, and a secondary peak can occur in autumn. In streams of Tennessee, daily chlorophyll-specific primary production peaked in the spring, and then chlorophyll concentrations decreased after leaf emergence, reached a minimum in summer due to shading and then increased again in the autumn. In these rivers, seasonal changes were primarily related to changes in light availability (Hill and Dimick 2002). In streams of Hubbard Brook Experimental Forest, New Hampshire, both light and N concentrations are higher in the spring before leaf-out, which likely explains higher biomass accrual rates in spring compared to summer and autumn (Bernhardt and Likens 2004). A factorial manipulation of grazers, nutrients, and irradiance demonstrated how factors limiting periphyton can change seasonally (Rosemond et al. 2000). Periphyton biomass was limited by light in fall and summer but not in spring, while nutrients limited periphyton when light availability was higher.

In tropical rivers, seasonality in hydrology can be important. In the Daly River, northern Australia, annual variation in benthic algae biomass is primarily controlled by seasonal changes in flows (Townsend and Padovan 2005). During the dry season, low velocities favored the colonization and growth of *Spirogyra*, which appeared in the river in mid-May, increased in biomass through July and August, and disappeared from the river at the beginning of the wet season in late October or early November (Figure 6.13). The frequent high flow disturbances that occurred during the wet season probably limited the colonization and growth of *Spirogyra*, primarily due to abrasion and dislodgment.

The spatial distribution of benthic algae at both reach and river basin scales reflects spatial patterns in environmental variables. A conceptual model of the control of periphyton biomass and composition in unshaded temperate streams considers flood disturbance and nutrient limitation to be the primary controls, and grazing is an important factor in stable systems (Biggs et al. 1998). Under low nutrient supply and stable flood conditions, this model predicts periphyton mats of low to medium biomass, dominated by green algae, cyanobacteria, red algae, and diatoms, mostly with filamentous and erect forms and small to medium cell size. In environments with high nutrient availability and low flows, filamentous algae with medium to large cells that form high biomass mats will be most abundant. In locations with moderate to unstable flood conditions and variable nutrient supply, taxa that colonize denuded habitats, like diatoms, will dominate. Grazers are an important factor controlling periphyton biomass and composition in locations with stable flow, primarily because larger and more effective grazers such as caddis flies and snails prefer habitats with slow current. Where the frequency of flooding is higher, mayflies dominate but appear less able to control periphyton.

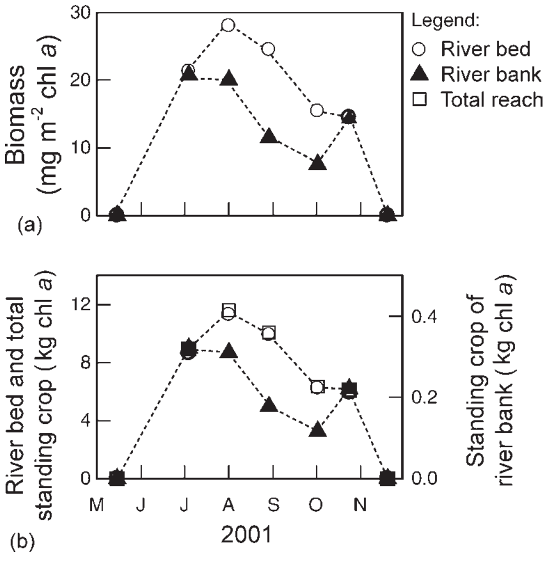

FIGURE 6.13 Seasonal variation in *Spirogyra* (a) biomass and (b) standing stock on river bed, river bank, and total reach along 17.5 km of the Daly River, Australia. (Reproduced from Townsend and Padovan 2005.)

6.1.3 Primary production by benthic algae

Autotroph primary production is measured by gas exchange or ^{14}C uptake in benthic chambers or by open stream gas exchange. Within closed benthic chambers, a stone with benthic algae or an enclosed area of substrate is incubated over time, so that both photosynthesis and respiration influence changes in oxygen levels during the day, whereas only respiration takes place at night. A pump circulates the water within the chamber to simulate current. Respiration (R) is estimated from the decline in oxygen concentrations that occurs in the dark, based on night measurements. Net primary production (NPP), which is the difference between photosynthetic release of oxygen and its consumption by respiration, is estimated from any change in oxygen during the day. Gross primary production (GPP) due to photosynthesis is the sum of R, estimated from night measurements, and NPP, estimated from day measurements (Bunn et al. 1999, Bott 2006).

Open stream gas exchange uses 24 h changes in O_2 within the stream itself to estimate NPP (during the day) and respiration (during the night), and so has the advantage of estimating rates of photosynthesis and respiration for the whole ecosystem (Lamberti and Steinman 1997).

This method includes not only the primary production of benthic algae, but from all submerged autotrophs in the stream. Originally applied to a highly productive spring (Odum 1956), the challenge is to accurately measure changes in oxygen concentrations due to biological activity in systems where production may be low and gas exchange due to turbulence is high. Methods to estimate diffusion between air and water include the use of upstream and downstream oxygen recorders to measure changes in oxygen concentration along the reach, and direct measurement of the reaeration coefficient by injecting a gas (propane) into the water column and measuring its release to the atmosphere (Marzolf et al. 1994, Mulholland et al. 2001). The single-station method is preferred for sites with low turbulence and high primary production while the two-station method is more accurate in fast-flowing water with low primary production (Young and Huryn 1998).

Both methods pose technical difficulties and require assumptions that are difficult to check. Nighttime oxygen fluxes are assumed to represent 24 h respiration. Respiration rates include microbes and other organisms in addition to the algae, which complicates the interpretation of GPP and NPP (discussed further in Section 12.4.2). In using benthic chambers, care must be taken to simulate current and irradiance appropriately and to avoid unnatural changes in nutrient and gas concentrations, including the formation of bubbles (Bott et al. 1997). In addition, benthic chambers can only be used with substrate of a certain size range, raising questions concerning how well they represent average conditions (Bott 2006).

Although not currently in use for stream benthic algae, the pulse-amplitude modulating (PAM) fluorometer has the potential to provide a noninvasive and compact method to measure photosynthetic rates in streams. Fluorescence correlates well with CO_2 uptake in higher plants, although for algae the relationship appears more variable (Gilbert et al. 2000, Jakob et al. 2005). However, the recent demonstration that fluorescence correlates well with photosynthesis measured under light limitation and nutrient saturation conditions for periphyton and phytoplankton suggests that fluorescence has the potential to become more widely used to estimate primary production in the future (Toepel et al. 2004).

Estimates of benthic algae primary production are relatively few, owing to the difficulty and expense of its measurement. Tentatively, it appears that maximal daily NPP in deciduous biome studies ranges from below 0.01 to $\sim 0.1\,\mathrm{g\ C\ m^{-2}\ day^{-1}}$ in shaded areas (Elwood and Nelson 1972, Hornick et al. 1981, Minshall 1967, Acuña et al. 2004), whereas values from 0.25 to $\sim 2\,\mathrm{g\ C\ m^{-2}\ day^{-1}}$ are common at sites where the canopy is open (Berrie 1972a, Bott 1983, Hill and Webster 1982, McDiffett et al. 1972, King and Ball 1966, Sumner and Fisher 1979, Mulholland et al. 2001). These values are consistent with estimates from laboratory streams provided with adequate light, where GPP was between 2.4 and $6\,\mathrm{g\ C\ m^{-2}\ day^{-1}}$, and NPP typically was slightly more than one half of GPP (McIntire and Phinney 1965). Estimates from streams flowing through grasslands (Prophet and Ransom 1974), in arid regions (Minshall 1978, Fisher et al. 1982, Mollá et al. 1996, Mulholland et al. 2001, Velasco et al. 2003), and open coniferous biome streams (Thomas and O'Connell 1966, Wright and Mills 1967) appear to give maximal values between 1 and perhaps $18\,\mathrm{g\ C\ m^{-2}\ day^{-1}}$ in systems receiving ample sunlight. Some very productive flowing water systems are reported to achieve daily GPP approaching $20\,\mathrm{g\ C\ m^{-2}\ day^{-1}}$ (e.g., Odum 1956, Duffer and Dorris 1966, Mulholland et al. 2001). Thus, estimates of daily primary production vary among sites, seasons, biomes, and climatic regions by as much as three orders of magnitude (Lamberti and Steinman 1997).

The river continuum concept (RCC) predicts that primary production will be lowest in forested headwaters, increase in more open, midsized rivers, and decline in turbid, higher-order segments (Vannote et al. 1980). This expectation is supported by higher estimates of primary production in unshaded as compared to shaded stream reaches, as just described. Estimates of GPP for 30 streams of order 1–7 located mainly in the northern hemisphere found that catchment area was the single best predictor, presumably because production responded to higher light levels and nutrient concentrations as rivers increased in size (Lamberti and Steinman 1997). There seems little doubt that periphyton production will decline in large, turbid rivers, because scant light reaches the river bed and stable substrate may be lacking as well. However, phytoplankton and macrophyte production tend to increase in the downstream direction, and so it is difficult to say how overall system production varies across rivers of order >7.

An ambitious effort to evaluate the RCC measured primary production over a range of stream sizes in four distinct biomes of the United States (Minshall et al. 1983). Each stream system was located in a relatively undisturbed catchment, had as its uppermost station a forested headwater site, and took for its lowermost station the largest stream site that was relatively undisturbed (seventh order). Oregon sites receive abundant precipitation, mostly as winter rain, and support dense conifer forests. Idaho sites lie in a cold arid region of the northern Rocky Mountains, where forest cover is less than other biomes and runoff is dominated by melt of the winter snowpack. Coniferous forest and scattered deciduous tree species are found at upper elevations, and sagebrush or grass vegetation at lower elevations. Michigan and Pennsylvania sites are in the eastern deciduous biome, with less-pronounced seasonality in precipitation and runoff than either of the western sites. Observed variation in the standing crop of periphyton among sites, seasons, and locations was consistent with what is known of the various factors that limit algae. GPP was lowest at the heavily forested Oregon sites, usually increased in the downstream direction, and was lowest in winter.

6.1.4 Fate of benthic primary production

Most periphyton production in flowing waters likely is consumed by herbivores or enters the pool of particulate detritus, either locally or after downstream transport. In addition, cells at times exude organic compounds, and these constitute inputs to the pool of dissolved organic carbon (DOC), although they are relatively small compared to allochthonous DOC sources. A complete reckoning of these quantities is not possible at present, but their inclusion should serve to emphasize that grazing of living plants is not the only fate of plant production.

Substantial downstream transport of sloughed periphyton has been observed in the laboratory and the field. In their year-long study of periphyton dynamics in laboratory streams, McIntire and Phinney (1965) recorded considerable export, particularly of filamentous green algae under higher light conditions and during periods of high turbidity of the inflowing water. Sycamore Creek, Arizona, was found to be a net exporter of organic matter during a 63-day recovery between floods (Fisher et al. 1982). Of the 56% of NPP not utilized at the site of production, the major amount was exported downstream and a smaller portion was stranded laterally by drying. Based on experiments conducted in laboratory streams exposed to different irradiance (20, 100, and 400 μmol m^{-2} s^{-1}) and grazing levels (240 snails m^{-2} or no snails), Lamberti et al. (1989) found that increased irradiance and grazing both enhanced algal export. At the highest irradiance algal export represented 72% of total algal biomass in ungrazed streams and 84% of the biomass in grazed streams, while under low irradiance, exports were only 7–24% of total biomass.

Energy budgets constructed for periphyton populations in laboratory streams demonstrate that substantial quantities of dissolved and colloidal matter may be exuded by live cells. Energy budgets (GPP should equal respiration + biomass accumulation + biomass export) revealed a discrepancy of 17–28% (McIntire and Phinney 1965), indicating a substantial export term, which the authors attributed to dissolved matter. Extracellular release by periphyton in White Clay Creek, Pennsylvania, was found to dominate DOC dynamics and resulted in a pronounced daily cycle in DOC concentrations at certain times of the year (Kaplan and Bott 1982). Particularly in the spring, when periphyton biomass was maximal, allochthonous inputs were few and discharge was low, extracellular release by autotrophs was estimated to account for as much as 20% of daily DOC export. Clearly, a substantial fraction of GPP can be exported as DOC under circumstances of high primary production.

6.2 Macrophytes

Flowering plants, mosses and liverworts, a few species of encrusting lichens, the Charales, and other large algal species constitute the macrophytes of flowing waters (Hynes 1970). Most groups can also be found in standing water, but as one proceeds to faster flows the flora becomes restricted to the small number of species able to withstand current. Taxa almost entirely restricted to very fast currents include two flowering plant families of the tropics: Podostemaceae and Hydrostachyaceae, and a number of bryophytes (Westlake 1975a). Macrophytes exhibit few adaptations to life in flowing water and are most successful in slow currents and backwaters. Certain characteristics permit establishment and maintenance of populations in appreciable current. Tough, flexible stems and leaves, firm attachment by adventitious roots, rhizomes or stolons, and vegetative reproduction typify most macrophytic species. However, Podostemaceae and Hydrostachyaceae of tropical torrential rivers possess aerial flowers and sticky seeds, and so are able to reproduce sexually.

Macrophytes can be classified according to their growth form, their manner of attachment, and even more specifically by the range of environmental conditions that a species inhabits. Four major growth forms are recognized by Westlake (1975a). Emergents occur on river banks and shoals. They are rooted in soil that is close to or below water level during much of the year, and their leaves and reproductive organs are aerial. Floating-leaved taxa occupy margins of slow rivers, where they are rooted in submerged soils. Their leaves and reproductive organs are floating or aerial. Free-floating plants usually are not attached to the substrate and can form large mats, often entangled with other species and debris, in slow tropical rivers. Submerged taxa are attached to the substrate, their leaves are entirely submerged, and they typically occur in midstream unless the water is too deep.

Particular species occur in specific habitats based on growth form and attachment characteristics, as well as other environmental factors. Bryophytes occur worldwide in relatively cool streams and characteristically are found in headwater regions, associated with high currents, high substrate stability, and low light (Bowden 1999). In a woodland stream in Tennessee, a liverwort and two mosses were the most abundant bryophytes. Whole-system photosynthesis was similar between bryophytes and periphyton in late summer and fall, but greater by periphyton in spring as the algae responded to increased irradiance (Steinman and Boston 1993). Along with some angiosperms, bryophytes are unable to use bicarbonate and require free CO_2, which is most available in turbulent soft waters. A combination of harder water and slower current allows rooted plants to become established, with a corresponding decline of bryophytes (Westlake 1975a). In longitudinal view, therefore, one expects the macrophyte assemblage to exhibit a downstream succession from bryophytes to freshwater angiosperms such as *Ranunculus*, to flowering plants such as *Potamogeton* and *Elodea* that are typical of slower and more fertile waters, to emergent and floating-leaved plants in the slowest and deepest sections. In rivers of

Southern Germany, bryophytes dominated shaded and fast-flowing streams while vascular plants and charophytes were more common in sites with slower current and higher light incidence (Passauer et al. 2002).

Macrophytes play an important role in lotic systems for both invertebrates and fish as habitat (Humphries 1996, Bowden 1999) and as refuge from predators (Grenouillet et al. 2000, Harrison et al. 2005). Macrophytes also may increase habitat heterogeneity for aquatic organisms by modifying water velocity across the stream channel and increasing its range of variation, including the provision of low flow areas (Champion and Tanner 2000). By slowing the current, macrophytes can trap sediments (Schulz et al. 2003) and particulate organic matter (Horvath 2004). However, these effects likely vary among macrophyte species, as Sand-Jensen (1998) reported for *Callitriche cophocarpa* and *Sparganium emersum* in Danish streams. *C. cophocarpa* forms a dense canopy whereas *S. emersum* has long and flexible leaves and forms more open patches. Current velocity decreased markedly near the bed of *C. cophocarpa*, which enhanced the accumulation of fine sediments and elevated the substrate surface (Figure 6.14). In contrast, the open canopy of *S. emersum* had less effect on current velocity, sediment composition, and topography. Organic matter and nutrient enrichment in the sediments was also higher in *C. cophocarpa* than in *S. emersum* patches, emphasizing that macrophytes should not be viewed as a homogenous ecological unit.

6.2.1 Limiting factors for macrophytes

In contrast to land, where coverage of the soil surface by vegetation often is near 100%, only a small percentage of the streambed supports growth of higher plants. As Hynes (1970) points out, aquatic botanists have an understandable bias toward studying areas where plants are fairly abundant. Even so, studies of macrophyte production in two midsized Appalachian rivers estimated cover between 27% and 42% (Hill and Webster 1983, Rodgers et al. 1983), and in Bavarian streams 37% of the area studied was found to have <10% cover (Gessner 1955). In a small Danish lowland stream, the combined area of *C. cophocarpa* patches covered up to 70% of the streambed. The remaining area apparently was unsuitable habitat due to a strong shear effect and coarse substrate that limited the growth of the plant (Sand-Jensen et al. 1999). Clearly, the amount of macrophyte cover varies enormously with locale, and in many stream habitats macrophytes are of little importance.

Where macrophytes do occur, the growing season can be quite long if water temperatures stay above freezing throughout winter. In British rivers, many species simply grow slowly or cease growth during winter, although others, emergent plants in particular, shed leaves and die back to rhizomes and stolons (Hynes 1970). In tropical waters there likely is little seasonality to growth, unless due to changes in river flow.

Hardness of water, or its correlates including calcium, alkalinity, and pH, influences the distribution of particular macrophyte species and also limits the occurrence of bryophytes, probably by affecting the availability of free CO_2. Indeed, the flora of British rivers can be reasonably categorized on the basis of hardness, current, and substrate with the result that certain taxa are regularly associated with particular environmental conditions (Hynes 1970).

Current and high-flow events strongly influence the presence of macrophytes. Riis and Biggs (2001) reported a negative correlation between macrophyte abundance and frequency of flood disturbance in unshaded streams of New Zealand. Similarly, the biomass of *Najas* in a fluvial pool of an intermittent stream in Brazil declined after floods, and larger floods resulted in longer periods before recovery of lost biomass took place. Where floods are frequent, common species may produce many propagules, an adaptation for recolonization (Maltchik and Pedro 2001).

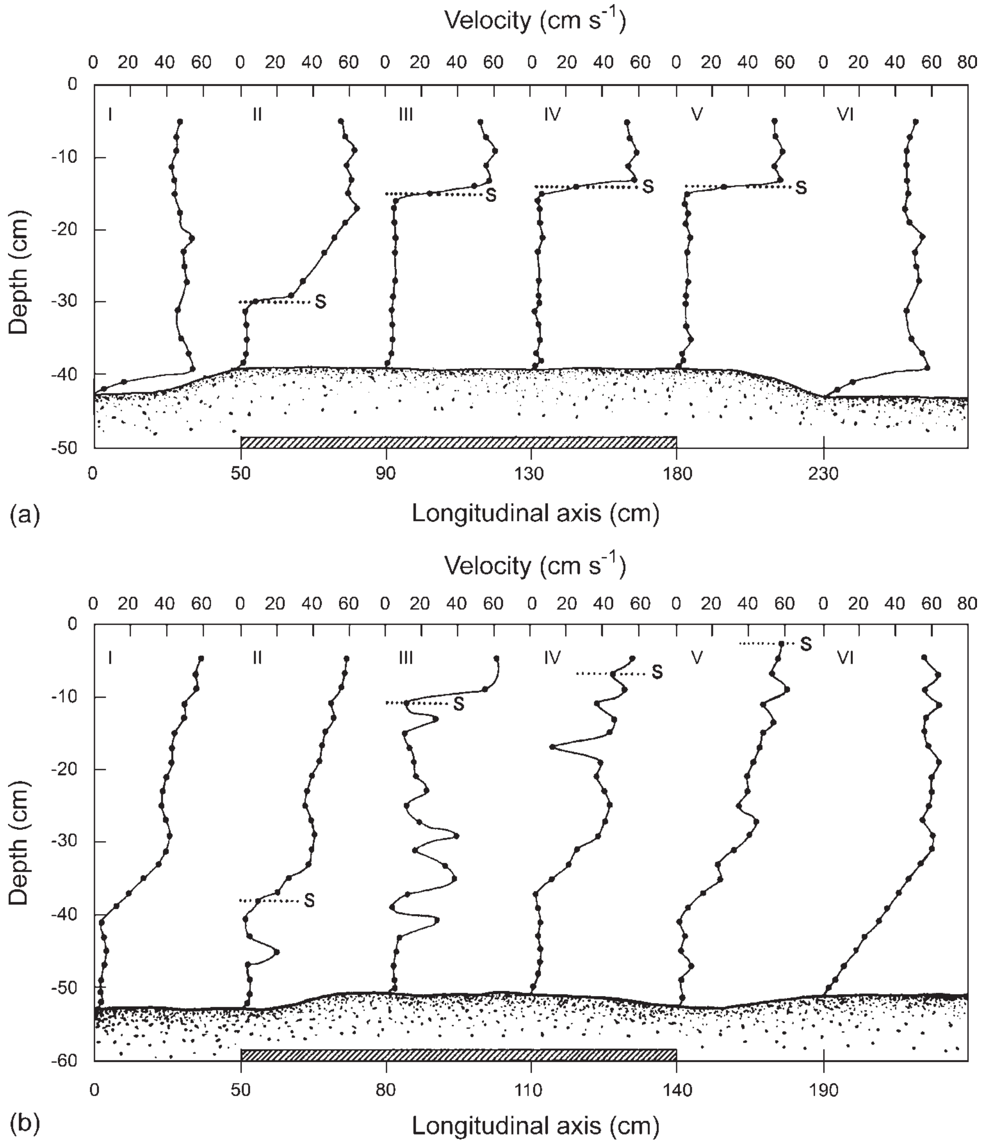

FIGURE 6.14 Vertical velocity profiles along a transect passing through the center of patches of (a) *Callitriche cophocarpa* and (b) *Sparganium emersum*. Velocity was measured at six positions: upstream from the patch (I), within the patch (II–V), and downstream from the patch (VI). The hatched line on the *x*-axis denotes the patch length, and the location of patch surface (S) is also shown. (Reproduced from Sand-Jensen 1998.)

Along with current, light is one of the most important factors limiting macrophytes. Heavy shade results in complete exclusion of angiosperms, prompting Bunn et al. (1998) to attempt to use shading as a control of an invasive aquatic macrophyte in Northern Australia. When light levels in the stream channel were reduced by 50% and 90% using shade cloth, plant biomass decreased significantly. The largest effect was observed under 90% shading, which reduced plant biomass by half. Light also attenuates with depth, which inhibits the establishment of macrophytes in deeper rivers, although the precise depth at which photosynthesis can no longer balance respiration varies with turbidity and species-specific light requirements. Some very turbid tropical rivers lack higher plants for this reason.

Major plant nutrients, particularly P but possibly N and potassium, can be limiting in nutrient-poor waters such as mountain streams. Lowland rivers, which often provide the most suitable flow and habitat conditions for macrophytes, typically are nutrient enriched due to human activities. Although a positive relationship between nutrients and macrophyte biomass has been shown in some rivers and streams (Chambers et al. 1991, Carr and Chambers 1998), other lotic systems have not shown such relationships (Peltier and Welch 1969, Kern-Hansen and Dawson 1978, Canfield and Hoyer 1988). Potential explanations for not observing a strong association between macrophyte growth and nutrients could be related to the influence of other factors including light (Canfield and Hoyer 1988), sediment type and texture (Barko et al. 1991), herbivory (Lodge 1991), or current velocity (Chambers et al. 1991), which could confound the association with nutrients. The relationship between nutrients and macrophytes is also influenced by macrophyte growth form because the latter determines the primary nutrient sources for the plants. In the case of rooted macrophytes, sediment N and P may be a better predictor of growth than water nutrient concentration because these plants acquire nutrients primarily from the sediments (Barko et al. 1991, Rattray et al. 1991, Carr and Chambers 1998).

Herbivory on freshwater macrophytes generally has been viewed as unimportant in limiting their growth and abundance (Hutchinson 1981). However, Nystrom and Strand (1996) showed that crayfish can have a strong negative impact on macrophyte biomass. Terrestrial herbivores feed on emergent vegetation, some river-dwelling vertebrates including waterfowl, manatees, and grass carp (see Chapter 9) consume submerged aquatic macrophytes, and others such as muskrats harvest plant material for construction of lodges (Westlake 1975b). However, few representatives of the major groups of aquatic invertebrates are able to graze on macrophytes until after death and decomposition of the plant. Interestingly, some insects are effective herbivores, but these are species phylogenetically allied with families and orders of insects that are primarily terrestrial (Newman 1991). Some of these herbivorous insects are successful agents of biological control, as is the manatee, against waterweeds that in many areas pose a serious nuisance.

6.2.2 Macrophyte production and its fate

Estimates of NPP indicate a maximum NPP of roughly $3\,\mathrm{g\ C\ m^{-2}\ day^{-1}}$ for submerged macrophytes compared to ~ 10–$20\,\mathrm{g\ C\ m^{-2}\ day^{-1}}$ for emergents, and with somewhat higher values in tropical compared to temperate environments (Westlake 1975b). Macrophyte primary production is generally estimated from biomass accrual over time. Macrophyte production generally is highest in rivers of medium size where light is ample, current is moderate, turbidity is low, and strong fluctuations in depth and discharge are minimal. Even in circumstances that favor their growth, macrophytes generally contribute only a small fraction of the total energy base (Fisher and Carpenter 1976). In a Mediterranean stream, for example, macrophyte production represented, on average, 8.9% of the reach GPP (Velasco et al. 2003). Exceptions include ditches and canals in fertile regions, as well as marshes and river mouths, where macrophytes may occupy virtually all available habitat.

The possible fates of macrophyte production include consumption as living tissue, secretion of dissolved organic matter, and decomposition. Very little is consumed as living plant biomass.

Exudates of DOC likely benefit epiphytic autotrophs and heterotrophs, and in addition an unknown amount enters the downstream pool of DOC. Wetzel and Manny (1971) suggest as a conservative estimate that 4% of GPP of macrophytes in lakes is released as exudate. The majority consists of labile compounds of low molecular weight. Experimental addition of DOC leached from alligator weed *Alternanthera philoxeroides* to Ogeechee River water (Findlay et al. 1986a) and from *Vallisneria americana* to Hudson River water (Findlay et al. 1992) increased bacterial production and yielded higher growth efficiency than did controls, suggesting that some macrophyte C is retained in microbial biomass.

The principal fate of macrophytic primary production is to enter the detritus food chain (Polunin 1984). In addition to seasonal dieback of plants, up to 50% of new biomass is lost during the period of growth (Westlake 1975a). Because macrophytic detritus is of relatively high quality, and appears when summer periphyton might be waning and prior to autumnal leaf fall, Hill and Webster (1983) argued that these inputs may be of greater importance to consumers than would be anticipated solely from the quantity produced. In support of this suggestion, a study of decomposition of aquatic macrophytes in the Atchafalaya River Basin, a large floodplain river in southern Louisiana, found amphipods and mayflies to be abundant on macrophyte detritus in fall and winter, and microbial respiration rates were high (Battle and Mihuc 2000). There is evidence, however, that food chains in the Amazon and Orinoco floodplain are fueled by phytoplankton and periphyton rather than by macrophytes, despite the abundance of the latter in these systems (Araujo-Lima et al. 1986, Hamilton et al. 1992).

6.3 Phytoplankton

The phytoplankton are algae suspended in the water column and transported by currents. Whether a river phytoplankton could be self-sustaining was in doubt for some time, because downstream flow would seem to prevent the persistence of their populations. It was suggested that any river plankton was the result of displacement of cells from the benthos, backwaters, and lakes or impoundments along the river's course, and reflected washout and export rather than a true "potamoplankton." These are indeed major sources of phytoplankton in rivers. In small, fast-flowing streams, sloughing of benthic algae likely is the primary source of phytoplankton, and any cells in the water column are simply eroded material in transit (e.g., Swanson and Bachman 1976). However, in sluggish, lowland streams, in side channels and within macrophyte beds, and in rivers of considerable length, the residence time of a water mass can be sufficient for true plankton to colonize and reproduce. Under these conditions phytoplankton and zooplankton almost always are present, and at times they can develop substantial populations.

It is doubtful that any planktonic organisms are restricted only to flowing water, and so the phytoplankton species found in rivers are drawn from the same pool of species found in standing water. Thus, the presence of lakes, ponds, and backwaters, and more recently the creation of impoundments, can be of great importance in seeding the river with plankton. Diatoms, particularly centric diatoms, have been found to dominate the composition of river phytoplankton in a number of studies (Mississippi, Baker and Baker 1979; Nile, Talling and Rzoska 1967; Thames, Lack 1971; Nakdong, Ha et al. 1998; Lower Paraná, O'Farrell et al. 1998; Columbia, Sullivan et al. 2001; San Joaquin, Leland 2003). A 300-mile section of the Sacramento River recorded 15 genera of cyanobacteria, 38 genera of chlorophytes, 13 flagellate genera, and 29 diatom genera (Greenberg 1964). Diatoms dominated numerically, however, averaging 75% and occasionally 99% of cell counts. In tropical rivers, desmids (a green alga) have the largest number of species while diatoms dominate the biomass, although to a lesser degree than in temperate rivers (Rojo et al. 1994). In the Baia River, a tributary of the Paraná, cyanobacteria and diatoms dominate phytoplankton biomass, whereas chlorophytes contribute the most species (Train and Rodrigues 1998). In the Orinoco River, diatoms, flagellates, and cyanobacteria dominate the phytoplankton (Lewis 1988). Cyanobacteria have been reported to form dense blooms in the Nile and during summer in temperate rivers (Talling and Rzoska 1967, Bennett et al. 1986), apparently in response to nitrate depletion. These studies establish that phytoplankton occur in virtually all major rivers examined. They are present throughout the year, even when not apparent, as Sze (1981) demonstrated by collecting samples of Potomac River water from which he successfully cultured several major phytoplankton groups. Interestingly, the order of appearance in culture was centric diatoms, then chlorococcolean green algae, then pennate diatoms, and finally the cyanobacteria, which paralleled their seasonal appearance in the river.

Variation in temperature, light availability, nutrients, and discharge influence seasonal variation in phytoplankton abundance. In temperate rivers, abundance is greatest in spring and summer (Aliakmon River, Greece, Montesanto et al. 2000; Columbia River, the United States, Sullivan et al. 2001; St. Johns River, Florida, Phlips et al. 2000). In the Columbia River, higher nutrient levels, lower flows, and higher light availability probably favor diatom abundance during the spring. In the St. Johns River, seasonal variation is related to light availability, which is primarily influenced by the color of the water. Less color and lower light attenuation are observed during spring and summer, and these conditions correspond with greatest abundance of phytoplankton. In tropical rivers, phytoplankton abundance responds to hydrologic seasonality, and is higher during periods of low water. In the Orinoco River and some of its tributaries, highest production and biomass of phytoplankton was observed during the periods of falling and low water, probably related to greater transparency, shallower depths, and lower flows (Lewis 1988). In the Baia River, phytoplankton biomass also peaked during low water and was dominated by heterocystous cyanobacteria. This was followed by an increase in diatoms, probably favored by an increase in rainfall and turbulence (Train and Rodrigues 1998).

6.3.1 Limiting factors for phytoplankton

Factors affecting the growth of phytoplankton in running waters include all the same variables that limit algal growth in lakes, such as light, temperature, and nutrients. However, discharge regime has a profound influence over river phytoplankton, and the influence of light and nutrients differ in some ways from what is seen in standing waters. In addition, adjacent stagnant waters are critical to the establishment of river phytoplankton, through their influence upon the size of the inoculum. This can be of considerable importance, especially when residence time of the water mass is short enough to limit the buildup of populations.

An inverse relationship between river discharge and phytoplankton abundance is perhaps the most common finding of detailed investigations of river phytoplankton (Décamps et al. 1984, Filardo and Dunstan 1985, Sullivan et al. 2001). As a mass of water moves downstream and the entrained plankton multiply, one expects maximal abundances to be associated with a water mass that is traveling slowly and is uninterrupted over a long distance. Talling and Rzóska (1967) estimated that a water mass traversed the 357 km section of the Blue Nile between Sennar Reservoir and Khartoum in 40 days at low flows, but required only 2 days at high flood. Since phytoplankton populations are capable of a maximum of about 1–2 doublings per day, the consequences for eventual population size are considerable.

Using a data set that included 345 sites on large rivers and 812 lakes and impoundments within the continental United States, Søballe and Kimmel (1987) concluded that rivers and lakes occupy two ends of a continuum, and impoundments fall in-between. Along the gradient from rivers to impoundments to lakes, residence time increased (mean values of 18.4, 528.5, and 1073.5 days, respectively), transparency increased, total P declined, and phytoplankton counts increased severalfold. Interestingly, water residence time appeared to act as a threshold factor, being of great importance at values <75–100 days, and of little importance when residence time was longer.

Although the usual effects of high flows are dilution and downstream transport, under certain circumstances floods might augment river plankton by washing in populations from stagnant areas. The lower Orinoco and several of its tributaries comprise a large tropical river system with fringing floodplain regions that are in contact with the river for up to 180 days in wet years. Lewis (1988) found that primary production per unit volume was greatest during the period of low water, but nonetheless was quite low, due to a combination of light limitation and the short residence time of river water. Total phytoplankton transport exhibited a minimum just as discharge began its seasonal increase and was maximal at high water. Lewis concluded that flushing of backwaters in or adjacent to the river channel accounted for increased transport during the rise of flood waters, and the floodplain contributed phytoplankton during the flushing and draining periods associated with peak and declining flood stages.

In a large river with ample nutrients and a transit time long enough to permit multiplication of phytoplankton, it is likely that the phytoplankton is limited by light via interactions among turbidity, depth, and turbulence. If the water column mixes to a depth greater than the photic zone, then an individual cell will spend part of the day at light levels too low to support photosynthesis (Figure 6.15). Cole et al. (1991) estimated that the average phytoplankton cell in the Hudson River would spend from 18 to 22 h below the 1% light level. Rather than growing, the cell would be expected to lose biomass. This is a real puzzle, because phytoplankton biomass does increase during the spring and summer. One possible explanation is that phytoplankton blooms originate only in river sections <4 m in depth (Cole et al. 1992). Similarly, Lewis (1988) reasoned that the bulk of phytoplankton biomass transported in the lower Orinoco system originates from stagnant waters in or adjacent to the channel, because once in the main channel, phytoplankton spent too little time at light levels sufficient for growth.

Turbidity and depth of mixing will of course vary from place to place and with seasons, greatly affecting the opportunities for growth of phytoplankton populations. Phytoplankton productivity was suppressed to a greater degree in the whitewater Apure River than in the blackwater Caura River, corresponding to differences in light penetration (Lewis 1988). Depth of the euphotic zone varies seasonally with the sediment load, and also due to self-shading when phytoplankton are abundant. In the Lot River of south-central France, the maximum depth at which photosynthesis can occur ranges between 0.7 and 5.3 m (Décamps et al. 1984), depending upon season. In the Blue Nile, passage of the flood crest reduces Secchi disk readings to zero (Rzóska et al. 1952). Reservoirs usually enhance the conditions for phytoplankton growth because greater water clarity results from settling of sediments. Under these conditions, self-shading by the plankton replaces sediments in suspension as the principal limitation to light penetration.

Nutrient limitation of river phytoplankton does not appear to be usual in free-flowing rivers. Downstream transport and light typically are overriding variables, and nutrient concentrations in rivers, and especially in lowland rivers, often are considerably higher than in lakes.

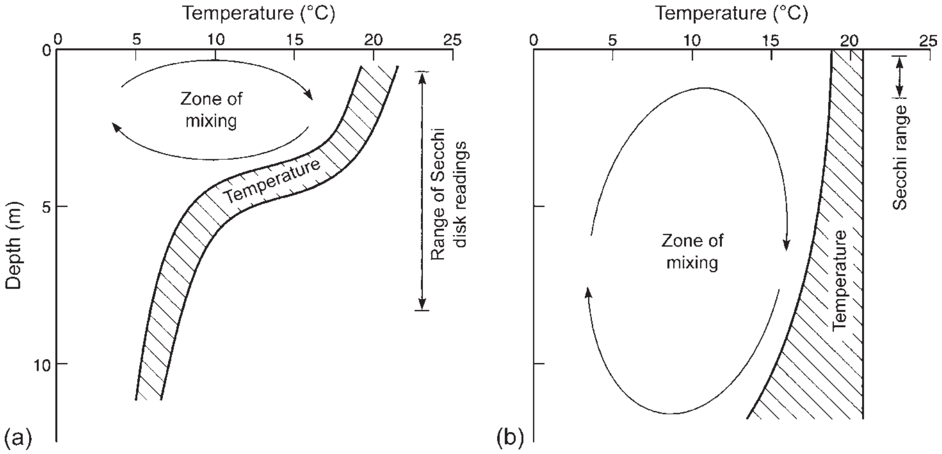

FIGURE 6.15 Schematic diagram comparing effect of depth of mixing on primary production in phytoplankton of a lake versus a river. In a lake (a), establishment of a temperature barrier between surface and deep waters restricts mixing to the upper few meters. In a river (b), temperature stratification is impeded by turbulence of flow, and the water column typically mixes from top to bottom. Depths of 5–20 m are common in large rivers. Rivers often carry substantial sediment loads, restricting light penetration to, at best, the upper 1–2 m.

In their survey of more than 100 sites on lakes, impoundments and rivers, Søballe and Kimmel (1987) observed a positive relationship between P concentrations and phytoplankton biomass, a well-established trend in lakes. However, river phytoplankton abundance was several times lower than would be expected based on P availability, and the relationship also was more variable, suggesting that factors other than nutrients exerted primary control. A similar pattern was observed by Basu and Pick (1996), who found a positive and significant correlation between chlorophyll and total P concentrations measured in 31 rivers in eastern Canada. Koch et al. (2004) determined experimentally that light and nutrients could limit phytoplankton grown in the Ohio, Cumberland, and Tennessee rivers. When irradiance was below a threshold, light limitation was frequently observed for the phytoplankton of the Ohio River, which is more turbid than the regulated Cumberland and the Tennessee. When irradiance was higher, P limitation was obtained for the Cumberland phytoplankton, while N and P were colimiting in the Tennessee and silicate was limiting in the Ohio River. In the River Rhine, a spring bloom of diatom-dominated phytoplankton reached very high abundances until dissolved silicate became depleted, which led to a population collapse (Vansteveninck et al. 1992).

6.3.2 Primary production by river phytoplankton

Phytoplankton primary production usually is measured by gas exchange or ^{14}C uptake in light and dark bottles, although how well conditions inside bottles represent the conditions of turbulence, light, and herbivory experienced by phytoplankton in rivers is a concern (Reynolds and Descy 1996). Very low phytoplankton production was recorded in the Orinoco River (4–43 mg C m^{-2} day^{-1}), as expected due to unfavorable environmental conditions of turbidity, depth, and swift current (Lewis 1988). Greater production has been recorded under impoundment conditions (Prowse and Talling 1958), and nuisance levels of phytoplankton have been reported under conditions of high nutrient loading (Bennett et al. 1986) and low flows (Décamps et al. 1984). Descy et al. (1988) reported a range of 0.6–1.68 g C m^{-2} day^{-1} for mean annual GPP for European Rivers.

Zooplankton grazing does not appear to constitute a major loss term for phytoplankton under most conditions (Reynolds and Descy 1996). Compared to lakes, rivers typically support a zooplankton biomass less than would be expected based on the amount of phytoplankton (Pace et al. 1992). In the Danube (Bothar 1987), the Apure (a whitewater tributary of the Orinoco, Saunders and Lewis 1988), and the Hudson (Pace et al. 1992), zooplankton grazing was believed to have little impact on phytoplankton. The largest species of microcrustaceans, which are capable of the highest filtering rates, are uncommon in rivers because their slow rates of population growth do not compensate for downstream transit. Rotifers and smaller crustaceans usually predominate because of their shorter generation times, and even these taxa can increase their numbers only during low flow periods. For example, Rzóska et al. (1952) reported transit times at moderate flows to be twofold to threefold longer in the White Nile compared to the Blue Nile. Crustacean zooplankton predominated in the former, while the Blue Nile contained mainly rotifers. Thus discharge conditions determine the species and size composition of zooplankton, and thereby constrain their ability to exert strong grazing pressure.

Nonetheless, grazing does consume significant amounts of phytoplankton production under some circumstances. In the fresh, tidal Potomac River in Maryland–Virginia, phytoplankton abundance was reduced 40–60% upon passage through a section of high densities of the Asiatic clam *Corbicula fluminea*. The filtering rates of these clams could reduce chlorophyll *a* from a river water sample by 30% in 2 h (Cohen et al. 1984). The zebra mussel *Dreissena polymorpha*, which first appeared in the Hudson River in 1991, quickly became so abundant that their populations were capable of filtering the entire volume of the Hudson estuary every 1–4 days during summer. Phytoplankton biomass fell by 85% due to direct consumption (Caraco et al. 1997), and the entire ecosystem was affected through associated changes in nutrients, water clarity, other grazers, and due to increases in submersed macrophytes (Strayer et al. 1999). Both examples involve invasive bivalves, and illustrate the potential for nonnative species to dramatically influence ecosystems. Because low grazing rates are the norm, however, under most circumstances the majority of the primary production of rivers is exported downstream.

6.4 Summary

Primary producers acquire their energy from sunlight and their materials from nonliving sources. The major autotrophs of running waters are the benthic algae and macrophytes, and phytoplankton also can be important in larger rivers. Benthic algae occur in intimate association with heterotrophic microbes within an extracellular matrix, referred to as periphyton, biofilm, and sometimes as *Aufwuchs*. Benthic algae are important in fluvial food webs, especially in headwater and midsized streams, and also influence the benthic habitat and nutrient cycling. Proximate factors that may limit benthic algal communities include light and nutrients which, along with temperature, influence biomass accrual; and disturbance and grazing, which are the factors that lead to algal dislodgement and biomass loss. The importance of any one factor to algal growth depends upon whether some other factor is in even shorter supply, and these environmental conditions vary with location and by season. Light often is the limiting factor in streams shaded by forest cover, as evidenced by lower benthic algal abundance in shaded versus unshaded streams, and by seasonal peaks before leaf-out and after leaves are shed. Phosphorus and N have each been shown to limit algal growth, sometimes in combination, but nutrient limitation can be overridden by low light or intense herbivory. Stream current has opposing effects on benthic algae accrual depending on growth form and architecture and is best described as a "subsidy-stress" response. The flow of water brings continual renewal of gasses and nutrients, and so current benefits algal growth by enhancing nutrient uptake. However, current also exerts a shear stress on benthic algae, which can cause cell sloughing, and high flows disturb and scour the substrate. Different temperatures apparently favor particular algal taxa, with filamentous green algae and cyanobacteria more abundant in warmer rivers; and growth rate of course increases with increasing temperatures. Substrate is a factor through its interaction with current, in that different areas of a stone may be more or less exposed to flow and smaller particles are more likely to be dislodged. Grazers can significantly limit benthic algae and influence community composition by selectively eliminating certain species and growth forms. The composition and biomass of the benthic algae varies temporally and spatially due to the interaction of these multiple environmental factors.

Macrophytes include flowering plants, bryophytes (mosses and liverworts), and some filamentous benthic algae. Macrophytes can be placed in four categories according to their growth form. These are emergent, submersed, and floating-leaved taxa, which are all rooted, and free-floating plants, which usually are not attached to the substrate and often form large mats. Angiosperms require moderate depths and slow currents, and so are most common in springs, rivers of intermediate size, and along the margins and in backwaters of larger rivers. Bryophytes are restricted in distribution but can be abundant in cool climates and in shaded headwater streams. Macrophytes are important to fish and invertebrates as habitat and as refuge from predators, and they can increase habitat heterogeneity for aquatic organisms by modifying water velocity and trapping sediments and organic matter. Herbivory on freshwater macrophytes usually is minor, and most biomass enters the detritus pool where its breakdown and utilization can be rapid.

The phytoplankton consists of cells and colonies of algae and cyanobacteria suspended in the water column and transported by currents. Light, nutrients, flow, and temperature all influence seasonal variation in phytoplankton abundance. Unable to maintain populations in fast-flowing streams, phytoplankton can become abundant in slowly moving rivers and backwaters where their doubling rates exceed downstream losses due to current. In large rivers, light penetration may be <1 m and so vertical mixing within a deep and turbid water column further limits the opportunity for photosynthesis. When compared with lakes, river phytoplankton populations are much less abundant for a particular nutrient concentration. Although invasive mollusks have been observed to dramatically reduce phytoplankton populations in some large rivers, grazing on phytoplankton typically is minor, as zooplankton doubling times are too slow to counter downstream losses. Thus, it appears that downstream export rather than in situ energy processing is the dominant fate of large river phytoplankton production.

Chapter seven

Detrital energy sources

Detritus includes all forms of nonliving organic carbon (C) including fallen leaves, the waste products and carcasses of animals, fragments of organic material of unknown origin, and organic compounds. Originally restricted to particulate matter, it now is considered to include dissolved organic matter (DOM) as well (Wetzel 2001). Nonliving organic C from diverse sources provides important energy inputs to most food webs, and this is especially true in fluvial ecosystems. While primary production by the autotrophs of running waters can be substantial (Chapter 6), much of the energy that supports fluvial food webs derives from particulate detritus and DOM. These energy pathways are referred to as detrital or detritus-based, and the immediate consumers of this material are decomposers and detritivores.

Plant litter and other coarse debris that falls or blows into stream channels, fine particulates that originate from many sources including the breakdown of plant litter, and DOM constitute the three main categories of nonliving OM in most situations (Table 7.1). Some of this material originates within the stream, such as dying macrophytes, animal feces, and extracellular release of dissolved compounds, and some is transported into the stream from outside the channel, such as leaf fall, soil particulates, and compounds dissolved in soil water. Collectively these sources can substantially exceed the energy fixed within streams by photosynthesis.

The division of nonliving organic energy sources into size classes is widely employed in studying detrital dynamics in streams. The usual categories are coarse particulate OM (CPOM, >1 mm), fine particulate OM (FPOM, <1 mm and >0.5 μm), and DOM (<0.5 μm). Each category can be divided further, but the dividing lines are arbitrary. In some instances, particularly the breakdown of forest leaves that enter streams, we have a detailed understanding of the processes involved. In other instances, such as the pathways involving fine particulates, we know considerably less. However, it is clear that the dynamics of OM in streams are complex, microorganisms are critical mediators of OM processing, and the surrounding landscape significantly influences what takes place within the stream.

7.1 The Decomposition of Coarse Particulate Organic Matter

The fate of CPOM is best known for autumn-shed leaves, which are major energy inputs to many small, forested streams. The topic is reviewed by Webster and Benfield (1986), and

TABLE 7.1 Sources of organic matter (OM) to fluvial ecosystems.

Sources of input	*Comments*
Coarse particulate organic matter (CPOM)	
• Leaves and needles	Major input in woodland streams, typically pulsed seasonally
• Macrophytes during dieback*	Locally important
• Woody debris	May be major biomass component, very slowly utilized
• Other plant parts (flowers, fruit, pollen)	Little information available
• Other animal parts (feces and carcasses)	Little information available
Fine particulate organic matter (FPOM)	
• Breakdown of CPOM	Major input where leaf fall or macrophytes provide CPOM
• Feces of small consumers	Important transformation of CPOM
• From DOM by microbial uptake	Organic microlayers on stones and other surfaces
• From DOM by physical–chemical processes	Flocculation and adsorption, probably less important than microbial uptake route
• Sloughing of algae*	Of local importance, may show temporal pulses
• Sloughing of organic layers	Little information available
• Forest floor litter and soil	Influenced by storms causing increased channel width and inundation of floodplain, affected by overland versus subsurface flow
• Stream bank and channel	Little known, likely related to storms
Dissolved organic matter (DOM)	
• Groundwater	Major input, relatively constant over time, often highly refractory
• Subsurface or interflow	More important during storms
• Surface flow	Possibly important during storms causing overland flow
• Leachate from detritus of terrestrial origin	Major input, pulsed depending upon leaf fall
• Throughfall	Smaller input, dependent on contact of precipitation and clouds with canopy
• Extracellular release and leachate from algae*	Of local importance, may show seasonal and diel pulses
• Extracellular release and leachate from macrophytes*	Of local importance, may show seasonal and diel pulses

Much OM originates outside the stream reach where it is measured. Some (sources marked with an asterisk) is produced by photosynthesis within the stream and subsequently enters the pools of dissolved or particulate OM.

methods of study are described by Boulton and Boon (1991) and Graca et al. (2005). The breakdown of macrophytes is similar to that of leaves of terrestrial origin, although some minor differences are noted below. The breakdown of woody material is, not surprisingly, much slower than that of leaves, and is of lesser importance to higher trophic levels. Other sources of CPOM that enter heterotrophic pathways in running waters and may be locally or seasonally important, such as flower parts, animal feces, and carcasses of large animals, have received less study.

Once CPOM enters streams it undergoes a breakdown process or is exported (Webster et al. 1999). Studies of OM breakdown start with the source material, often using leaves picked from riparian trees just prior to abscission, and follow its disappearance over time. As the process advances, leaves release solutes and are colonized by microorganisms and invertebrates, which enhance fragmentation and mineralization (the conversion of organic C compounds into inorganic carbon dioxide [CO_2]). The original leaf is transformed into several products including microbial and shredder biomass, FPOM, DOM, nutrients, and CO_2 (Gessner et al. 1999). DOM and FPOM can undergo further microbial degradation or be transported downstream.

The loss of leaf mass over time is approximately log-linear (Figure 7.1), although some data have been interpreted as linear or as consisting of two or more distinct stages. Webster and Benfield (1986) argue that a simple exponential model provides a general description of the breakdown process,

$$W_t = W_i e^{-kt} \tag{7.1}$$

where W_t = dry mass at time t, W_i = initial dry mass, and t is time, measured in days. The statistic k (in units days^{-1}), which is the slope of the plot of the natural logarithm of leaf mass versus time, provides a single measure of breakdown rate.

The rate of leaf breakdown is determined by intrinsic chemical and structural differences among leaves, a number of environmental variables, and the feeding activity of detritivores. Petersen and Cummins (1974) suggested a continuum of decomposition rates from slow to fast, based on the breakdown of leaves from six deciduous tree species in a small Michigan stream. They also recognized that this variation in leaf decomposition rates, which they termed a "processing continuum," had important consequences for invertebrate consumers by extending the time interval over which microbially colonized leaf litter was available. The wide variation in the breakdown rate of the leaves of different plant species has now been amply documented (Figure 7.2). Nonwoody plant leaves decompose much more quickly, on average, than do leaves of woody plants (mean half-lives in Figure 7.2 are approximately 65 days and 100–150 days, respectively). Submerged and floating macrophytes are among the fastest to decay, presumably because they contain the least amount of support tissue and often the highest concentration of potentially limiting elements such as nitrogen (N) and phosphorus (P).

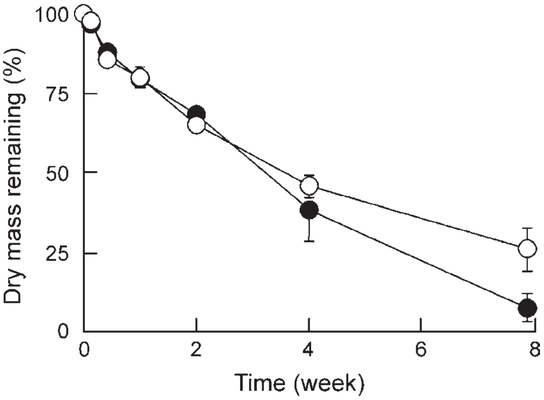

FIGURE 7.1 Leaf dry mass remaining (as %) from alder (●) and willow (○) leaf packs in an experiment conducted in a Black Forest stream, Germany. Error bars represent 95% confidence intervals. (Reproduced from Hieber and Gessner 2002.)

A number of environmental factors also influence breakdown rate. Although leaf breakdown can occur at near-zero temperatures (Short et al. 1980), breakdown rates generally are faster at warmer temperatures (Abelho et al. 2005). Faster breakdown also occurs in more nutrient-rich systems, apparently due to the greater availability of N. Laboratory studies typically show acceleration of leaf breakdown in response to N addition (Meyer and Johnson 1983). Higher nitrate concentrations partly explain higher leaf decomposition rates in streams in logged catchments (Benfield et al. 2001). Rosemond et al. (2002) found that variation in leaf breakdown rates along a stream in Costa Rica correlated with a natural gradient in P concentrations. Experimental addition of N and P to a stream at the Coweeta Hydrologic Laboratory in the southern Appalachians enhanced the loss of wood mass and increased microbial respiration and fungal biomass (Gulis et al. 2004). However,

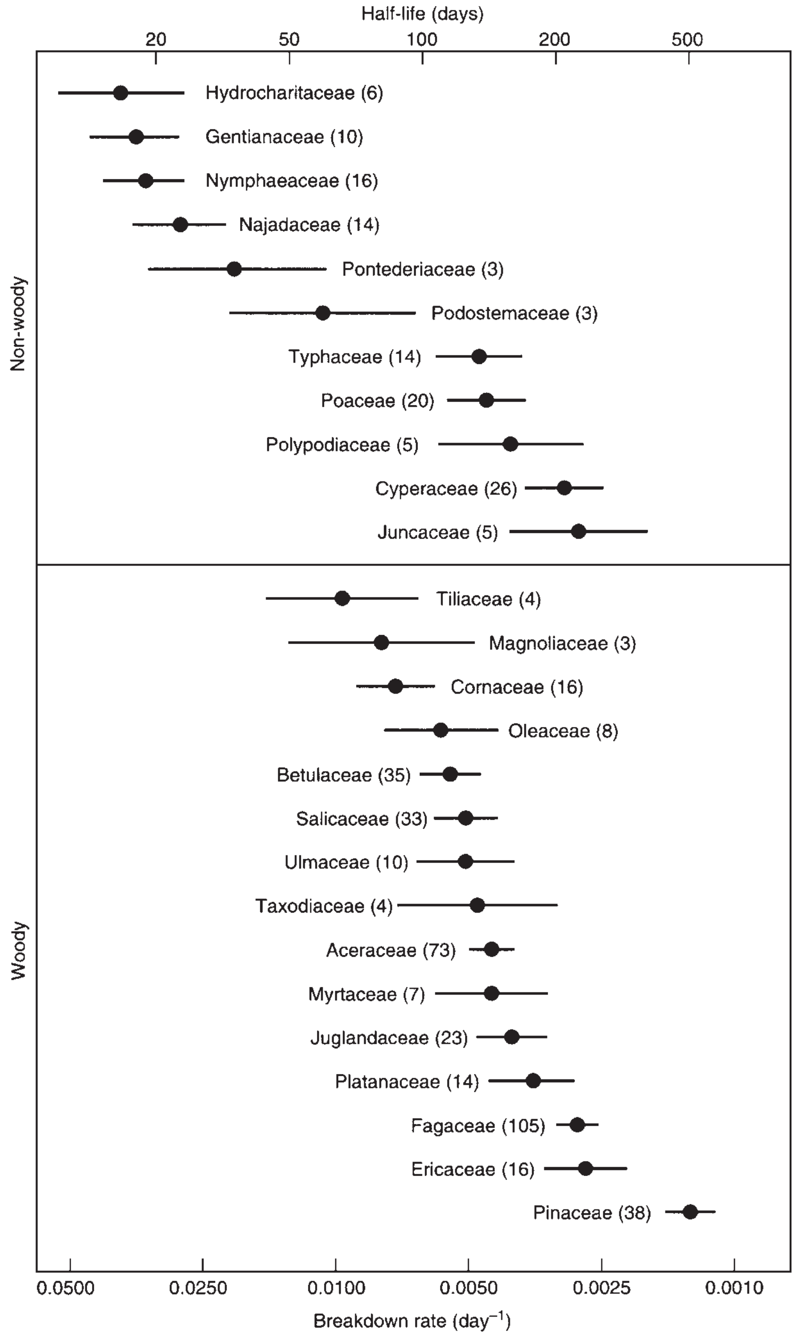

FIGURE 7.2 The breakdown rates for various woody and nonwoody plants, based on 596 estimates compiled from field studies in all types of freshwater ecosystems. Means ± 1 standard error are shown, and the variation is due to (at least) effects of site, technique, and numerous environmental variables. The number of individual rate estimates is shown in parentheses. (Reproduced from Webster and Benfield 1986.)

nutrient additions to a stream in the Caribou National Forest in southeast Idaho did not affect leaf breakdown, suggesting that microorganisms were not nutrient limited due to relatively high ambient nutrient concentrations (Royer and Minshall 2001). Low pH retards decomposition by inhibiting the activity of microorganisms and invertebrates (Dangles et al. 2004a). Hydrologic fluctuations can cause abrasion and fragmentation, which may expose more surface area to microbial action (Benfield et al. 2001), and burial, which can reduce microbial activity by reducing the availability of oxygen (Sponseller and Benfield 2001). Metal pollution can decrease decomposition rates by negatively affecting shredders and microorganisms (Niyogi et al. 2001, Duarte et al. 2004, Carlisle and Clements 2005).

7.1.1 Stages in the breakdown and decay of CPOM

The sequence in the breakdown of CPOM, well documented for autumn-shed leaves in temperate streams (see reviews by Bärlocher 1985, Webster and Benfield 1986), is illustrated in Figure 7.3. Leaves fall directly or are windblown into streams, become wetted, and commence to leach soluble organic and inorganic constituents. Most of the leaching occurs within a few days and is followed by a period of microbial colonization and growth, causing numerous changes in leaf condition. The next stage, fragmentation by mechanical means and invertebrate activity, usually follows some period of softening of tissue by microbial enzymes, and is complete when no large particles remain. Although the general model suggests sequential stages, leaf decomposition is a complex process and some of the events can occur simultaneously. For example fragmentation can occur during microbial colonization and not just at the end of the process, and invertebrate colonization may begin shortly after leaves enter the stream (Gessner et al. 1999, Hieber and Gessner 2002).

As much as 25% of the initial dry mass of freshly abscised leaves is lost due to leaching in the first 24 h. Constituents lost during leaching are primarily soluble carbohydrates and polyphenols (Suberkropp et al. 1976). Leaves of different plants show species-specific leaching rates: alder (*Alnus rugosa*) lost only about 4% of dry mass over several days whereas elm (*Ulnus americana*) lost 16% in an early study by Kaushik and Hynes (1971). Release of DOC

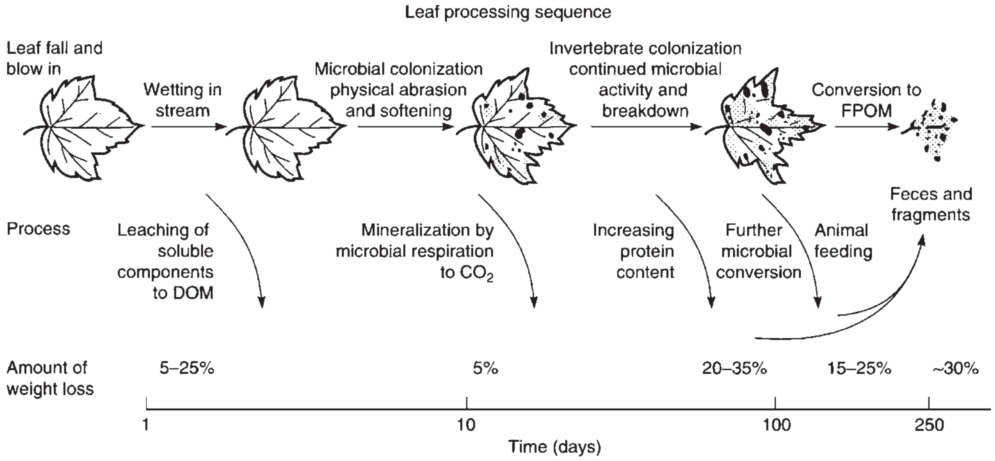

FIGURE 7.3 The processing or "conditioning" sequence for a medium-fast deciduous tree leaf in a temperate stream. Leached DOM is thought to be rapidly transferred into biofilms by microbial uptake.

by leaves of several plants in a stream in British Columbia, Canada, also revealed substantial differences in leaching rates (McArthur and Richardson 2002). During the first day, Western hemlock needles (*Tsuga heterophylla*) lost 14% of the total DOC released over a 7-day period, compared with 30% for western red cedar (*Thuja plicata*) and 74% for red alder (*A. rubra*) (Figure 7.4). By the end of the experiment, hemlock and cedar had released 40% and 20%, respectively of the DOC released by alder.

Differences in leaf chemistry and structure result in wide variation in breakdown rates (Webster and Benfield 1986). Leaves with a high initial nutrient concentration decompose more rapidly than leaves of lower nutrient content. For example, Kaushik and Hynes (1971) established a positive relationship between initial N concentration and rapidity of breakdown. Comparison of the decomposition rates of litter from red alder, western red cedar, and western hemlock also showed a positive correlation with initial N content and a negative correlation with C/N ratios (Richardson et al. 2004). Conversely, a high lignin content slows breakdown. A combination of initial N and lignin proved to be an effective predictor of breakdown rate of six species of leaves in the terrestrial litter of a New England forest (Melillo et al. 1982) and of wood chips from five species of trees in streams in eastern Canada (Melillo et al. 1983). Leaf chemistry explained differences in decomposition of *Croton gossypifolius* (Euphorbiaceae) and a species of *Clidemia* (Melastomataceae) in an Andean stream (Mathuriau and Chauvet 2002). Higher decomposition rates in *Croton* than in *Clidemia* appeared to be related to lower tannin and higher N content in *Croton*, which resulted in earlier peaks in ergosterol (a compound found primarily in fungi), sporulation activity, and macroinvertebrate colonization. Lastly, chemical inhibitors impede leaf decay in several ways. Tough outer coatings such as the cuticle of conifer needles slow fungal invasion (Bärlocher et al. 1978), and complexing of protein to tannins is a principal cause of slow breakdown in many broadleafed woody plants. Toxic effects of chemical constituents also may influence breakdown rates (Webster and Benfield 1986), just as secondary plant compounds defend against terrestrial herbivores, although evidence is scant. Somewhat surprisingly, chemical measures of tannins (total phenolics and condensed tannins) of 48 deciduous trees were unrelated to published breakdown rates (Ostrofsky 1993). However, Canhoto et al. (2002) found that oils of *Eucalyptus globulus* inhibited the growth of hyphomycetes and the activity of their enzymes, which could explain the delayed decomposition of eucalyptus in rivers.

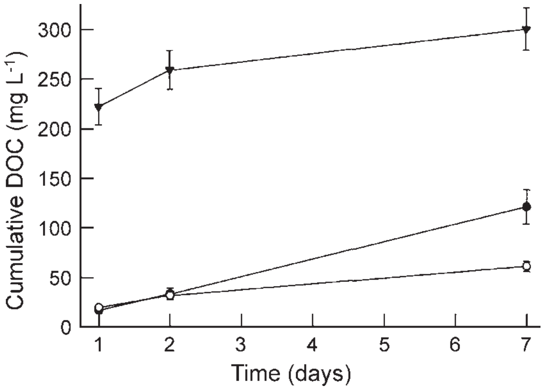

FIGURE 7.4 Cumulative DOC release from hemlock (●), cedar (○) and alder (▲) litter. Data shown are means, and error bars represent one standard deviation. (Reproduced from McArthur and Richardson 2002.)

As leaf processing advances, microbial populations colonize and proliferate on the leaf substrate. Microbial colonization plays an important role in altering the palatability of leaves for detritivores (Arsuffi and Suberkropp 1984) and in the fragmentation of leaf material. This colonization is primarily by fungi and bacteria, although protists also can be important (Ribblett et al. 2005). In addition to the conversion of leaf tissue into more edible material for shredders and the production of FPOM, microbial activity softens plant tissue, favoring the release of compounds that can be incorporated into microbial biomass (Gessner et al. 1999, Graca 2001). Fungi can degrade the polysaccharides present in the cell walls of the leaves by the production of extracellular enzymes (Jenkins and Suberkropp 1995), and their hyphae also penetrate leaf tissue, facilitating the softening process (Wright and Covich 2005).

Suberkropp and Klug (1976) followed in detail the succession of dominant microorganisms on oak and hickory in a Michigan stream from November until June. Fungi, primarily aquatic hyphomycetes, dominated during the first half (12–18 weeks) of the processing period. Bacteria, whose numbers gradually increased throughout, dominated the terminal processing stage and perhaps were benefited by fungal-induced changes in leaf surface area or by the release of labile compounds. In a stream in the Black Forest of Germany, fungal and bacterial biomass both increased during the first 4 weeks (Figure 7.5) and then remained constant for the next 4 weeks of the study (Hieber and Gessner 2002). Fungal colonization of leaves takes place primarily in the water, because freshly abscised leaves exhibit low fungal biomass (measured as ergosterol content) before entering the stream (Gessner and Chauvet 1997, Hieber and Gessner 2002). Propagules of soil fungi, although commonly carried into the stream on shed leaves, appeared to contribute little to decomposition (Suberkropp and Klug 1976). Bärlocher (1982) reported that typically 4–8 species of aquatic fungi dominate throughout the decomposition of leaves, while a similar or larger number of rare species appear erratically. Apparently no particular succession occurs on a single leaf; whichever fungal species arrives first as a waterborne spore establishes numerical dominance. Hieber and Gessner (2002) identified 30 species of hyphomycetes on decomposing leaves of alder and willow, but two species, *Flagellospora curvula* and *Tetrachaetum elegans*, were dominant. Bacteria from biofilms growing on decomposing leaves in a stream in Ohio were mostly of one type known as *α-Proteobacteria,* although representatives of *β-Proteobacteria* were occasionally abundant (McNamara and Leff 2004).

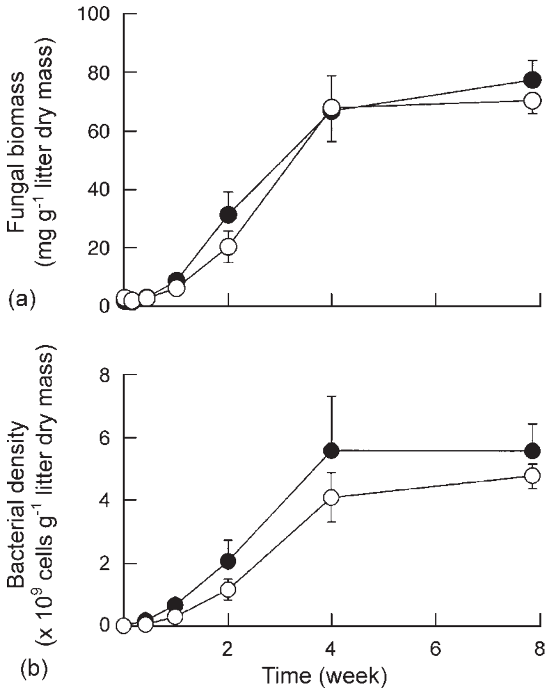

FIGURE 7.5 Fungal (a) and bacterial biomass (b) in a leaf decomposition experiment conducted with alder (●) and willow (○) leaves in a Black Forest stream, Germany. Error bars represent 95% confidence intervals. (Reproduced from Hieber and Gessner 2002.)

The relative influence of fungi and bacteria upon the decomposition process likely varies with substrate and habitat. Although fungal biomass was found to be several times greater than bacterial biomass on alder and willow leaves in a stream in Germany's Black Forest region (Figure 7.6), the fungal contribution to leaf mass loss was only about twice that of bacteria, whose shorter turnover times partly compensated for their lower biomass (Hieber and Gessner 2002). Findlay et al. (2002) found that fungi dominated microbial biomass in large OM such as wood and leaves whereas bacterial biomass was dominant

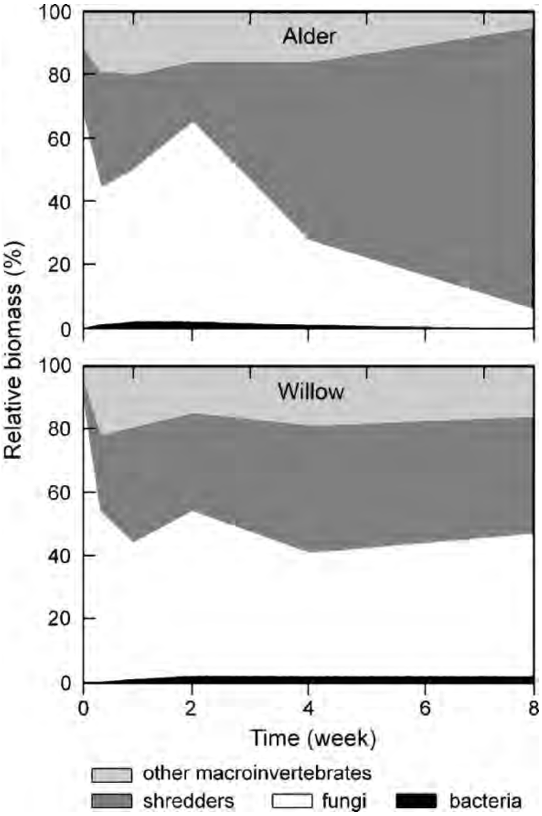

FIGURE 7.6 Proportions of biomass of bacteria, fungi, shredders, and other macroinvertebrates during alder and willow leaf decomposition in a Black Forest stream, Germany. (Reproduced from Hieber and Gessner 2002.)

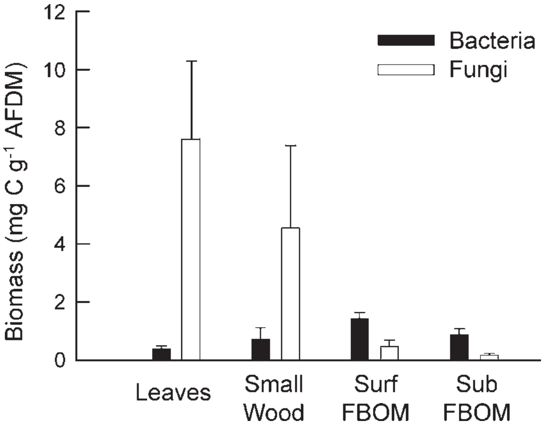

FIGURE 7.7 Biomass of fungi and bacteria on leaves, wood, and surface and subsurface fine benthic organic matter (FBOM). Means and standard deviations of 7–9 streams are shown. (Reproduced from Findlay et al. 2002.)

in fine benthic OM (Figure 7.7). Because fine benthic OM was more abundant than coarse detritus at the study sites, when bacterial biomass was weighted for the abundance of detritus in the reach, it was similar to or higher than that of fungi. In addition, bacterial biomass was less variable per unit of OM mass than fungal biomass, suggesting that bacteria could be a more reliable food resource than fungi.

Bacteria and fungi may interact synergistically and antagonistically during POM decomposition. In their study of decomposing leaf litter under low and high nutrient levels, Gulis and Suberkropp (2003) reported that microbial biomass and production were always dominated by fungi. The bacterial contribution increased in treatments where fungi were excluded, suggesting competition between bacteria and fungi for resources. This interaction may be symbiotic as well, as Gulis and Suberkropp (2003) also found evidence that bacteria may benefit from fungal activity during leaf decay. When leaf disks that were treated with antibacterial and antifungal solutions were incubated in two tropical streams in Venezuela, results indicated that fungi contributed more to total microbial biomass than did bacteria, while bacterial were responsible for a higher proportion of total microbial respiration (Abelho et al. 2005). In a tropical headwater stream in Puerto Rico, leaf decomposition rates were faster when both bacteria and fungi were present, compared with treatments in which one was excluded. However, fungi reached higher biomass alone than in the presence of bacteria, suggesting an antagonistic effect (Wright and Covich 2005). This indicates that the interaction between bacteria and fungi can be synergistic in facilitating leaf decomposition but antagonistic in the mutual demand for a C source.

Leaves undergo a number of chemical changes as they decay. Nitrogen typically increases as a percent of remaining dry mass and sometimes increases in absolute terms as well. Because protein complexed to lignin and cellulose is very resistant to breakdown, N compounds remain while other leaf constituents are lost, resulting in a relative increase. Microbial immobilization from external sources can also lead to increases in either relative or absolute quantities of N or P. When increases in total N are recorded, this immobilization of N usually is attributed to an increase in microbial biomass and incorporation of N from the surrounding water into new protein. In a headwater stream reach in Coweeta Hydrologic Laboratory, North Carolina, that received additions of ammonium, nitrate, and phosphate, N content of maple (*Acer rubrum*) and rhododendron (*Rhododendron maxima*) leaves increased significantly relative to a control (Figure 7.8), suggesting higher microbial biomass under enrichment conditions (Gulis and Suberkropp 2003). The slower breakdown of rhododendron leaves compared to maple is attributable to their lower initial N content and lower surface area relative to leaf volume. In a study of oak and hickory leaves incubated in a Michigan stream over the winter (Suberkropp et al. 1976), cellulose and hemicellulose declined at about the same rate as total leaf mass, while lignin was processed more slowly and increased as a percentage of remaining weight. Lipids were lost more rapidly than total mass, and thus were a declining fraction of remaining dry mass of leaf material.

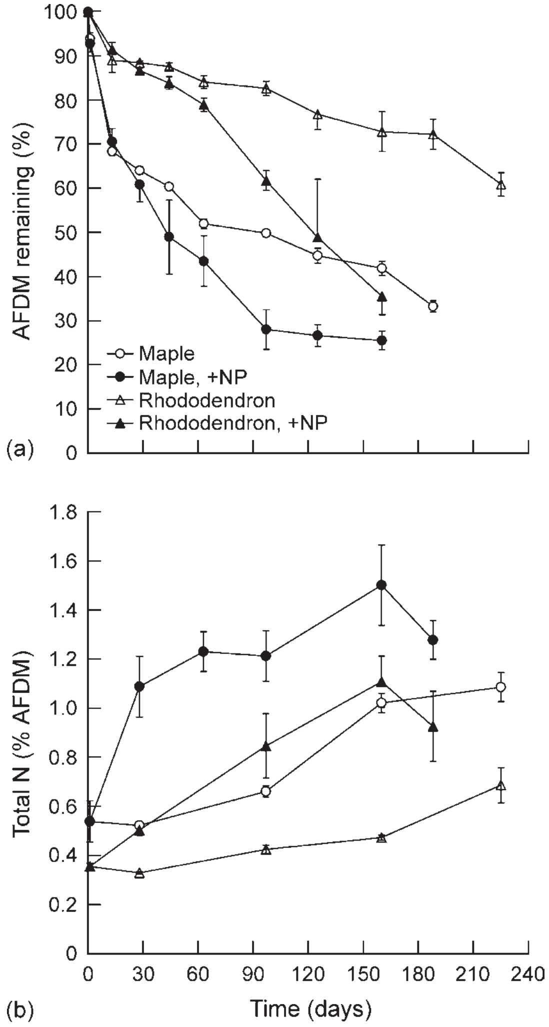

FIGURE 7.8 (a) Ash free dry mass (AFDM) and (b) total nitrogen content in an experiment using maple and rhododendron leaves in control and nutrient-enriched reaches of a headwater stream at the Coweeta Hydrologic Laboratory, North Carolina. (Reproduced from Gulis and Suberkropp 2003.)

Because of variation in timing of leaf fall, species-specific rates of leaf conditioning by fungi, and the diversity of fungi present, leaves on the streambed are a mosaic of patches of microbial populations. The extent of this variation is shown by Bärlocher's (1983) study of a Swiss stream flowing through an alder–willow–maple forest. The standing crop of CPOM was maximal in October–November, and by April only veins and petioles remained for an 85% loss of leaf mass. Soluble protein also decreased after November, indicating that nutritional value declined from that time on. However, on any one date, the quality of individual leaves was so variable that the amount of soluble protein in the richest 10% of leaves in mid-April exceeded the median value of leaves sampled in mid-November. Detritivores capable enough or fortunate enough in patch choice could enjoy food quality well above average.

7.1.2 The influence of detritivores on litter decomposition

The fragmentation of leaves by invertebrate feeding and abrasion constitutes another important stage in leaf breakdown. Aquatic insects and crustaceans are the most common consumers of CPOM. During the decomposition of autumn-shed leaves in temperate woodland streams, microbial populations play a central role not only in decomposing the leaf substrate, but also in altering the chemical nature of the leaf material, rendering it more palatable and nutritious to consumers. In turn, the feeding activities of detritivores significantly accelerate the decomposition process. Their contribution to the fragmentation of coarse particles through feeding activities and production of feces significantly accelerates breakdown rates and influences subsequent biological processing of the original CPOM inputs.

Several lines of evidence indicate that shredders accelerate the breakdown of leaves in streams (Webster and Benfield 1986). The finding that leaf packs in mesh bags decomposed more slowly than those tethered to bricks with fishing line indicated that the former method underestimated breakdown rate. Exclusion of detritivores is a likely cause of this difference, and leaf breakdown is more rapid when bags with larger mesh size are used (e.g., Benfield et al. 1979, Wright and Covich 2005), presumably because invertebrate access is greater. Furthermore, breakdown rates are higher where invertebrates are more abundant (Graca 2001, Sponseller and Benfield 2001), and there is a positive relationship between invertebrate preferences and decay rates (Webster and Benfield 1986). Hieber and Gessner (2002) estimated that 64% of mass loss in alder and 51% in willow leaves were due to shredders that colonized leaves early in the experiment (Figure 7.9).

Comparison of decay rates in experiments with and without insect detritivores establishes that as much as half of leaf degradation can be attributed to the presence of animals. Processing rates in two experimental streams, one lacking invertebrates and another stocked with detritivores (*Tipula*, *Pycnopsyche*, and *Pteronarcys*) at densities believed to represent natural maxima, indicated that 21–24% of the loss of hickory leaves was due to the influence of detritivores (Petersen and Cummins 1974). The contribution of macroinvertebrates to the breakdown of *Phragmites*, a macrophyte, was comparable

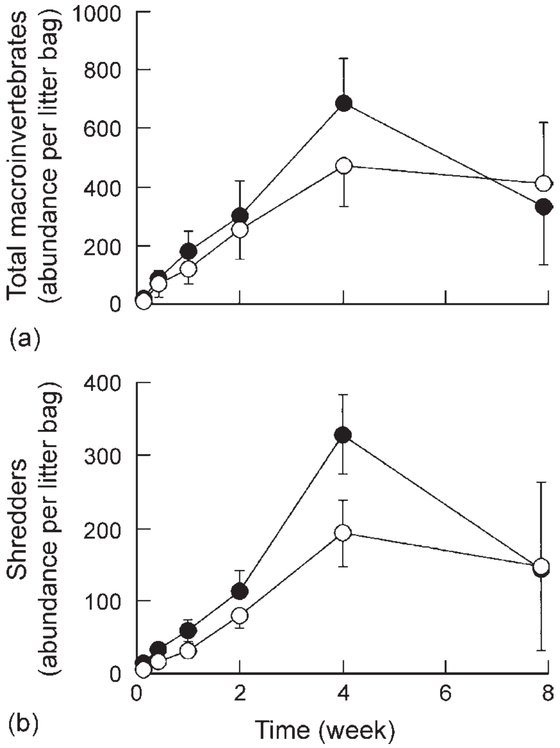

FIGURE 7.9 Colonization of alder (●) and willow (○) leaf packs by (a) macroinvertebrates and (b) shredders in a Black Forest stream, Germany. Error bars represent 95% confidence intervals. (Reproduced from Hieber and Gessner 2002.)

(Polunin 1982). In an Appalachian stream, exclusion of macroconsumers, primarily crayfish, using electric fences resulted in lower breakdown rates of rhododendron leaves (Schofield et al. 2001). When present, crayfish were responsible for 33% of leaf breakdown in summer and 54% in autumn. Sponseller and Benfield (2001) observed faster leaf breakdown with higher shredder density and biomass (Figure 7.10). In addition to direct consumption, possible influences of detritivore feeding include release of nutrients and DOM, comminution of litter, and modification of water circulation (Polunin 1984). The freshwater shrimp *Xiphocaris elongata*, a consumer of large leaves in tropical streams, increased the concentration of both total dissolved N and dissolved organic carbon (DOC), and also the concentration and transport of POM (Crowl et al. 2001).

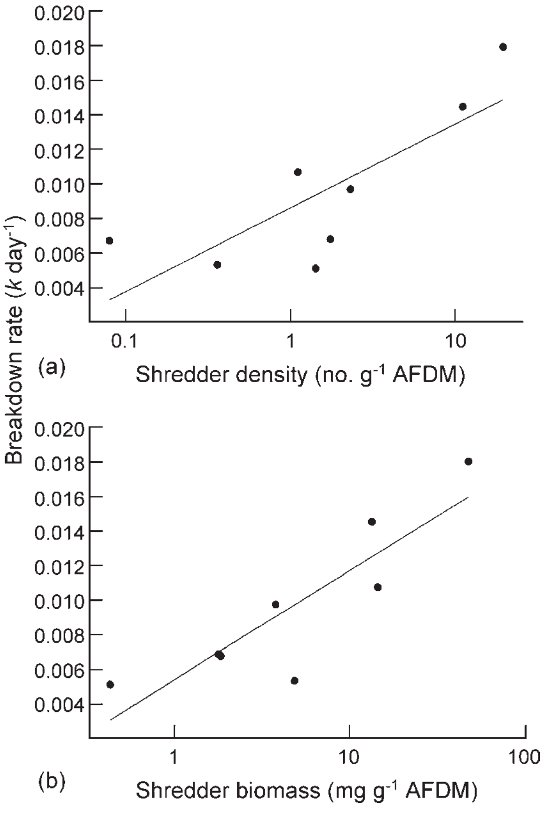

FIGURE 7.10 Correlations between leaf breakdown rates and (a) density and (b) biomass of shredders expressed per gram of leaf AFDM. (Reproduced from Sponseller and Benfield 2001.)

The experimental removal of detritivorous insects from a small mountain stream in North Carolina provides a particularly convincing demonstration that animal consumers regulate rates of litter decomposition. Wallace et al. (1982a, 1991) added the insecticide methoxychlor to one small stream in February, with supplemental treatments in May, August, and November. Massive downstream drift of invertebrates occurred and insect densities subsequently were reduced to <10% of numbers in an adjacent, untreated reference stream, while oligochaetes increased roughly threefold. Leaf breakdown rates were significantly slower in the treated stream, presumably due to the great reduction in insect density, and the magnitude of the effect was greatest for the most refractory leaf species (Table 7.2). Export of suspended fine particulates also was reduced in the treated stream, consistent with the finding of reduced leaf processing.

Most research on the role of detritivores in leaf breakdown has been conducted in the temperate zone, and less is known from other latitudes. Studies conducted in Colombia, Costa Rica, Venezuela, Papua New Guinea, and Kenya found that insect shredders were scarce, despite the fact that densities of other invertebrates were similar to those reported in the temperate zone (Yule 1996, Dobson et al. 2002, Rincon et al. 2005, Wantzen and Wagner 2006). In these studies, shredders represented <7% of total macroinvertebrate abundance, while in European rivers this value ranged from 10% to 43% (Dobson et al. 2002, Hieber and Gessner 2002). Nonetheless, leaf breakdown rates in streams in Costa Rica (Rosemond et al. 1998) and in Colombia (Mathuriau and Chauvet 2002) were rapid, suggesting a greater role of microorganisms in tropical streams. Possible explanations for these findings include higher temperatures in the tropics, lower quality

TABLE 7.2 Estimated half-lives (days) based on exponential decay in ash-free dry mass of four leaf species in a stream treated with an insecticide, compared to a reference stream. (From Wallace et al. 1982a, b.)

	Reference stream	*Treatment stream*	*Change in half-life*
Dogwood (*Cornus florida*)	41.0	65.4	1.6×
Red maple (*Acer rubrum*)	50.2	135.9	2.7×
White oak (*Quercus alba*)	64.2	173.3	2.7×
Rhododendron (*Rhododendron maxima*)	128.4	577.6	4.5×

of leaves due to the presence of defensive compounds, incorrect allocation of tropical invertebrates to trophic roles, or failure to detect the presence of large shredders (Irons et al. 1994, Schofield et al. 2001, Wantzen et al. 2002). In contrast to some reports of low shredder density in tropical streams, Cheshire et al. (2005) found that shredders represented 20% of total macroinvertebrate abundance in the Australian tropics, similar to values reported from the temperate zone. These authors suggested that shredder scarcity may reflect historical biogeography rather than a strict latitudinal effect, because in some temperate regions such as New Zealand, shredder insects also are scarce. Where shredder insects are rare or absent, other organisms may play a similar role. Fish and shrimp enhanced leaf breakdown in a Costa Rican stream (Rosemond et al. 2002), as did shrimp and macroinvertebrates in a stream in Puerto Rico (Wright and Covich 2005). In New Zealand headwater streams, the crayfish *Paranephrops zealandicus* has a strong influence on the decomposition of leaf litter and the production of POM (Usio and Townsend 2001).

7.1.3 Other CPOM

Macrophytes are an important source of detritus where they are abundant, typically in larger rivers and in floodplains (Section 6.2). Polunin (1984) reviewed studies of the decomposition and fate of this material, which is similar to that of terrestrial leaves. Breakdown rates are relatively fast, although less so for emergent macrophytes that contain more support tissue. Bacteria appear to play a greater role in macrophyte decomposition than is true for leaves of terrestrial origin (Webster and Benfield 1986).

Wood ranging from small branches to large tree trunks is abundant in small to midsized streams flowing through forested landscapes. Wood influences channel structure and stream habitat in a number of ways (Section 5.2.2), and also contributes to the nutrition of some consumers (Anderson and Sedell 1979). Not surprisingly, wood decays very slowly. The high lignin and cellulose content of wood fiber, combined with low concentrations of N and P, relatively small surface area, and low penetrability, results in very slow breakdown with microbial activity confined to surface layers. Even small wood chips (0.75–1.5 cm size range) placed in coarse mesh bags in Quebec streams showed very slow loss rates (Melillo et al. 1983). Alder chips (*A. rugosa*) had a half-life of about 7 months, while spruce (*Picea mariana*) chips would require roughly 17 years to undergo a 50% reduction in weight. Anderson et al. (1978) retrieved sticks (2.5 × 2.5 × 92 cm) of alder, hemlock (*Tsuga*), and Douglas fir (*Pseudotsuga*) after 15 months in an Oregon stream, with similar results. Webster et al. (1999) estimated breakdown rates for sticks of different diameter (<20 mm, 20–25, and >25 mm) of yellow poplar (*Liriodendron tulipifera*), white pine (*Pinus strobus*), and red oak (*Quercus rubra*) in a 5-year experiment conducted in streams at Coweeta Hydrologic Laboratory. Breakdown rates were more rapid for sticks of smaller diameter, and for poplar relative to the pine and oak. Breakdown rates for sticks were 1–2 orders of magnitude slower than those reported for leaves of woody plants. Logs (20–32 cm diameter) that were placed in this stream lost their bark after 4–5 years and showed some signs of surface decomposition after 8 years, but still no differences in density were detected. Natural wood pieces, such as branches and twigs, have slower decomposition rates than commercial wood substrates such as chips, sticks, cubes, and disks, probably because of the latter having a higher surface to volume ratio and because leaching losses are higher from the processed surfaces of wood products (Spanhoff and Meyer 2004).

Nutrient availability may have some influence on wood decomposition. Comparison of alder, pine, oak, and eucalyptus branches at three sites in the Aguera River, Spain, that differed in nutrient levels suggested P limitation of wood breakdown (Diez et al. 2002). An initial weight loss (5–9%) due to leaching occurred during the first few weeks, and P was rapidly lost during the first 6 weeks in all but eucalyptus. Breakdown rates were most rapid for alder, followed by oak and eucalyptus, and then pine, which also showed the lowest values of ergosterol. In two streams in Germany the decomposition rate for black alder (*A. glutinosa*) was higher and the half-life shorter at a site with higher nitrate and phosphate levels (Spanhoff and Meyer 2004). Experimental addition of nutrients enhanced the decay of wood (oak veneers and natural maple sticks), more so for veneers than sticks (Gulis et al. 2004). The faster breakdown rate of the veneers was accompanied by higher N and ergosterol content and microbial respiration, which was thought to be primarily fungal (Figure 7.11).

7.2 Fine Particulate Organic Matter

Less is known about the energy pathways involving FPOM than CPOM. One source of FPOM obviously is the breakdown of leaf litter (Figure 7.3) as fragments from mechanical breakdown and shredder activity enter the water column. When one includes the production of feces and the eventual contribution of leached DOC to formation of fine particles (discussed below), it is apparent that a large fraction of leaf litter eventually becomes fine particulate matter. In addition, microbial activity on the leaf can result in the release of leaf and bacterial cells and the hyphae and conidia of fungi (Gessner et al. 1999). FPOM also is transported into streams from the terrestrial landscape by wind and runoff, and can be formed from DOM primarily by the incorporation of DOC into microbial biomass. These sources are difficult to trace and potentially of greater magnitude than FPOM derived from leaf fragmentation. The term seston includes all suspended particles, and so organic seston is used synonymously with FPOM.

The presence and activity of microbial populations on fine particulates is measured in a number of ways. Cell counts and ATP concentrations provide estimates of biomass, while respiration rates, enzyme assays, denitrification potential, N-fixation rates, and uptake of labeled substrate provide estimates of metabolic activity (Bonin et al. 2000, Findlay et al. 2002). Because bacteria become more abundant in the later stages of CPOM processing, and the small size of FPOM suggests a reduced role for fungal hyphae, bacteria are likely to dominate microbial populations on fines. This expectation is supported by a study conducted in nine headwater streams in the United States, where bacteria were found to dominate fine benthic OM whereas fungi were more abundant in larger material (Findlay et al. 2002). However, compared to the extensive data on leaf breakdown, less is known about the eventual fate of FPOM (Ward and Woods 1986, Ward et al. 1990).

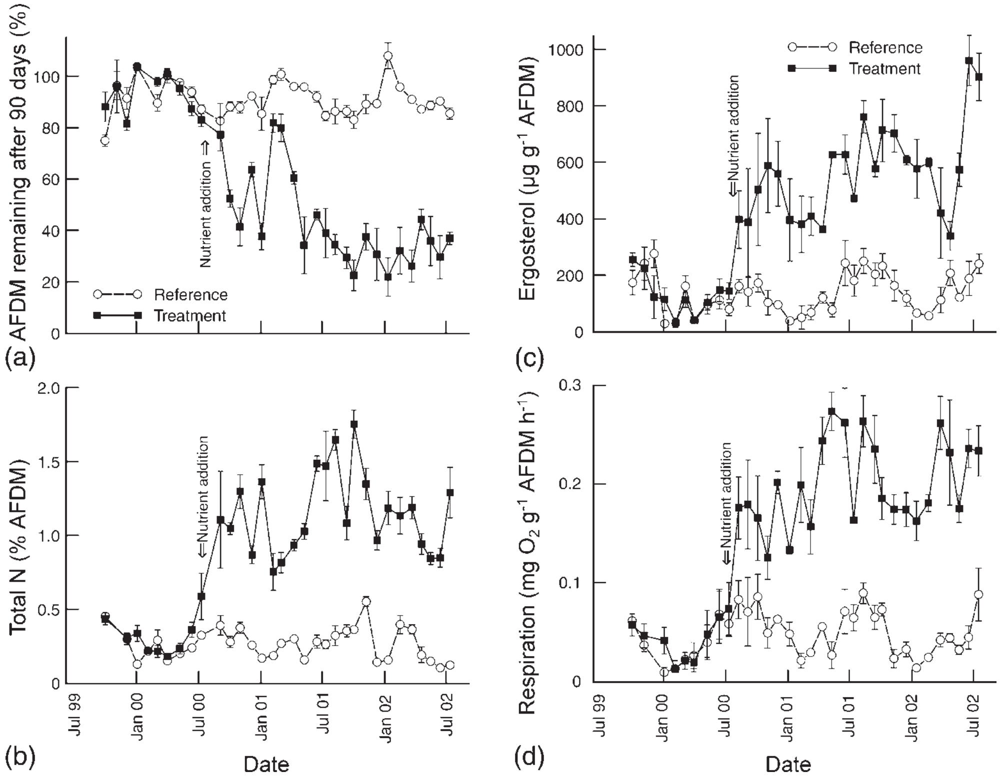

FIGURE 7.11 Variation in (a) AFDM, (b) total N (as % of AFDM), (c) ergosterol and (d) respiration during a 90-day decomposition experiment using oak veneers incubated in a treatment stream (nitrogen and phosphorus additions) and a reference stream (no nutrient addition). (Reproduced from Gulis et al. 2004.)

Rates of processing, resemblance between FPOM and its source, nutritive value, and eventual fate all are poorly understood.

7.2.1 FPOM originating from leaf decomposition

Feeding by leaf-shredding insects produces FPOM not only by fragmenting larger particles into smaller ones but also through the production of feces. With assimilation efficiencies ~10–20% and ingestion rates in the range of the animal's mass per day (Golladay et al. 1983), many consumers of CPOM produce copious amounts of feces. Coprophagy has been reported to be a dietary mainstay in some instances (Hynes 1970) and an important supplement in others (Wotton 1980). Some stream-dwelling invertebrates such as amphipods and isopods produce pellets enclosed in a peritrophic membrane, while most insects apparently produce feces that are less discrete and more variable in size (Shepard and Minshall 1981). Ladle and Griffiths (1980) provide a pictorial description and commentary on size, shape, texture, cohesiveness, and so forth. Most such particles appear to vary between 100 and 1,000 µm in longest dimension, but since a correlation exists between size of particles and the organisms that produced them, the smallest invertebrates probably produce even smaller fecal particles.

Consumers differ in how they attack leaf material, which can affect the appearance of resultant FPOM. Larvae of the crane fly *Tipula* and many limnephilid caddis flies eat all parts of the leaf, both mesophyll and venation, while the peltoperlid stonefly *Talloperla cornelia* avoids venation and concentrate mainly on mesophyll, cuticle, and epidermal cells (Ward and Woods 1986). Fecal pellets from *Tipula* visually resembled macerated leaf fragments and were similar to source material in lignin, hemicellulose, and cellulose content. If one included the noningested fragments, resultant FPOM even more faithfully resembled its source. In contrast, *T. cornelia* produced a macerated FPOM in which lignin content was substantially reduced, especially from leaves with highest initial concentrations. Cellulose was also reduced, while hemicellulose either remained similar or increased.

In addition to their role in changing the palatability and nutritional content of CPOM, aquatic fungi generate substantial amounts of FPOM in the form of asexual spores called conidia. Gessner and Chauvet (1997) determined that nearly half of fungal production is allocated to the production of conidia, which are released into the water and so available to fine-particle feeders. Maximum production of conidia occurred shortly after leaf colonization.

Because the most readily assimilated material is likely to be processed in the steps prior to FPOM production (Figure 7.3), much of what remains is likely to be quite refractory. This is born out by the finding that the respiration rate associated with native detritus was much lower than that of conditioned and mechanically ground oak and hickory leaves (Ward and Cummins 1979). As FPOM is decomposed and reduced in size, one might expect particles to become more refractory to microbial action and lower in nutritional value. A study of the chemical composition and microbial activity of FPOM in relation to particle size supports this expectation (Peters et al. 1989). As particle size decreased from 500 to 10 μm, organic content declined while lignin and cellulose content increased.

Black fly larvae ingest FPOM and DOM and produce larger particulate material in the form of fecal pellets (Wotton et al. 1998). Hershey et al. (1996) observed a 28% increase in the AFDM of FPOM and an alteration of the particle size distribution downstream of a filtering black fly aggregation. Each larva can produce on average 575 pellets per day, and so in dense aggregations ($\sim 600{,}000\,\mathrm{m}^{-2}$ within a 40 m reach of an Arctic tundra stream), the daily production of pellets was estimated at $1.3\text{–}9.2 \times 10^9$. About one third of this material deposits on the streambed and is available to other benthic consumers, thus larval black flies represent an important link between FPOM, DOM, and consumers in benthic communities (Wotton et al. 1998, Malmqvist et al. 2001).

7.2.2 Other sources of FPOM

However tentative is our understanding of the dynamics of FPOM originating in leaf litter, even less is known about other FPOM sources, which could be of equal or greater magnitude (Table 7.1). DOC enters the particulate pool via a number of pathways, and probably in substantial amounts. Input of fine particulates from the forest floor, soil water, and banks and channel of the streambed all can be substantial. Algal cells sloughed from periphyton mats and washed out of lakes and beaver ponds also contribute to total FPOM.

The quality of FPOM originating from terrestrial ecosystems is influenced by the composition of the terrestrial vegetation, position along the river network, and temporal variation in discharge. Several characteristics of fine benthic OM (FBOM) differed among Oregon stream sites in old growth forest dominated by Douglas fir and western hemlock, and young growth stands of Douglas fir and herbaceous vegetation with abundant deciduous trees in the riparian zone (Bonin et al. 2000). The FBOM of streams flowing through young growth stands had lower C/N ratios and higher denitrification potential, as well as greater extractable ammonium, phosphatase activity, and respiration rates, suggesting higher substrate quality and microbial activity compared with streams in older stands. The quality and amount of inputs of terrestrial POM likely are higher at young growth sites, and an observed increase in microbial activity following a storm is evidence of system response to a pulsed input. Benthic respiration and thus microbial activity have also been observed to increase as one proceeds downstream (Webster et al. 1999), which may be the result of changes in OM quality as well as higher temperatures, greater nutrient availability, and increases in substrate quality related to higher algal POM inputs (Figure 7.12).

Not surprisingly, the origin of fine particulates is difficult to infer simply by examining FPOM. However, studies using a variety of techniques give us some insight into the importance of the multiple sources of FPOM just described (Ward et al. 1990). Inspection of fine particles by scanning electron microscopy sometimes allows identification of source material. Another approach makes use of the fact that neither algae nor bacteria contain lignin, and so its presence establishes that the material originated as vascular plant tissue. Lignin oxidation products are indicative of the type, concentration, and degree of preservation of the plant source. Stable C isotope ratios distinguish C-4 grasses from other plants, and the atomic C/N ratio is highest (~20) in relatively unaltered plant detritus, whereas lower values (~10–12) are characteristic of well-decomposed soil OM (Hedges et al. 1986, Devol and Hedges 2001).

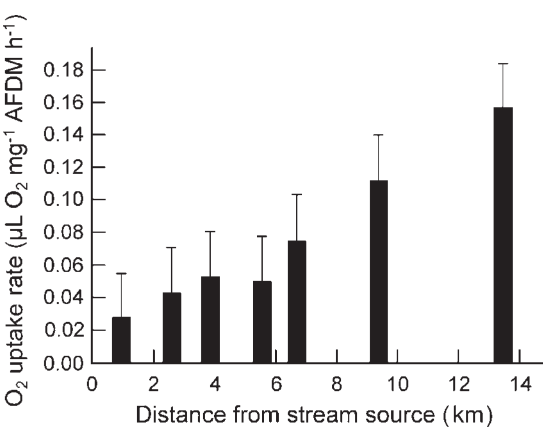

FIGURE 7.12 Downstream variation in benthic FPOM respiration in Ball Creek-Coweeta Creek at the Coweeta Hydrologic Laboratory. Values shown are means and standard errors for all sampling dates for each site. (Reproduced from Webster et al. 1999.)

Employing such techniques, Hedges et al. (1986) analyzed FPOM from the Amazon River by comparing the signatures of river particles to various potential organic sources. They concluded that the majority originated as soil humic material, and at least for large rivers, this conclusion appears to be general (Onstad et al. 2000, Bernardes et al. 2004, Townsend-Small et al. 2005). Based on the ratio of C/N atoms in river seston worldwide (Meybeck 1982), the majority of riverine FPOM most closely resembles soil OM. Lower C/N ratios in FPOM than CPOM and DOM could be related to the presence of microbial biomass or clay minerals (Hedges et al. 1994, Devol and Hedges 2001). Even in headwater streams, our detailed knowledge of the leaf breakdown process not withstanding, it seems likely that most FPOM originates from sources other than fragmentation of leaves. Based on rough calculations of the magnitudes of inputs attributable to soil OM and the breakdown of wood, Ward and Aumen (1986) concluded that leaves and needles were minor sources of FPOM. Sollins et al. (1985) used flotation to separate organomineral particles from fragmented plant material collected from small forested streams in Oregon. The majority of detrital C and N was present as organic material adsorbed on mineral surfaces, rather than as plant fragments.

7.3 Dissolved Organic Matter

DOM typically is the largest pool of organic C in running waters (Fisher and Likens 1973, Karlsson et al. 2005), and fluctuations in quantity and quality can strongly affect microbial metabolism and community structure (Bott et al. 1984, Judd et al. 2006). All DOM originates as natural biological products. Some derives from instream processes described previously, including leachate from leaves and other POM, and by extracellular release from algae and higher plants. In addition, soil and groundwater are major pathways of DOM transport from terrestrial vegetation and wetlands into river water. While the size of the DOM pool indicates its potential importance to heterotrophic energy pathways, much of this material is highly refractory and thus of low bioavailability on timescales relevant to stream transport. However, river water also contains labile DOM, and this material constitutes a potentially important energy source for microbial production and possibly for higher consumers as well.

DOM includes a variety of organic compounds that are potential C sources for microorganisms, and for this reason and because many studies now rely on automated C analysis by combustion of water samples, it often is reported as DOC. For all practical purposes these terms can be interconverted by assuming that DOM is 45–50% organic C by mass. Organic forms of N and phosphorous can be quantitatively significant fractions of DOM, and potentially are available for uptake by algae and heterotrophs.

The size division between FPOM and DOM is one of convenience, usually determined by what passes a 0.45 μm filter. In reality the dissolved fraction is likely to include some smaller bacteria, viruses, and some colloidal OM. Lock et al. (1977) used ultracentrifugation to examine the colloidal fraction, which was defined by a sedimentation coefficient and estimated to correspond to a spherical diameter between 0.021 and 0.45 μm (perhaps 0.01–0.5 μm should be considered the general size range for colloidal OM). In water from a variety of sources in Canada, the colloidal fraction constituted between 29% and 53% of total DOC. According to Thurman (1985), however, the colloidal fraction typically is <10%.

From 10% to 25% of DOM consists of identifiable molecules of known structure: carbohydrates and fatty, amino, and hydroxy acids. The remainder (50–75%, up to 90% in colored waters) can be placed in general categories such as humic and fulvic acids, and hydrophilic acids. Humic acids separate from fulvic acids by precipitating at a pH <2 while fulvic acids remain in solution. Fulvic acids are also smaller than humic acids, which often form colloidal aggregates of high molecular weight (HMW) and may be associated with clays or oxides of iron and aluminum. Fulvic acids generally are the majority of humic substances (Thurman 1985). In the Amazon, for example, fulvic acids were approximately 50% and humic acids 10% of riverine DOC (Ertel et al. 1986).

Primary producers can be important sources of DOM in streams and rivers, releasing mainly low molecular weight (LMW) and labile matter as exudates and from cell lysis (Bott et al. 1984, Bertilsson and Jones 2003). This organic C source may be most available during episodes of high primary production when exudates are produced, and within surface biofilms where exudates and products of cell lysis become concentrated. During springtime periphyton blooms, stream DOC concentrations have been noted to increase as much as 37% from a predawn minimum to a late afternoon maximum, apparently due to extracellular release by algae (Kaplan and Bott 1989).

Leachate from leaf litter and other POM including fish carcasses is a high quality source of DOM that may be seasonally pulsed, as occurs with autumn leaf fall into woodland streams. Some 42% of the autumnal DOC inputs to a small New England stream were attributed to this source (McDowell and Fisher 1976). Exclusion of leaf litter inputs to a stream at the Coweeta Hydrological Laboratory resulted in lower DOC concentrations than in a nearby, untreated reference stream (Meyer et al. 1998).

Instream generation of DOC from leaf litter was estimated to contribute approximately 30% of daily DOC exports, and to be greatest in autumn and winter and during periods of increasing discharge rather than at baseflow. DOC concentrations were higher during the fall and early winter in a deciduous woodland stream in Tennessee (Mulholland 2003).

Soil OM originating in aboveground and belowground terrestrial production is a quantitatively important source of DOC to fluvial ecosystems. Grasslands contain the highest soil OM, deserts the least, and forests are intermediate. The interstitial water of soils usually contains high DOC concentrations, in the range of 2–30 mg L^{-1}, due to solubilization of organic litter (Thurman 1985). Most soil DOC is produced in the organic horizon and from leaf litter and root exudate and decay. Enzymes released by soil microorganisms also contribute to the soil DOC pool (Aitkenhead-Peterson et al. 2003).

DOC that reaches stream channels by surface and shallow subsurface flowpaths is of higher quality and concentration than groundwater DOC, where low concentrations are a consequence of biological and chemical degradation of OM and of physical adsorption. Mineral soils can also adsorb organic molecules, and an increase in the content of clay, aluminum, and iron oxides is usually accompanied by higher adsorption of DOC (Aitkenhead-Peterson et al. 2003). Median values for groundwater DOC are usually <1–2 mg L^{-1} (Thurman 1985), whereas the DOC in shallow soil water can be considerably higher. In small streams in North Carolina, Meyer and Tate (1983) recorded DOC concentrations of 2–12 mg L^{-1} in soil water in contact with the active root zone, compared to 0.2–0.7 mg L^{-1} in subsurface seeps. Similarly, in the catchment of an Alberta stream, the median DOC concentration in soil interstitial waters was 7 (range 3–35) mg L^{-1}, whereas shallow groundwater in the saturated zone contained 3 mg L^{-1} DOC (Wallis et al. 1981). DOC of terrestrial origin is rich in aromatic components such as lignin and tannins because these compounds are abundant in terrestrial vegetation (Benner 2003), and as we shall see these compounds are less accessible to microorganisms.

Precipitation is a highly variable source of DOC, influenced by contact with dust and pollen (Aitkenhead-Peterson et al. 2003). When rain water is intercepted by leaves of the forest canopy, leaching removes significant amounts of OM. Fisher and Likens (1973) estimated an average value of 17.8 mg L^{-1} for canopy drip in a hardwood forest in New England. Precipitation indirectly affects riverine DOM through its influence over soil moisture and hydrologic flowpaths. Water that moves near the soil surface has greater contact with the organic horizon of soils, resulting in higher DOC concentrations (Mulholland 2003). Flowpaths also influence the temporal response of DOC concentrations to increases in rainfall. In well-drained soils, an increase in streamwater DOC during a storm is expected due to shallow subsurface flowpaths and flushing of soil DOC. In contrast, in streams draining wetlands, surface flow is dominant and increased rainfall may produce a decrease in DOC concentrations as a dilution effect (Mulholland 2003).

7.3.1 Uptake of DOC

DOM is removed from streamwater by both abiotic and biotic processes. The principal biotic processes are uptake by microorganisms, assimilation of the organic C into microbial biomass, consumption of this heterotrophic production, and its eventual remineralization to CO_2 by community respiration. DOC is also removed from the water column by abiotic sorption and transformed into other compounds by photodegradation. Dahm (1981) estimated that adsorption onto clays and chemical complexing with oxides of aluminum and iron accounted for up to one third of the initial removal of DOC from the water column. Over a period of several days, however, microbial uptake was responsible for the majority of DOC disappearance from the water column into the sediment layer. Photochemical degradation results in the transformation of DOC into other inorganic and organic compounds. Although it is not clear whether these organic products are more or less available to bacteria than the initial DOC, most studies conducted in freshwater systems using humic compounds or DOC from vascular plants have found that photochemical degradation enhances biological availability (Moran and Covert 2003).

The incorporation of DOC into microbial biomass is of interest because of its potential as an energy input into stream food webs. It is a central tenet of this chapter that detrital energy pathways can be as or more important than primary production, and DOC can be a major C source for heterotrophic microorganisms. Bacteria likely play an even greater role in this regard than do fungi, but it is also apparent that different microorganisms are intimately intertwined with various OM sources as well as with algae in complex energy-processing sites known as biofilms (Figure 7.13). Experimental study of the response of bacterial abundance and biomass to different C sources and nutrient levels is the basis for most current knowledge, but rapid advances in microbial ecology including the ability to assay for key enzymes and to survey microorganisms for the functional genes that encode particular enzymes promise new insights

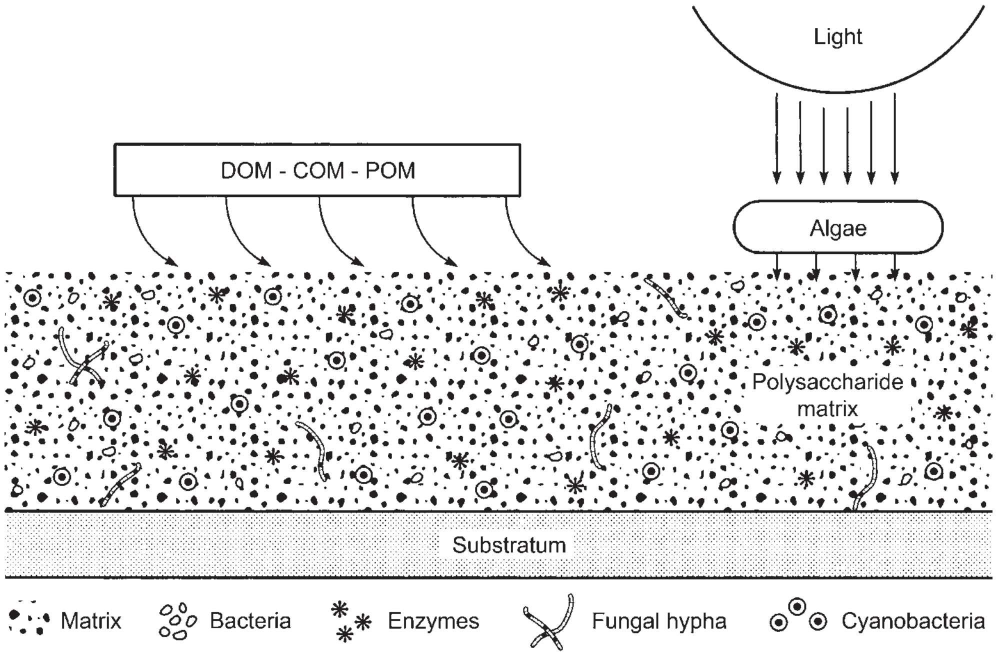

FIGURE 7.13 A structural and functional model of the organic microlayer-microbial community found as a surface biofilm on stones and other submerged objects in streams. The matrix of polysaccharide fibrils produced by the microbial community binds together bacteria, algae, and fungi, and is inhabited by protozoans and micrometazoans that graze on this material. Detrital inputs include dissolved, colloidal, and fine particulate organic matter, while light energy is trapped by algal photosynthesis. Within the matrix, extracellular release and cell death result in enzymes and other molecular products that are retained due to low diffusion rates and thus available for utilization by other microorganisms. (Modified from Lock 1981.)

into such processes as leaf breakdown and biofilm activity (Findlay and Sinsabaugh 2006, Zak et al. 2006).

In addition to surface biofilms, bacteria in the water column of rivers and attached to particles can process available DOC and potentially be important in food webs. Bacteria are responsible for a large proportion of ecosystem respiration in large rivers (Richey et al. 1990; Benner et al. 1995), and the quantity of C lost by respiration is nearly 13 times greater than total organic C transported by the Amazon River to the ocean (Richey et al. 2002). Carbon is generally considered to be an important limiting resource for bacterial production, and so variation in the quantity and quality of DOC and POC sources is of considerable importance. In addition, nutrients, temperature, oxygen, and many other environmental factors will influence the incorporation of these C sources into microbial biomass. The following sections summarize current knowledge of microbial utilization of DOM, primarily by bacteria, on and within the streambed and in the water column. Because microorganisms commonly are associated with particulate matter, utilization of DOM does not separate easily from utilization of fine POM.

7.3.2 Biofilms

Assemblages of microorganisms (bacteria, fungi, and algae) growing on the streambed and other surfaces are called biofilms. Biofilm formation involves the conditioning of surfaces by macromolecule sorption, followed by the attachment of bacteria, the production of a polysaccharide matrix and the development of the biofilm itself, including the growth and later detachment of autotrophic and heterotrophic microorganisms (Fischer 2003). Biofilms are embedded in an exopolysaccharide matrix produced by microorganisms and forming on surfaces of stones, sediments, plants, decaying wood and leaves, and on suspended particles in larger rivers. This matrix binds together algae, bacteria, fungi, detrital particles, various exudates, exoenzymes, and metabolic products in an organic microlayer (Figure 7.13). Additional organic compounds, including proteins, nucleic acids, and humic compounds also occur in the matrix (Sinsabaugh and Foreman 2003). Energy transformations within biofilms include the conversion of light to chemical energy by algal photosynthesis, adsorption and microbial uptake of heterotrophic C, and internal transfers due to extracellular release and cell lysis. Both autotrophs and heterotrophs are likely to benefit from the internal fluxes of this highly symbiotic association.

Properties of the polysaccharide matrix of the biofilm have the potential to influence energy and mineral transfers. By reducing diffusion rates, the organic microlayer tends to retain and concentrate compounds, particularly those of higher molecular weight. In addition, the polysaccharide matrix can act as an ion exchange system, attracting and binding charged organic molecules, anions, and cations (Lock 1981, Lock et al. 1984). DOC is adsorbed by the matrix and later diffuses into the biofilm, where it can be used by microorganisms. LMW organic compounds can be taken up directly by bacteria from above or within the biofilm, whereas larger molecules require hydrolysis by extracellular enzymes prior to bacterial uptake (Pusch et al. 1998, Fischer 2003).

Exoenzymes and enzymes derived from cell lysis may be retained and remain active, facilitating the release of molecular products. The accumulation of exoenzymes within the microlayer permits surface film bacteria to divert resources from enzyme synthesis to microbial growth, thereby reducing energy demands on microorganisms for enzyme synthesis. Sampling of biofilm from the surfaces of stones (Sinsabaugh et al. 1991) and organic substrates (Golladay and Sinsabaugh 1991) has documented that exoenzyme accumulation occurs as suggested under the Lock model. This has the beneficial effect that enzyme activity can be spatially distant from the microorganisms that produced the original enzymes, enhancing the availability of organic C to microorganisms and helping to maintain growth in an environment where C and nutrient sources are variable (Pusch et al. 1998).

Under environmental conditions that favor a well-developed algal component of the biofilm, such as stony substrates receiving ample light, heterotrophic bacteria benefit from the presence of algae. Periphyton can provide substantial amounts of dissolved organics for bacterial uptake (Kaplan and Bott 1982) and probably are responsible for secreting most of the "slime" structure. Geesey et al. (1978) found that measures of bacterial biomass (ATP) and periphyton biomass (chlorophyll *a*) in the epilithon fluctuated together, and suggested that bacterial populations were dependent upon the periphyton for their establishment and maintenance. An evaluation of 69 streams from sites in Kentucky and Michigan using algal biomass, DOC, and nutrients as possible predictors of bacterial cell density found that algal biomass was the best predictor, but the relationship was not evident at low algal biomass (Rier and Stevenson 2001).

Although biofilms can develop both in the light and in the dark, and thus on the undersides of stones, within the sediment profile and even within caves (Simon et al. 2003), biofilm structure and function exhibit distinct differences between light and dark environments. Comparison of a biofilm in an open channel to one inside a dark pipe within the stream channel documented greater DOC uptake in the former (Romani et al. 2004). The light-grown biofilm supported greater biomass and activity of bacteria due to its higher algal biomass, exudates, and development of a polysaccharide matrix. The dark-grown biofilm, in contrast, was highly dependent on the supply and quality of OM and was more efficient in the uptake of labile molecules. Indeed, labile DOC from streamwater may play an important role in bacterial growth during initial colonization, while DOC from algae may enhance bacterial growth at later stages of biofilm development (Sobczak 1996).

Biofilms readily develop on the surfaces of leaves and wood. Microbial biomass and exoenzyme accumulation were greater on wood (ice-cream sticks of white birch) than sugar maple leaves in a boreal river in upper New York State (Golladay and Sinsabaugh 1991), suggesting that wood may be an important site of biofilm development in streams. McNamara and Leff (2004) tested the response of several bacteria species to leachate from sugar maple leaves at various stages of decomposition using an agar substrate that allowed the leachate to diffuse through filters on which bacteria were enumerated. Species differed in their response to components of leaf leachate such as tolerance to phenolic compounds, demonstrating how the composition of microbial assemblage can influence its ability to utilize the mixture of labile, refractory, and inhibitory compounds. Measurements of uptake of tree-tissue leachate in streambed sediments within recirculating mesocosms found that most DOC was bioavailable, and by extrapolation to bacterial demand for DOC in White Clay Creek, Pennsylvania, could support up to half of community respiration (Wiegner et al. 2005). Tank and Webster (1998) reported higher microbial respiration, fungal biomass, and extracellular enzyme activity in wood biofilms in a litter-excluded stream compared with a reference stream, suggesting competition for C or nutrients between microorganisms associated with leaf and wood substrates.

The bioavailability of DOC (assayed as micrograms of bacterial biomass produced per milligram of DOC present) ranges over two orders of magnitude (Meyer 1994), varying with the composition of the DOC source, with nutrients, current, and other environmental factors, and possibly with changes in the composition of the microbial assemblage. Biofilm development on nutrient diffusing artificial substrates has demonstrated that bacterial taxa differ in their responses to various combinations of DOC (glucose, leaf leachate, and algal exudates) and inorganic nutrients (nitrate and phosphate), and these response patterns vary seasonally (Olapade and Leff 2005). The greatest response was to glucose, a highly labile, LMW form of DOC. Extracellular enzyme activity of hyporheic bacterial communities was also greatest when treated with labile DOC (glucose, bovine serum albumin), compared with refractory (tannic acid) and natural (leaf leachate) DOC sources (Findlay et al. 2003).

Microbial response to terrestrially supplied DOC supports expectations that DOC bioavailability varies with catchment vegetation and flowpaths. Benthic microbial communities in streamside microcosms along a forested stream responded immediately and positively to increases in terrestrially derived DOC, and more so to DOC extracted from upper soil horizons than from deeper soils (Kreutzweiser and Capell 2003). Findlay et al. (2001) compared water draining from pasture, native forest, and pine plantation in the Whatwhata catchment on the North Island of New Zealand to evaluate the effects of catchment vegetation on the ability of DOC to support bacterial growth. Water from the pasture surface flowpath supported twice as much bacterial production as pasture groundwater, and differences among the three vegetation types were detected from surface flows but not from groundwater.

Nutrients may limit microbial production when an abundant C source supports high microbial production. Microbial respiration on wood biofilms increased in response to nutrient addition in a reference stream but not in a litter-excluded stream, suggesting lowered nutrient immobilization and thus higher nutrient availability in the absence of decomposing leaf litter and its microbial flora (Tank and Webster 1998). A comparison of nutrient limitation of biofilm algae and fungi in ten streams in North America found that fungi responded more to nutrient addition than did algae, although for both autotrophs and heterotrophs, N limitation was more common than P limitation (Tank and Dodds 2003).

Using streamside flumes to observe biofilm development under slow and fast current velocities, Battin et al. (2004) found that slow velocities favored thicker biofilms in which internal cycling of C was more important, based on DOC uptake and microbial growth rates. Manipulation of substrate heterogeneity resulted in an immediate and significant increase in the respiration of the benthic biofilm of a Virginia piedmont stream, probably due to changes in near-bed flow velocity and turbulence intensity (Cardinale et al. 2002b).

Biofilm studies have focused primarily on surfaces that have some contact with current, and less is known about the role of biofilms within the sediments and into the hyporheic zone. Permeability of the sediments and the hydraulic residence time of the infiltrating water will strongly affect how much water column DOC exchanges with pore water. Battin (2000) showed that water velocities affected transport of solutes into surface biofilms, and higher velocities helped overcome diffusional limitation of material exchange. At least in some instances the availability of POC rather than infiltration of DOC is likely to determine hyporheic microbial metabolism (Brugger et al. 2001). A synthesis of numerous studies of bacterial production documented a significant positive relationship with the amount of OM in the sediments (Cole et al. 1988). Findlay et al. (1986b) reported daily bacterial production to be an order of magnitude higher in sediments of backwater areas than in sandy regions of two blackwater rivers of the southeastern United States, corresponding to differences in organic content between sites. Similarly, bacterial production was higher in an Appalachian mountain spring (Crocker and Meyer 1987) and in a Pennsylvania stream (Kaplan and Bott 1989) than in the two blackwater rivers, and sediment OM content also was higher at the former sites.

The relative contributions of POM versus DOM to bacterial production within sediments

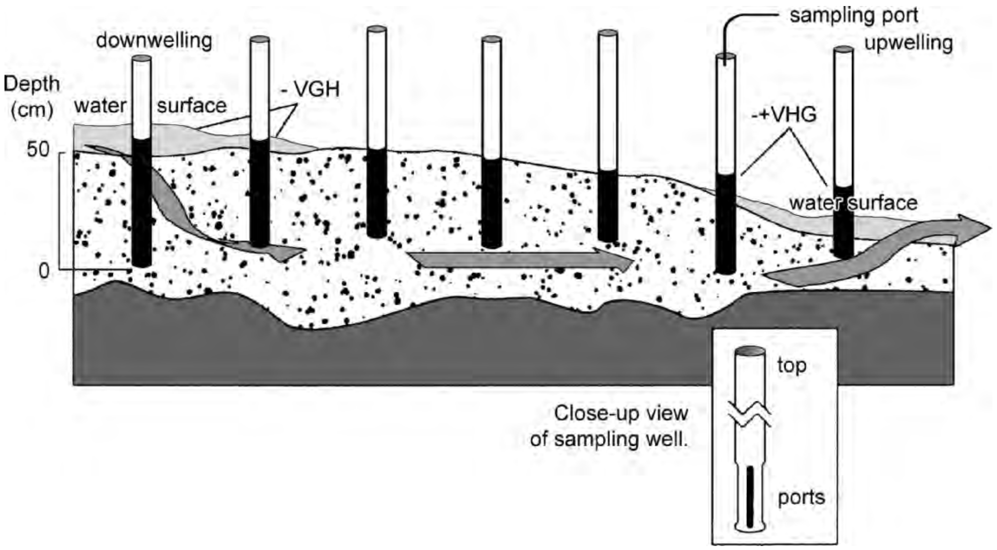

FIGURE 7.14 Sampling wells positioned along a hyporheic flow path to evaluate DOC transfer from the water column to benthic biofilms. Negative vertical hydraulic gradient (−VHG) indicates down-welling of surface water while a positive gradient (+VHG) indicates upwelling of hyporheic water. (Reproduced from Sobczak and Findlay 2002.)

will vary with the supply of each, and with hyporheic flowpaths and water residence time (Findlay and Sobczak 2000). Within the hyporheic interstices of the Toss River, a gravel-bed stream in Switzerland, highest bacterial production occurred within interstices dominated by surface water inflow, and an attenuation of bacterial abundance was observed in deeper sediment strata (Brunke and Fischer 1999). The abundance of several hyporheic invertebrate taxa, taxon richness, and total invertebrate density correlated with bacterial abundance and production, indicative of a consumer response to resources. In the Spree River, Germany, bacterial production rates in the sediments (1.3–5.4 μg C cm^{-3} h^{-1}) were nearly three orders of magnitude higher than in the water column (0.9–3.9 μg C L^{-1} h^{-1}), and bacterial respiration was sufficiently high to metabolize a large proportion of the organic C retained in the sediments (Fischer and Pusch 2001). To evaluate the influence of hyporheic flowpaths on the availability of streamwater DOC within the sediments beneath the streambed, Sobczak and Findlay (2002) sampled DOC and oxygen concentrations in wells located along transects on gravel bars, where down-welling of surface water was indicated by negative hydraulic gradient (Figure 7.14). About 38–50% of the surface water DOC was removed, and declines in DOC along the flowpath were accompanied by decreases in oxygen concentration and bacterial activity, suggesting that DOC removal was due to bacterial metabolism.

In lowland rivers where sediments tend to be finer and water circulates less freely, microbial metabolism within the streambed is likely to show a vertical profile, more so if the sediments are vertically stratified and less so if they are shifting. Based on the rapid turnover of organic C in sediments, Fischer et al. (2002) concluded that sediment dynamics significantly foster organic C metabolism in lowland rivers and thus strongly influence the metabolism of the whole ecosystem. Comparing biofilms growing on stones and on sandy substrata in a Mediterranean stream in northeastern Spain, Romani and Sabater (2001) observed higher extracellular enzymatic activity in episammic compared with epilithic biofilms, indicating the much greater availability of POC in sandy substrates relative to gravel, and the likely importance of sand habitats to OM processing.

7.3.3 Bacterioplankton

Heterotrophic bacteria within the water column of rivers obtain C from organic molecules that are part of the DOC pool. Bacterioplankton production is expected to be of importance mainly in lowland rivers, where bacterial doubling times potentially can exceed washout rates, provided that DOC is of sufficient quality and quantity and other environmental conditions are favorable. However, microbial production in the water column generally is much less than benthic production. In the case of the River Spree, mentioned earlier, bacterial production in the sediments was nearly three orders of magnitude higher than in the water column. Estimates of production by bacterioplankton vary over at least two orders of magnitude (Figure 7.15), ranging from 0.14–0.52μg C L^{-1} h^{-1} in blackwater rivers in the southeastern United States, the Amazon and Orinoco Basins (Benner et al. 1995, Castillo et al. 2004) to 40–75 μg C L^{-1} h^{-1} in anthropogenically enriched rivers like the Maumee and the Ottawa in Ohio (Sinsabaugh et al. 1997). Values for planktonic bacterial abundance are less variable than bacterial production, ranging between 0.05×10^6 cells mL^{-1} in the Kuparuk River in Alaska and 5×10^6 cells mL^{-1} in more disturbed systems like the Hudson River and the River Rhine (Findlay et al. 1991, Admiraal et al. 1994).

Environmental variables likely to influence planktonic bacterial production, in addition to the amount and quality of DOC, include nutrients, temperature, and pH. Greater availability of nutrients can directly enhance bacterial production whenever the OM that serves as a C source has a low nutrient content, thus forcing bacteria to obtain nutrients from elsewhere (Findlay 2003). Nutrient supply can also benefit bacterial production indirectly, by enhancing primary production and thus the C supply. The addition of various combinations of nutrients to bacterioplankton samples cultured in situ has shown

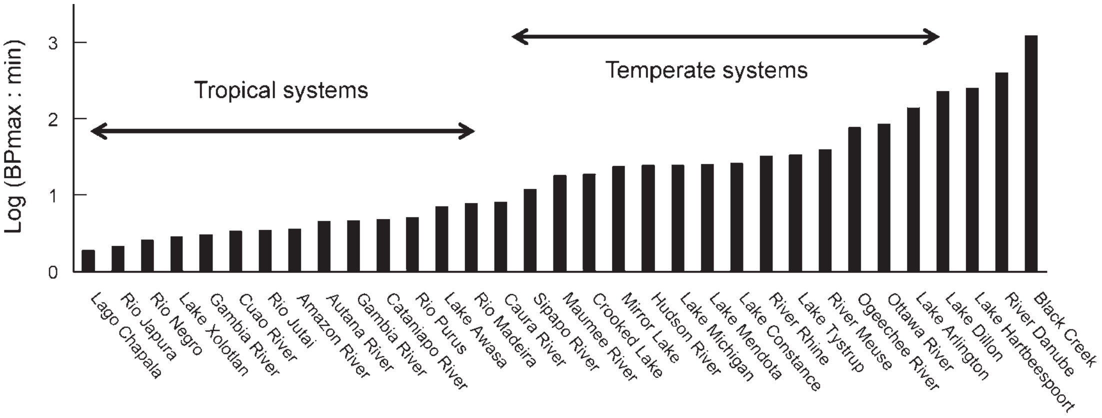

FIGURE 7.15 Annual variation in bacterial production (BP) measured as the maximum: minimum for several freshwater systems. A logarithmic transformation was applied to the vertical axis to reduce the scale. (Reproduced from Castillo et al. 2004.)

P limitation in clearwater rivers of the Amazon basin (Farjalla et al. 2002) and in clear and blackwater rivers draining the Guayana Shield in the Orinoco Basin (Castillo et al. 2003). In the Río Negro, a blackwater tributary of the Amazon River, bacterial production was enhanced by the simultaneous addition of glucose, ammonium, and P (Benner et al. 1995), which suggests that C, N, and P were available in approximately the stoichiometric ratio needed by bacteria. The influence of temperature is reflected in seasonal variation in bacterial metabolism, with higher values during the warmer months (Edwards and Meyer 1986, Findlay et al. 1991). The effect of pH is ambiguous, as some studies suggest that bacterial extracellular enzymes can be negatively affected by acidification (Benner et al. 1989, Schoenberg et al. 1990); however, some exoenzymes exhibit an optimum at low pH (Münster et al. 1992). Low pH may also affect the availability of DOC to bacteria because the cell membrane is more permeable to hydrophilic compounds, and at very low pH, humic compounds become more hydrophobic and thus are less permeable substrates (Edling and Tranvik 1996).

DOC quality and composition likely are the most important factors limiting production of bacterioplankton. In fact, correlations of bacterial production with total DOC are rare (Findlay 2003), probably because bacterial production reflects the amount of labile DOC rather than the total (Findlay et al. 1998). The evidence suggests that some constituents of the heterogeneous mix of molecules that comprises DOC are more available than others, and preferential removal of LMW DOC has been reported in several studies (Kaplan and Bott 1982, Meyer et al. 1987, Kaplan and Bott 1989). Peptides and sugars support a large fraction of bacterial production, evidence of the high bioavailability of these compounds, which can be found free or forming complexes with humic molecules (Foreman et al. 1998, Findlay and Sinsabaugh 1999). Bioavailability is also related to the proportion of aliphatic compounds, which are more abundant in algal and macrophyte leachate than in leachate from woody plants (Sun et al. 1997). However, there is evidence that bacteria can utilize humic substances, which are rich in aromatic components (Moran and Hodson 1990, Tranvik 1990, Wetzel 1995), but at a lower growth efficiency compared to LMW DOC (Amon and Benner 1996).

Direct measurement of the amount of labile DOC is difficult because DOC is composed of many different compounds, many of which are not well characterized (Volk et al. 1997, Seitzinger et al. 2005). DOC lability can vary with its sources and the type of molecules (Findlay and Sinsabaugh 1999) and be influenced by nutrient availability and the composition of the bacterial assemblage (Cottrel and Kirchman 2000, Findlay 2003). Moreover, the timescales of inputs can vary dramatically, ranging from highly episodic storm-induced transport to gradual leaching of organic material into stream channels or adjoining sediments. Although different methods have been used to directly measure the concentrations of individual compounds or sources of DOC, the amount of labile DOC routinely is estimated from bacterial production and respiration over extended incubations (Meyer et al. 1987, Amon and Benner 1996). DOC lability has also been measured as the decline in DOC concentrations due to bacterial uptake in batch incubations (Meyer et al. 1987) or in biofilm reactors where indigenous bacterial populations are maintained over time (Kaplan and Newbold 1995, Volk et al. 1997). One can also relate DOC composition to bacterial growth by measuring the activity of extracellular enzymes, because they are an indicator of substrate availability when C is limiting (Sinsabaugh et al. 1997).

Estimates of labile DOC availability based on bacterial growth in batch incubations suggest that, on average, 19% of riverine DOC is labile, although this value could be <1% in blackwater rivers (Søndergaard and Middleboe 1995). Because this study included some large European rivers that receive wastewater inputs, the average value of 19% labile DOC may not be representative of less disturbed rivers. Amon and Benner (1996) estimated that 1.4–7.5% of DOC in the Amazon was labile. Based on DOC disappearance in batch incubations, del Giorgio and David (2003) estimated that on average 10% of riverine DOC was consumed during 1–3 day incubations; and this estimate was low compared with lakes and marine systems, possibly because the origin of DOC in the terrestrial landscape and its flow path into riverine systems provide ample opportunities for processing in soils. Using a biofilm reactor, Volk et al. (1997) estimated that on average 25% of DOC of a headwater stream was labile; the composition of the labile portion included humic substances (75%), carbohydrates (30%), amino acids (4%), and DOC $>$ 100 kDa (39%). Carbohydrates were mostly polysaccharides and were bonded to humic compounds, as were most of the amino acids. Although only 25% of streamwater humic compounds were consumed in the bioreactor, they represented a large fraction of the labile DOC (75%), which contradicts the general view that humic substances are refractory.

Although the supply of organic C and nutrients in lotic ecosystems likely is limiting to bacterioplankton growth much of the time, microbial respiration in the water column and sediments of higher-order rivers may nonetheless be sufficient to mineralize large amounts of DOC. The lower Hudson River is almost always supersaturated with CO_2, evidence of an excess of respiration over production, and DOC concentrations decline as one proceeds downriver, evidence of its mineralization by microbial activity (Cole and Caraco 2001). In the lower sections of large rivers, significant quantities of organic C in transit are returned to the atmosphere by CO_2 evasion. These results suggest that although some fraction of DOC likely is incorporated into aquatic food webs through bacterial production, a greater fraction of riverine DOC is converted to CO_2 by instream respiration.

7.4 Summary

Particulate and DOM originating both within the stream and in the surrounding landscape is an important basal resource to fluvial food webs. Detritus-based energy pathways can be particularly important, relative to pathways originating from living primary producers, in small streams shaded by a terrestrial canopy and in large, turbid rivers with extensive floodplains. Coarse, fine, and dissolved OM originate from a myriad of sources. Leaves, fruits, and other plant products that fall or are transported by wind and gravity into the stream are major CPOM inputs, and the carcasses and feces of insects and larger animals also contribute. Most FPOM originates from the fragmentation of larger particles, particularly terrestrial vegetation, and is likewise transported into the channel or is produced by the breakdown of larger particles within the stream. Soil water is usually the major source of DOM, which is a heterogeneous pool of molecules of widely varying bioavailability. The quality and accessibility of nonliving OM as a basal resource typically depends on the presence of bacteria or fungi whose degradative activity can alter palatability or accessibility of OM to consumers. Microorganisms are critical mediators of OM pathways, aiding in the processing of POM and uptake of DOM, and markedly increasing the energy available to consumers both small and large.

Autumn-shed leaves are a primary CPOM input to forested streams in temperate regions, and their decay serves as the primary model of CPOM processing. Leaves, which serve as the OM or C substrate, quickly release DOM when wetted, and soon are colonized by microorganisms and invertebrates, which enhance fragmentation and mineralization. The original leaf is transformed into several products including microbial and shredder biomass, FPOM, DOM, nutrients, and CO_2. Leaf breakdown rates vary considerably and as a consequence the supply of CPOM to the stream food web, although pulsed seasonally, is less so than would be the case if all leaves had similar breakdown rates. Temperature, oxygen availability, and nutrient supply are key environmental variables that influence the decomposition process. Colonization by microorganisms, particularly fungi, is critical to leaf decomposition as well as the leaf's nutritional value, although bacteria play a greater role as particle size diminishes and the presence of leaf-shredding invertebrates is also important. When detritivorous invertebrates are excluded, the breakdown process is significantly slowed.

FPOM is an amorphous collection of particles <1 mm, originating from instream CPOM breakdown, sloughed cells of algae, invertebrate fecal pellets, and fragments derived from the terrestrial environment. The uptake of DOM within biofilms provides another avenue for FPOM production. Black fly larvae, by consuming bacteria and very small FPOM and producing fecal pellets that are larger than some of the material that they ingest, illustrate yet another pathway for the generation of organic particles. The sources, processing, and eventual fate of FPOM are less well accounted for than is the case for CPOM. Although the breakdown of CPOM within the stream is the best-studied pathway, it seems likely that FPOM originates from many other sources. Because of the small size of FPOM, bacteria likely are more important than fungi in microbial processing.

DOM typically is the largest pool of organic C in running waters and is incorporated into POM due primarily to uptake by microorganisms. Soil and groundwater are major pathways of DOM transport from terrestrial vegetation and wetlands into river water, whereas leachate from leaves and from extracellular release by algae and higher plants can be temporally important instream sources. Because it comprises a heterogeneous mix of bioavailable, refractory, and perhaps inhibitory compounds, total DOM is a poor predictor of microbial metabolism. DOM is removed from streamwater by both abiotic and biotic processes, and DOM uptake appears to be greatest in biofilms, which are symbiotic assemblages of bacteria, fungi, and algae that interact both synergistically and antagonistically in their demand for C and nutrients. Because biofilms are embedded in a polysaccharide matrix, exoenzymes and exudates resulting from cell lysis and extracellular release are held within the matrix by low diffusion rates, allowing microorganisms to benefit from available compounds and possibly permitting bacteria to shift energy from enzyme production to cell growth. Biofilms can develop in the dark, in which case the algal contribution is negligible, but heterotrophic microorganisms benefit most when algal production within the biofilm is vigorous. Biofilm development on substrates and to a lesser degree on suspended POM depends greatly on the presence of labile DOM compounds and in some circumstances on nutrient availability as well. LMW DOM such as glucose can greatly stimulate uptake and growth by microorganisms, and at present the most effective assay of DOM bioavailability is via microorganism response.

Particulate and DOM are important energy sources in almost all lotic ecosystems and frequently can be the dominant energy source. Detritus and the associated microbial biomass, along with algae and other primary producers, form the basal resources for the various trophic levels occupied by invertebrates, fishes, and other consumers in stream food webs. We turn now to the diversity of consumers and the feeding adaptations that govern their effectiveness with the diverse producer and detrital resources described in this and the preceding chapter.

Chapter eight

Trophic relationships

The network of consumers and resources that comprise fluvial food webs is supported by a diverse mix of energy supplies that originate within the stream and beyond its banks. These include the living resources of algae and higher plants, and the nonliving resources of particulate organic matter (POM) and dissolved organic matter (DOM). Microorganisms are important mediators of organic matter availability and there is increasing evidence of their importance as a resource to both small and large consumers. Additionally, energy subsidies in the form of falling terrestrial arthropods and the eggs and carcasses of migrating fish contribute to the support of many stream-dwellers. Nor is all of the energy provided within a stream reach consumed within that reach, as downstream export, insect emergence, and fish movements supply energy to distant ecosystems.

Trophic organization in river ecosystems can be complex and indistinct. Many consumers are polyphagous rather than monophagous, and exhibit considerable overlap with one another in their diets. The gut contents of invertebrates usually are difficult to distinguish, so these consumers often are characterized by the unspecific term of herbivore–detritivore. At least in temperate waters, the vast majority of fishes eat invertebrates. As a consequence, while a particular species may be classified solely on the basis of what it eats – herbivore, predator, detritivore, and so on – the resulting categories are of limited usefulness because they offer very few distinctions among feeding roles. However, further resolution can be achieved by distinguishing among feeding roles on the basis of how the food is obtained, rather than solely in terms of what food is eaten. When several species consume a common resource and acquire it in similar fashion, they are considered members of the same guild. Thus, a fish species that captures invertebrate prey directly from the bottom would occupy a different guild from another species that consumes the same prey, but captures them from the water column.

The guild concept is useful because it provides a reasonable degree of subdivision in feeding roles for both invertebrate and vertebrate consumers in streams, where the high degree of polyphagy frustrates adequate subdivision using food type alone. The particular species in a guild may change seasonally or geographically with, one presumes, little effect on trophic function. When invertebrates are divided into feeding guilds on the basis of what is eaten and how the resource is obtained, we refer to these categories as functional feeding groups (FFGs) (Cummins 1973), but the meaning is the same. It is important to note that members of different invertebrate functional groups may consume the same resource: for example, fine particulate organic matter (FPOM) can be captured from the water column or collected from depositional locales. The main difference is not the resource, but the organism's method of acquiring it.

Historically, the study of trophic relationships has emphasized the larger animal consumers, but a growing appreciation of the role of microorganisms coupled with methodological advances have led to a better understanding of the importance of microbial food webs. Biofilms, in particular, have been shown to be important energy complexes where algae and microorganisms living in close association are able to capitalize on the energy obtained from sunlight and from organic matter, and so autotrophic and heterotrophic pathways can be closely linked. The smallest consumers of microbial populations are protozoans and micrometazoans, and these continue to be an understudied component of fluvial food webs.

8.1 Microbial Food Webs

Bacteria and fungi utilize nonliving organic matter as a carbon (C) source, fueling microbial production and remineralizing that C as CO_2. In the case of POM, such as decomposing leaves, microbial activity may make the organic substrate more accessible to large consumers such as leaf-shredding insects by softening the tissues, and the fungi and bacteria are themselves an easily assimilated source of C. The uptake of DOM by microorganisms provides a pathway for an abundant C source to enter fluvial food webs. Studies of lake and marine systems (Pomeroy and Weibe 1988) and more recently of rivers and streams (Hall and Meyer 1998) document that C flux through microbial food webs is much greater than was previously recognized.

Microbial production can be consumed directly by those organisms capable of ingesting individual cells and biofilms, or it can be ingested through its association with larger particles, including FPOM and coarse particulate organic matter (CPOM). Ingestion of individual bacterial cells implies a food chain of small and then larger microconsumers before eventually reaching macroinvertebrates and fish, raising the possibility that the original microbial production is largely dissipated within a "microbial loop." Thus, a key question has been whether the microbial food web is of interest primarily in its own right and for its role in recycling nutrients and remineralizing C, or whether it also is important as a pathway of energy flux to higher trophic levels. Current evidence supports both possibilities.

The likely primary consumers of microbial production, especially of bacteria (it has long been recognized that fungi are consumed along with leaf fragments by macroinvertebrates), are the meiofauna. These are protozoans and metazoans <0.5 mm in length, and possibly as small as 10 μm. The early instars of macroinvertebrates may be included as "temporary" meiofauna if they fall within this size range. These are an often neglected component of the fauna and may contribute half or more of the diversity and abundance of stream ecosystems, particularly due to rotifers and larval midges of the Chironomidae (Robertson et al. 2000). Most of the meiofaunal groups, including protozoans, gastrotrichs, rotifers, nematodes, microturbellarians, small oligochaetes, and microcrustaceans, are suspension feeders or browsers feeding on bacteria or on small particles coated with biofilm. Very few studies have examined this feeding link, although Perlmuter and Meyer (1991) documented significant consumption of bacteria by a harpacticoid copepod. Some studies have shown that flagellates and ciliates are able to exert significant grazing pressure on bacteria in streambed sediments (Bott and Kaplan 1990) and in the water column (Carlough and Meyer 1990). The effectiveness of direct meiofaunal consumption likely varies with the composition of the assemblage, and has been found to be greater when large ciliates and rotifers are present (Borchart and Bott 1995). Predator–prey linkages within the meiofauna also are little studied, although many taxa of predaceous habit are known from among the rotifers, cyclopid copepods, oligochaetes, microturbellarians, mites, and nematodes. The larger members of the meiofauna may be consumed by predaceous invertebrates such as predatory tanypod midges (Schmid and Schmid-Araya 1997), larger predators such as *Sialis* and *Plectrocnemia* (Lancaster and Robertson 1995), and even by fish, as Rundle and Hildrew (1992) document for the stone loach *Noemacheilus barbatulus* in English streams. Because members of the meiofauna are small and soft-bodied, assessing their presence in the guts of predators obviously is a challenge, and the resultant data are qualitative rather than quantitative (Schmid-Arraya and Schmid 2000).

Bacterial production within the water column usually is modest (Figure 7.15), although it can be important in larger rivers, especially those with floodplains and back channels (Meyer 1990) or receiving organic enrichment (Admiraal et al. 1994). Even under the most favorable assumptions for suspended bacteria, however, benthic bacteria dominate community respiration (Edwards et al. 1990). Some filter feeders are capable of direct capture of bacterial cells, including mollusks, cladocerans, and black fly larvae, but it is doubtful that water column bacterial production is important to the macroconsumers of river ecosystems, and instead the primary function of bacterial production is C mineralization.

In benthic food webs the presence of biofilms and association of bacterial cells with POM in sediments and on substrates facilitates the direct ingestion of microbial biomass by macroconsumers (Lodge et al. 1988, Meyer 1994). This potentially allows microbial C to bypass a lengthy food chain and reach macroinvertebrates in sufficient quantity to contribute significantly to the support of higher trophic levels, as has been nicely demonstrated by a whole stream addition of ^{13}C sodium acetate to label the benthic bacteria of a small stream at the Coweeta Hydrologic Laboratory (Hall and Meyer 1998). The label soon appeared throughout the food web, including in invertebrate predators. Macroinvertebrates derived from 0% to 100% of their C from bacteria and this amount was significantly related to the percent of amorphous detritus in invertebrate guts (Figure 8.1), so it is likely that biofilm was ingested incidentally through the consumption of particles of FPOM and CPOM. The assimilation of bacterial C may also have resulted from consumption of bacterial exopolymers secreted within the "slime" and consumed by the grazing of substrate surfaces. Enrichment of stream ecosystems with highly labile dissolved organic carbon (DOC) provides further evidence of a direct connection to higher trophic levels. When the amount of bioavailable C was increased in a small stream by the addition of dextrose, the density, growth, and respiration of epilithic bacteria increased in a treatment reach compared to the control, and growth rates of chironomid larvae also increased (Wilcox et al. 2005).

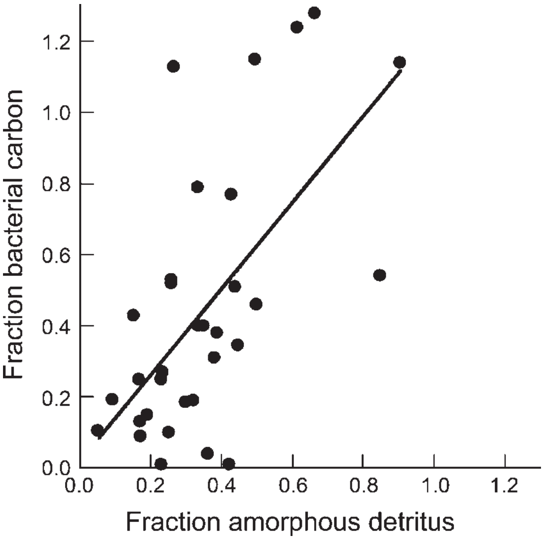

FIGURE 8.1 Relationship between the fractions of invertebrate carbon derived from bacteria and the fraction of amorphous detritus in invertebrate guts. (Reproduced from Hall and Meyer 1998.)

Figure 8.2 summarizes our best current understanding of the relationships among microbial

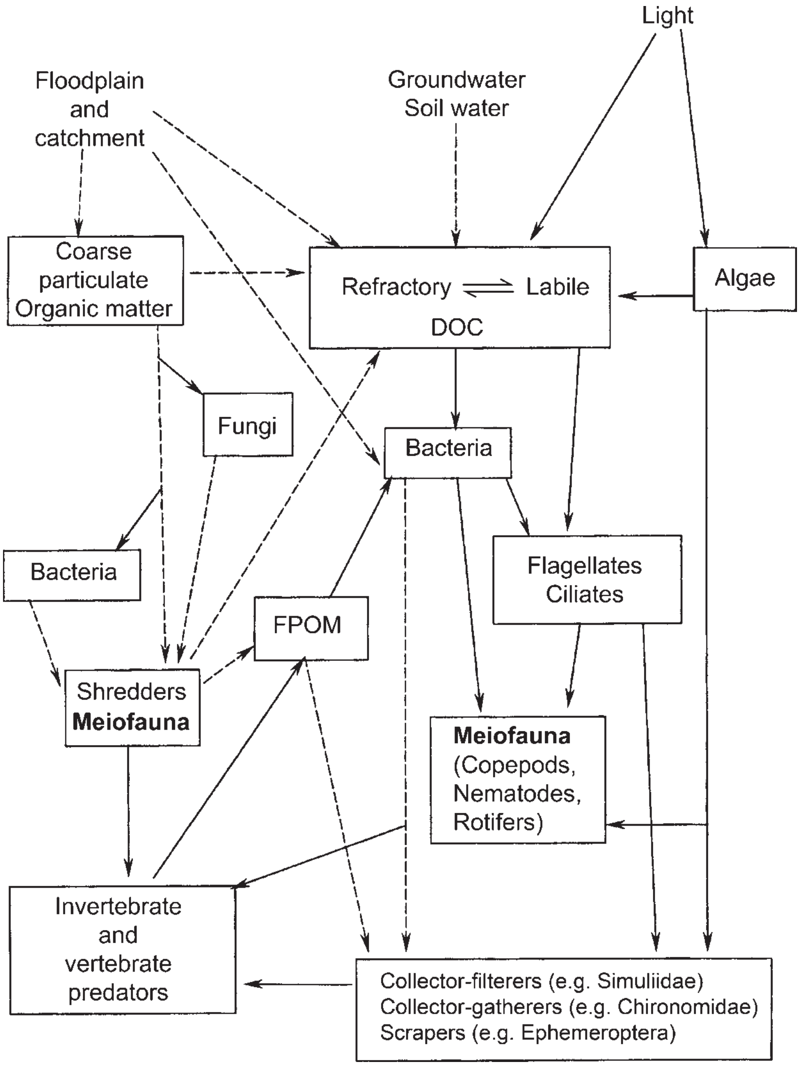

FIGURE 8.2 A fluvial food web emphasizing the role of the meiofauna and microbial production. Dotted lines are flows within the microbial web. (Reproduced from Schmid-Araya and Schmid 2000, adapted from Meyer 1994.)

production and the meiofauna within stream food webs (Schmid-Araya and Schmid 2000). The number of trophic links in the microbial web is strongly influenced by the small size of its members and especially the size of a bacterial cell, which is about 0.5 μm. Because few suspension feeders are able to capture particles of this size (Wotton 1994), the ingestion of bacteria by flagellates (~5 μm) and ciliates (~25 μm) provides a microconsumer pathway for this energy to reach larger consumers. On the other hand, bacteria associated with biofilm in a surface microlayer may be ingested directly by benthic consumers of surface films and by deposit feeders that pass organic matter and associated microbes directly through their guts. Clearly, the number of trophic transfers between bacterial production and macroinvertebrate consumer can be one or many, with significant consequences for energy dissipation, and this may vary between water column and benthic habitats. It is conceivable that in some habitats the microbial and metazoan webs are linked, and in others the microbial loop is an energy sink, internally dissipating whatever energy is obtained from dissolved and particulate C sources. Elucidation of the magnitude of the "link versus sink" role of the microbial loop is an important current challenge in lotic ecology.

8.2 Invertebrate Feeding Roles

The feeding roles of invertebrates of fluvial ecosystems are categorized according to food sources and mechanisms of food acquisition, which in turn are related to morphological and behavioral adaptations of the consumer (Table 8.1). These FFGs (Cummins 1973, Merritt and Cummins 2006) reflect the four most important food resources found in streams: periphyton, CPOM, FPOM, and animal prey. Shredders feed on CPOM, collectors feed on FPOM either from the water column or the streambed, scrapers ingest periphyton, and predators consume prey. However, this classification has limitations. Most macroinvertebrates likely function as collectors in their early instars, so FFG designations apply best to late instars. FFG classification usually is at the level of genus, raising the question of species-level differences. The food resources do not separate cleanly; for example, a leaf enriched by fungi may support a surface film of algae, and biofilms are not well incorporated into the FFG classification.

TABLE 8.1 The functional feeding groups (FFGs) of macroinvertebrate consumers in streams. See Cummins and Klug (1979) for further explanation.

Feeding role	*Food resource*	*Feeding mechanism*	*Examples*
Shredder	Nonwoody CPOM, primarily leaves; and associated microbiota, especially fungi	Chewing and mining	Several families of Trichoptera, Plecoptera, Crustacea; some Diptera, snails
Shredder/gouger	Woody CPOM and microbiota, especially fungi; primarily surficial layers are utilized	As above	Occasional taxa among Diptera, Coleoptera, Trichoptera
Filterer-collector/ suspension feeder	FPOM and microbiota, especially bacteria and small autotrophs in water column	Collect particles using setae, specialized filtering apparatus, or nets and secretions	Net-spinning Trichoptera, Simuliidae and other Diptera, some Ephemeroptera
Collector-gatherer/ deposit feeder	FPOM and microbiota, especially bacteria, and biofilm	Collect surface deposits, browse on amorphous material, burrow in soft sediments	Many Ephemeroptera, Chironomidae, and Ceratopogonidae
Grazer	Periphyton, especially diatoms; and biofilm	Scraping, rasping, and browsing adaptations	Several families of Ephemeroptera and Trichoptera, some Diptera, Lepidoptera, and Coleoptera
	Macrophytes	Piercing	Hydroptilid caddis larvae
Predator	Animal prey	Biting and piercing	Odonata, Megaloptera, some Plecoptera, Trichoptera, Diptera, and Coleoptera

Nonetheless, FFGs have proven to be a useful and durable classification system, and tabular summaries are available for many taxa (see Merritt and Cummins 2004, Tachet et al. 2002, Poff et al. 2006). The ability to view a macroinvertebrate assemblage as a collection of FFGs provides valuable insight into which food resources are prevalent, and allows one to observe how different groups of organisms respond to environmental variables. The distribution and abundance of these resources are influenced by size of stream or river, shading, substrate, and many other variables discussed previously, and it has been suggested that the relative availability of food resources changes predictably from headwaters to river mouth (Vannote et al. 1980). Thus, food webs also should vary in a predictable fashion: shaded headwater streams will favor organisms that consume POM, whereas grazers of algae should flourish in unshaded, stony streams, and fine particle collectors are likely to dominate in large, turbid rivers (Figure 1.7). FFG ratios also hold promise as indicators of stream ecosystem attributes. For example, an ecosystem whose metabolism derives mainly from autotrophy should have a high ratio of scrapers to shredders plus collectors (Merritt et al. 2002).

8.2.1 Consumers of CPOM

Figure 8.3 depicts the shredder–CPOM linkage typical of a small stream in the temperate zone. The series of events culminating in the disappearance of leaf CPOM has already been discussed (Section 7.1), and the critical role that microorganisms play both directly and indirectly in influencing the nutritional quality of this resource is elaborated below. CPOM that becomes available in wetlands and larger rivers following macrophyte dieback enters the decomposer trophic web in a very similar fashion (Polunin 1984). Wood is the coarsest of CPOM; few taxa are able to consume this material and its rate of utilization is very slow (Anderson et al. 1978).

The consumption of autumn-shed leaves in woodland streams by the invertebrates termed shredders is the most extensively investigated trophic pathway involving CPOM (Cummins and Klug 1979), and shall serve as our model here. Invertebrates that feed on decaying leaves include crustaceans (especially amphipods, isopods, crayfish, and freshwater shrimp), snails, and several groups of insect larvae. The latter includes crane fly larvae (Tipulidae), and several families of the Trichoptera (Limnephilidae, Lepidostomatidae, Sericostomatidae, and Oeconesidae), and Plecoptera (Peltoperlidae, Pteronarcidae, and Nemouridae). The leaf-shredding activities of insect larvae and gammarid amphipods are particularly well studied (Table 8.2). *Tipula* and many limnephilid caddis larvae eat all parts of the leaf including mesophyll and venation, whereas peltoperlid stonefly nymphs avoid venation and concentrate mainly on mesophyll, cuticle, and epidermal cells (Ward and Woods 1986). The radula of snails and mouthparts of *Gammarus* are most effective at scraping softer tissues, and the bigger crustaceans are able to tear and engulf larger leaf fragments (Anderson and Sedell 1979).

Selection of food by shredders is based on several characteristics of leaves such as toughness, nutrient content, the presence of plant chemical defenses, and the degree of conditioning by microorganisms (Graca 2001). The nutritional quality of leaves is intimately linked with the microorganisms that contribute so greatly to leaf breakdown. Much effort has been directed at determining how microorganisms directly (as food) and indirectly (by modifying the substrate) contribute to the nourishment of CPOM consumers, and what capabilities these detritivores possess to digest the various components of their diet. Invertebrate detritus feeders unquestionably prefer leaves that have been "conditioned" by microbial colonization in comparison with uncolonized leaves. When presented with elm leaves that were either autoclaved or cultured with antibiotics to inhibit microbial growth versus normal

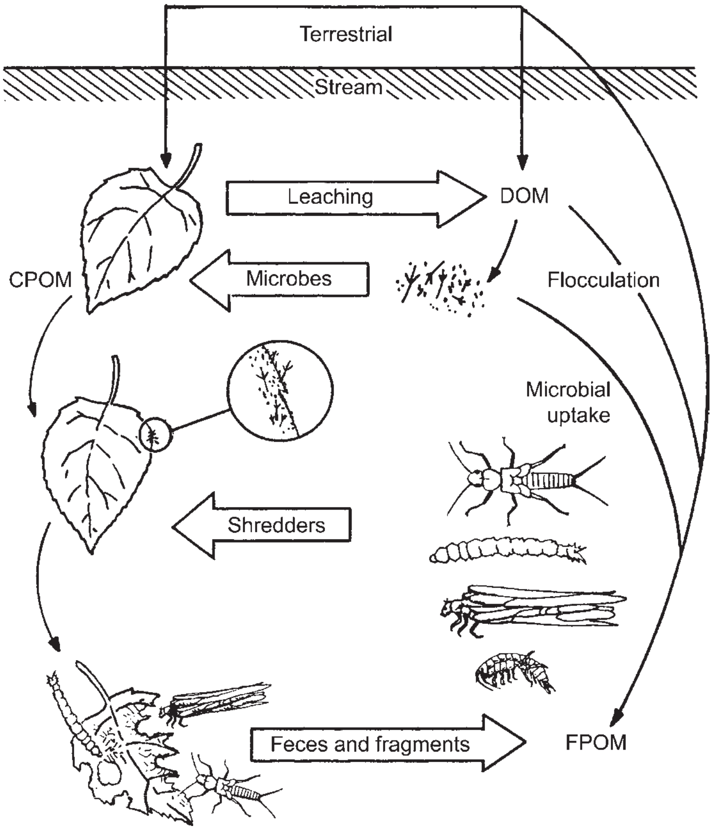

FIGURE 8.3 The shredder–CPOM linkages for a small stream within a temperate deciduous forest. Physical abrasion, microbial activity (especially by fungi), and invertebrate shredders reduce much of the CPOM to smaller particles. Chemical leaching, microbial excretion, and respiration release DOM and CO_2, but much of the original carbon enters other detrital pools as feces and fragmented material. (Reproduced from Cummins and Klug 1979.)

TABLE 8.2 The contrasting feeding strategies of two CPOM detritivores. (Adapted from Barlöcher 1983.)

	Gammarus fossarum	*Tipula abdominalis*
Feeding mechanism	Scrapes at leaf surface	Chews entire leaf
Gut pH and digestive biochemistry	Anterior gut slightly acid Its own enzymes and fungal exoenzymes attack leaf carbohydrates Posterior gut is alkaline, can digest microbial proteins and some leaf proteins	Foregut and midgut highly alkaline (up to 11.6) Results in high proteolic activity but inactivation of fungal exozymes, thus little activity toward leaf carbohydrates
Efficiency	Highly efficient at processing conditioned leaves at low metabolic cost	Less dependent upon stage of conditioning, probably good at extracting protein, but at high metabolic cost
Other attributes of feeding ecology	Highly mobile	Low mobility

colonized leaves, *Gammarus* consumed far more of the latter (Kaushik and Hynes 1971). Subsequent work has confirmed that preference is greatest for leaves at the stage of conditioning that roughly corresponds to the period of greatest microbial growth (Arsuffi and Suberkropp 1984, Suberkropp and Arsuffi 1984). The benefits to the consumer include greater efficiency in converting ingested leaf biomass into consumer biomass and a higher individual growth rate.

Preference trials that compared shredders from tropical and temperate locations provided with conditioned (leaves submerged in the stream for 2 weeks) and unconditioned leaves from a temperate and a tropical tree found that all shredders preferred conditioned over unconditioned leaves regardless of the region of origin of either the shredders or the leaves (Figure 8.4). In addition, all grew faster when provided with the conditioned leaves (Graca et al. 2001).

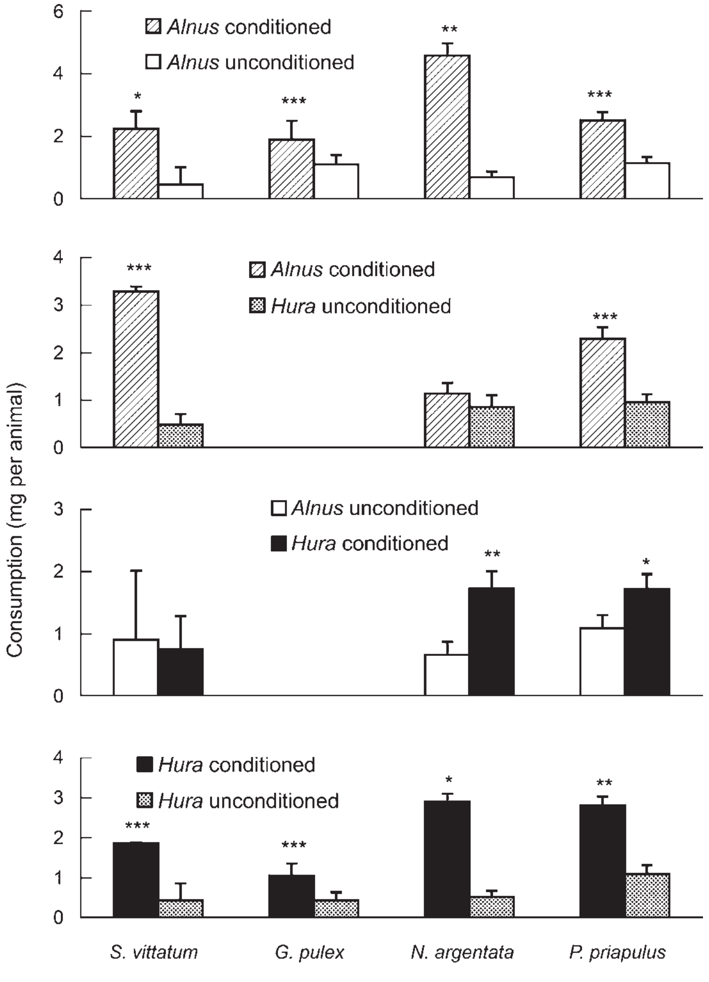

FIGURE 8.4 Preference of tropical (*Nectopsyche argentata*, *Phylloicus priapulus*) and temperate (*Sericostoma vittatum*, *Gammarus pulex*) zone shredders for tropical (*Hura crepitans*) and temperate (*Alnus glutinosa*) conditioned and unconditioned leaves. Mean and one standard deviation are shown. * = $P<0.05$; $^{**}<0.01$; $^{***}<0.001$. (Reproduced from Graca et al. 2001.)

Considering that the leaves of the temperate tree (alder, *Alnus glutinosa*) have been shown to be a preferred food in a number of studies, whereas the tropical tree (*Hura crepitans*, Euphorbiaceae) produces a milky juice used by Amerindians to make poison darts, a general preference for alder leaves is no surprise. More surprising is the observation that *Gammarus* showed no preference among conditioned leaves, and shredders grown on *Alnus* and *Hura* did not differ in survival and growth rates, indicating that leaf conditioning was more important than leaf type. In contrast, a study conducted in Australia found that shredders preferred native *Eucalyptus* leaves over leaves from sugar cane *Saccharum* and para grass *Urochloa*, despite the lower C/N ratios and presumed higher quality of the latter. When supplied only with *Eucalyptus* leaves, the caddis larva *Anisocentropus kirramus* showed low consumption and assimilation rates (Clapcott and Bunn 2003). Green and senescent leaves differ in their phenol, lignin, and nutrient content, and thus in their quality as food. Larvae of another caddis, *Lepidostoma complicatum*, grew more slowly on green than senescent leaves and none reached maturity, whereas 70% of larvae fed senescent leaves reached the adult stage (Kochi and Kagaya 2005). However, larvae that were provided with both senescent and green leaves had a faster growth rate than those provided with senescent leaves only, probably due to the higher nitrogen (N) content of green leaves. The freshwater shrimp *Xiphocaris elongate* was found to prefer leaves of *Dacryodes excelsa* over *Cecropia schreberiana*, despite their higher secondary compound content and firmness, apparently because of the lower lignin content of *Dacryodes* leaves (Wright and Covich 2005).

Microorganisms may enhance the palatability and nutritional quality of leaves in at least two distinct ways (Barlöcher 1985). One, termed microbial production, refers to the addition of microbial tissue, substances, or excretions to the substrate. Because assimilation efficiencies on fungal mycelia and mixed microflora have been shown to exceed 60%, while values for conditioned and unconditioned leaves average near 20% (Barlöcher 1985, Martin and Kukor 1984), indications are that the nutrient content per unit mass in microorganisms can be severalfold greater than that of the leaf substrate. The second potential role for microorganisms is microbial catalysis, and encompasses all of the changes that render the leaf more digestible. This includes partial digestion of the substrate into subunits that detritivores are capable of assimilating, and production of exoenzymes that remain active after ingestion. As support for this proposition, Barlöcher (1985) pointed out that structural carbohydrates (cellulose, hemicellulose, and pectin) may be partially digested by microorganisms into intermediate products which the gut fluids of invertebrates are then able to degrade. Indeed, leaves subjected to partial hydrolysis with hot HCl were preferred by *Gammarus pseudolimnaeus* over untreated leaves (Barlöcher and Kendrick 1975). Barlöcher (1982) also showed that fungal exoenzymes extracted from decomposing leaves remained active in the presence of gut enzymes of *G. fossarum* for up to 4 h at the foregut's pH, indicating that ingested exoenzymes can aid in the digestion of polysaccharides.

Some shredders may be able to actively discriminate between fungi and leaf material. In feeding trials with the freshwater detritivores *G. pulex* and *Asellus aquaticus*, Graca et al. (1993) found that both species discriminated between fungal mycelia, fungally colonized, and uncolonized leaf material. *A. aquaticus* selectively consumed fungal mycelia, whereas *G. pulex* fed preferentially on leaf material, and for the latter species fungi appeared to be more important as modifiers of leaf material. Experiments using radiotracers to separate the microbial versus substrate contributions to individual growth corroborate that the bulk of the energy is obtained from the leaf. Using radiolabelled food sources and inhibitors of DNA synthesis, Findlay et al. (1984, 1986c) demonstrated that only 15% of the respired C in the freshwater isopod *Lirceus* and 25% in the stonefly *Peltoperla* was met by consumption of microbes, primarily fungi. In addition, while insect larvae may lack the ability to synthesize cellulytic enzymes, Sinsabaugh et al. (1985) demonstrated using radiolabelled cellulose substrate that leaf-shredding insects indeed were able to digest and assimilate plant cell wall polysaccharides. Sinsabaugh et al. (1985) inferred that digestion was aided by ingested exoenzymes in the case of *Pteronarcys*, and by endosymbionts in the distinctive rectal lobe of the hindgut of *Tipula*. Leaf-shredding crustaceans produce enzymes that enhance their ability to digest leaf litter of terrestrial origin. The amphipod *G. pulex* produces phenol oxidase and cellulase activity in the hepatopancreas, whereas in the isopod *A. aquaticus* these enzymes are produced by endosymbiotic bacteria (Zimmer and Bartholme 2003).

Algae and bacteria of biofilms associated with leaf litter may contribute substantially to shredder nutrition. The exclusion of leaf litter from experimental stream reaches forced greater reliance on biofilms, and the shredders *Tallaperla* and *Tipula* derived on average 32% and 14% of their C from bacteria, respectively, probably in the form of bacterial exopolymers (Hall and Meyer 1998). Shredders can also obtain C from algae growing on leaf biofilms, where the algae can increase the food quality of leaf biofilms and also stimulate microbial production by the release of exudates, and thereby enhance the growth of shredders (Franken et al. 2005). Fungi contribute the majority of microbial biomass associated with decaying leaves, however, and even in large rivers where bacteria might be expected to increase in importance relative to fungi, fungal biomass greatly exceeds bacterial biomass (Baldy et al. 1995).

The importance of wood as a geomorphic agent in stream channels, altering flows and increasing habitat diversity, was discussed in Section 3.2. Wood can contribute 15–50% of total litter fall in small, deciduous forest streams and even more in coniferous regions (Anderson and Sedell 1979). Wood is considered to be a minor energy resource because few invertebrates feed on it directly and wood appears to be a poor food. Although its importance diminishes downstream and it is utilized only very slowly (a residence time of at least years to decades, in comparison with weeks to months for leaves), wood provides food and habitat for a number of species. Anderson et al. (1978) found some 40 taxa associated with this resource in wood-rich Oregon streams. Prominent aquatic xylophages included a midge (*Brilla*) which was an early colonizer of phloem on newly fallen branches, two species that gouged the microbially conditioned surface of waterlogged wood (the elmid, *Lara*, and the caddis, *Heteroplectron*), and a crane fly (*Lipsothrix*) that consumed nearly decomposed woody material. In comparison with leaves, invertebrate standing crop biomass on wood was about two orders of magnitude lower per kilogram of substrate.

Lotic consumers are relatively unspecialized for xylophagy. The beetle *Lara avara* possesses robust mandibles capable of slicing away thin strips of wood, but apparently lacks digestive enzymes or gut symbionts to aid digestion. Microscopic inspection of material progressing through the gut indicated no change to the wood (Steedman and Anderson 1985); presumably the larva is nourished by microbiota and their exudates occurring on the wood surface. Not surprisingly, *L. avara* grows very slowly and requires 4–6 years to attain maturity. Wood fibers represented a high fraction (63%) of the gut contents of the caddis *Pycnocentria funerea* in streams draining a pine forest in New Zealand, and stable isotope analysis also indicated that most of its nourishment was derived from pine wood (Collier and Halliday 2000). In streams in agricultural settings in Michigan and Minnesota where wood was comparatively rare, the presence of wood increased faunal diversity (Johnson et al. 2003). From a trophic perspective wood may be important primarily as a resting and feeding platform (Dudley and Anderson 1982), and a site of biofilm development and thus a food source for scrapers (Hax and Golladay 1993). Of the taxa found predominantly associated with wood in the study of Johnson et al. (2003), most were collectors, and predators were disproportionately common.

8.2.2 Consumers of FPOM

The collector–FPOM linkage (Figure 8.5) depends on FPOM captured from suspension or from substrates. As discussed in Chapter 7, FPOM is a poorly characterized food source, and it originates in a number of ways. Categories considered to be richest in quality include sloughed periphyton and biofilm, and particles produced in the breakdown of CPOM. Morphological and behavioral specializations for suspension feeding including setae, mouthbrushes, and fans are diverse and well studied (Wallace and Merritt 1980), whereas the mechanisms of deposit feeding appear to be less elaborate (Wotton 1994).

Caddis larvae in the superfamily Hydropsychoidea (comprised of the Philopotamidae, Psychomyiidae, Polycentropodidae, and Hydropsychidae) spin silken capture nets in a variety of elegant and intricate designs. Most net-spinning caddis are passive filter feeders, constructing nets in exposed locations, but some nets act as snares (*Plectrocnemia*) or as depositional traps where undulations by the larvae create current (*Phylocentropus*, Wallace and Malas 1976). Filter-feeding hydropsychids vary considerably in mesh size and microhabitat placement of their nets (Wallace et al. 1977, Wallace and Merritt 1980). Brown et al. (2004) studied the properties of the net silk of *Hydropsyche siltalai*, finding that it has a very low tensile strength, placing it among the weakest of natural silks; however, it is strong relative to the forces it experiences and it has high extensibility,

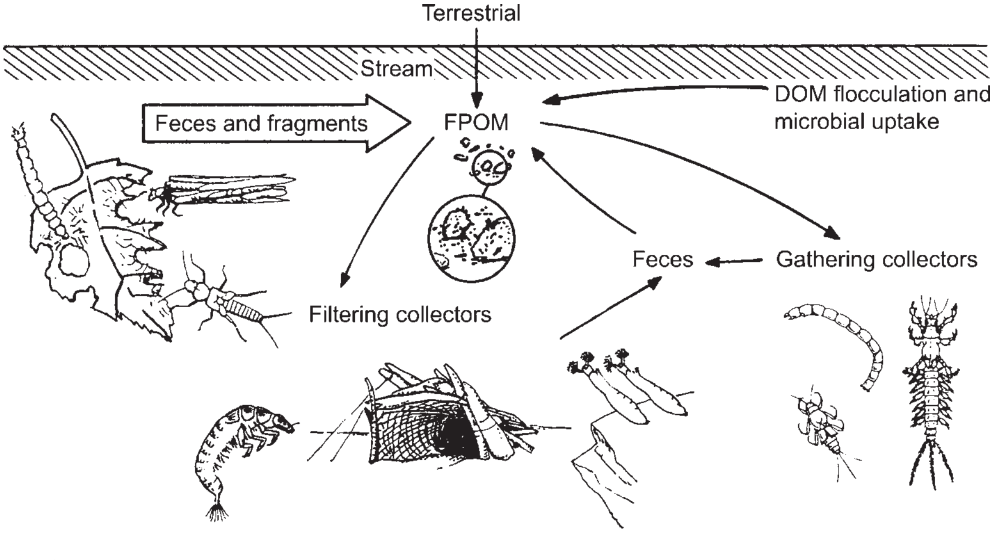

FIGURE 8.5 The collector–FPOM linkages for a small stream within a temperate deciduous forest. Sources of detrital particles <1 mm include CPOM fragments, terrestrial inputs, animal feces, and sloughed algal cells and biofilm material. FPOM and associated microorganisms are ingested from the water column by filter feeders and from the streambed by collector-gatherers. (Reproduced from Cummins and Klug 1979.)

doubling its length before breaking. There is evidence that catch nets of larger mesh tend to be found at higher velocities and capture larger prey, whereas fine mesh nets occur in microhabitats of low velocity and retain smaller particles (Wiggins and Mackay 1978). Members of the Arctopsychinae spin coarse nets, capture a good deal of animal prey and larger detritus, and tend to occur in headwaters. The Macronematinae occur in larger rivers, spin fine nets, and capture small particles. The Hydropsychinae are intermediate in net mesh size, more widely distributed, and perhaps because of the broad range of resources utilized, also are richer in genera.

Edler and Georgian (2004) examined the efficiency of particle capture in *Ceratopsyche morosa* (net mesh size 160 × 229 μm) and *C. sparna* (150 × 207 μm) by releasing food items of different sizes including *Artemia* nauplii (mean length 528 mm), and pollen of corn (*Zea mays*, mean diameter 84 mm) and paper mulberry (*Broussonetia papyrifera*, 12.5 mm). Both caddis species ingested more of the largest particles despite the greater availability of smaller particles in suspension (Figure 8.6), but particles smaller than mesh openings were retained as well. Selective capture of larger particles might be expected to be energetically rewarding, and this is supported by the finding that *H. siltalai* nets retained a larger range of particles size (1–40 mm) than those present in the water (1–25 mm) (Brown et al. 2005). Because some captured particles were smaller than the mesh size of *H. siltalai's* net, adherence of particles to the silk apparently has some role in overall particle retention.

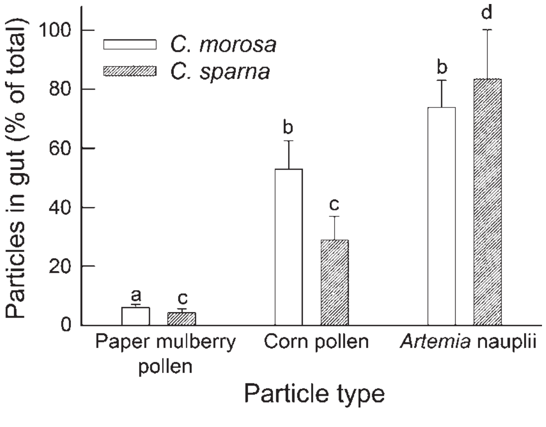

FIGURE 8.6 Particles found in the guts of fifth-instar larvae of *Ceratopsyche morosa* and *C. sparna* as fractions of total. For each species, bars marked with the same letter are not significantly different. (Reproduced from Edler and Georgian 2004.)

The impressive nets of caddis larvae are but one of the many specialized adaptations for capturing particles from suspension that have arisen frequently and repeatedly among aquatic invertebrates (Wallace and Merritt 1980). Larval black flies (Diptera: Simuliidae) are highly specialized suspension feeders (Figure 8.7). They have been studied extensively because the adults include important disease vectors as well as nuisance pests (Malmqvist et al. 2001). Black fly larvae attach to the substrate in rapid, often shallow, water and extend their paired cephalic fans into the current (Chance 1970, Currie and Craig 1988). Particles apparently are snared by sticky material on the primary fans, which are the main suspension-feeding organs, while secondary and medial fans act to slow and deflect the passage of particles. Food items are removed by the combing action of mandibular brushes and labral bristles, further adaptations to a filtering existence and lacking in some black fly species that scrape substrates instead. Fans are opened when feeding and closed at other times (Crosskey 1990). The four species studied by Chance (1970) ingested particles from <1 to >350 μm. Field studies generally report the majority of ingested particles to be <10 μm in diameter (Merritt et al. 1982).

Visualization of the fields of flow surrounding individual simuliid larvae indicates that they position their fans for maximum filtering effectiveness, and may be able to manipulate flow vortices to enhance feeding (Chance and Craig 1986, Lacoursiere and Craig 1993). Palmer and

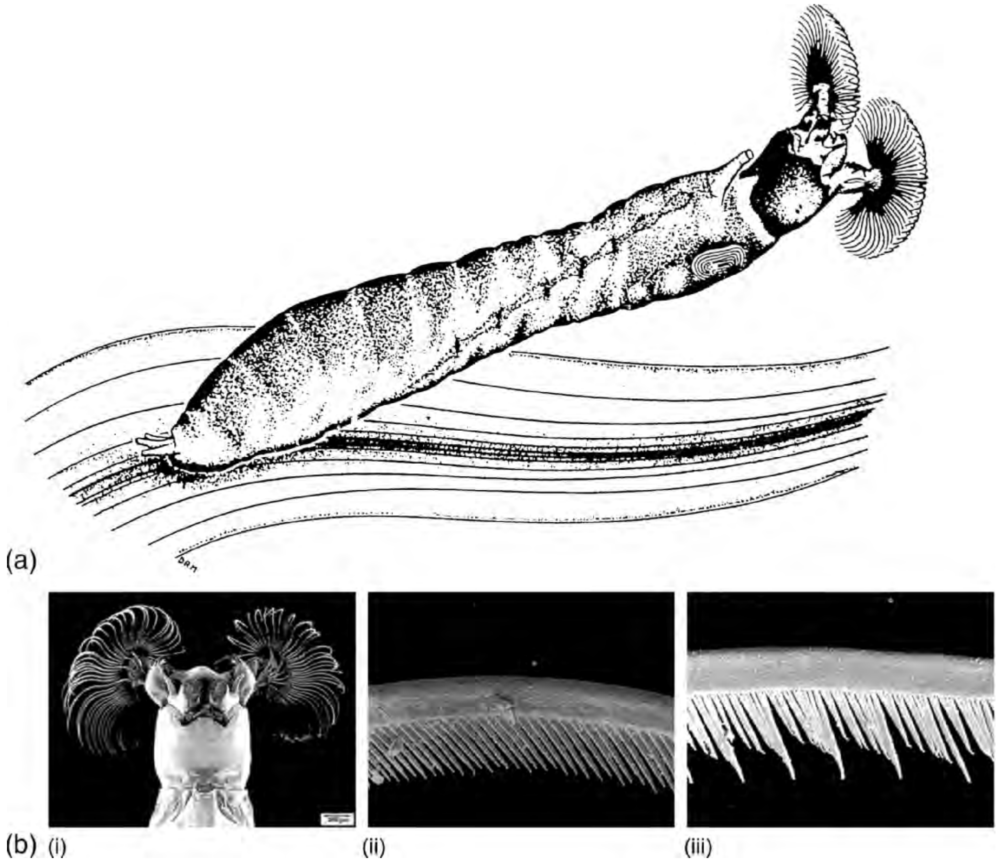

FIGURE 8.7 (a) The typical filtering stance of a black fly larva (*Simulium vittatum* complex). The larval body extends downstream at progressively greater deflection from vertical with increasing current velocity, and is rotated 90° to 180° longitudinally as can be seen by following the line of the ventral nerve cord. The position of the paired cephalic fans is upper and lower, rather than side by side. The boundary layer (depth where $\bar{U}$ falls below 90% of mainstream flow) begins at roughly the height of the upper fan (Chance and Craig 1986). (b) Details of cephalic fans: *left*: head of a normal larvae seen from beneath, with cephalic fans fully open; *middle*: *Simulium atlanticum* with uniform fringe of microtrichia; *right*: *S. manense* with long and short microtrichia. (Reproduced from Crosskey (1990) and SEM photographs of DA Craig.)

Craig (2000) suggest that black fly larvae occurring in fast-flowing, particle-rich water will tend to have strong fans with a porous ray structure, whereas larvae found in slow-flowing, particle-poor water will tend to have weak fans with a complex structure. Despite the evident elegance of the adaptations of larval simuliids for suspension feeding, this is by no means the only feeding mode employed. Currie and Craig (1988) state that scraping the substrate using mandibles and labrum is the second most important method of larval feeding, not including species that lack cephalic fans and are obligate scrapers. In addition, black fly larvae occasionally ingest animal prey, and Ciborowski et al. (1997) demonstrated that black fly larva grow when supplied only with DOM. This diversity is a useful reminder that even those taxa displaying great specialization for a particular trophic role also may be capable of great versatility.

As mentioned in Section 7.2.1, larval black flies not only are important for their ability to filter very fine particles, but also for their production of fecal pellets (Wotton and Malmqvist 2001). In northern rivers and particularly at lake outlets where very dense black fly aggregations occur, fecal pellet loads of several tons of C per day have been reported (Malmqvist et al. 2001). These pellets are available to filter feeders when in suspension, and to deposit feeders after they have sedimented. When Wotton et al. (1998) induced black fly larvae to produce labeled fecal pellets by adding paint to a lake outlet stream, the guts of midge larvae, oligochaetes, and black fly larvae contained abundant label, and lesser amounts were found in baetid mayfly larvae and the isopod *Asellus*.

Fecal pellets likely are an under-appreciated source of FPOM. Feces usually contain undigested food items and often are bound into discrete pellets although some are diffuse (Wotton and Malmqvist 2001). Pellet size varies with the size of the animal that produced them, and can be as small as 6 × 9 μm in protozoans. Although most organisms produce fecal pellets that are smaller than the food they consume, some suspension feeders such as larval black flies can ingest very small food items and so produce fecal pellets larger than the food they ingest.

Other dipteran families with representatives adapted to a suspension-feeding existence in running waters include the Culicidae, Dixidae, and Chironomidae (Wallace and Merritt 1980). Some Chironomidae construct tubes or burrows with catchments and create current by body undulations; others such as *Rheotanytarsus* passively suspension-feed by means of a sticky secretion supported by rib-like structures on the anterior end of the case.

Bivalved mollusks are effective filter feeders, capable of removing very small particles (10 μm and smaller) from their respiratory water current using sieve-like modified gills and mucus to filter and trap particles. Bivalves can remove large amounts of FPOM from the water column, including detritus, bacterioplankton, phytoplankton, and zooplankton (Strayer et al. 1999). Roditi et al. (1996) reported that zebra mussels removed phytoplankton and nonfood particles at the same rate, but other studies suggest that mussels can be selective within the FPOM pool. Based on stable isotope analyses, Nichols and Garling (2000) determined that unionids, which are the dominant group of freshwater mollusks, used bacteria as their main C source, although algae were found in the gut and provided vitamins and phytosterols. Christian et al. (2004) also found that mussels were using a bacterial fraction of FPOM as their food source based on stable isotope and digestive enzyme analyses. Although bivalves are traditionally seen as suspension feeders, Raikow and Hamilton (2001) reported that stream unionids obtained 80% of their food from deposited material versus 20% from suspended material. These unionids were probably assimilating the microbial and algal components of the suspended or benthic organic matter rather the bulk material.

Mechanisms of FPOM feeding by collector-gatherers either are less diverse in comparison with suspension feeding, or less is known about the subject. Nonetheless, this feeding role is well represented in most stream ecosystems in numbers of both individuals and species. Among the macroinvertebrates in swifter streams, representatives of the mayflies, caddis flies, midges, crustaceans, and gastropod mollusks are prominent deposit feeders. In slow currents and fine sediments one would also expect to find oligochaetes, nematodes, and other members of the meiofauna. It would be surprising if these animals all fed in the same way and consumed the same food. In addition to their particular food-gathering morphologies, these taxa differ in their ability to produce mucus, in mobility and body size, in their digestive capabilities and in whether they are surface dwellers or live within the sediments.

Browsing on easily assimilated biofilms may allow consumers to meet their energy needs without having to ingest large quantities of material. This is not the case for animals that ingest low-quality POM mixed with sediments. Many deposit feeders "bulk-feed," processing each day from one to many times their body mass of sediments and assimilating a low fraction of what they ingest. The burrowing mayfly *Hexagenia limbata* ingests more than 100% of its dry mass daily (Zimmerman and Wissing 1978). Estimates of assimilation efficiencies for FPOM deposit feeders in streams are scant, but numerous studies of leaf-shredding insects document assimilation efficiencies in the range of 10–20% (range: 1–40%, McDiffett 1970, Golladay et al. 1983) and daily ingestion rates in excess of one body mass per day. The assimilation efficiency of FPOM collectors in Sycamore Creek, Arizona, was estimated at 7–15%, and they consumed the equivalent of their body weight every 4–6 h (Fisher and Gray 1983).

Under the reasonable assumption that detritus varies widely in food value, one may ask whether deposit feeders adjust to different feeding opportunities. Taghon and Jumars (1984) argue that selection can be accomplished by either differential ingestion, which usually involves some method of particle rejection in the buccal region, or differential digestion, based on digestive physiology and gut retention time. High-quality foods that can be absorbed rapidly should favor high feeding rates and short retention times, whereas feeding should slow to allow longer digestion of poor-quality foods. Calow (1975a) demonstrated an inverse relation between ingestion rate and absorption efficiency in two freshwater gastropods. When starved, snails slowed the rate of passage of food through the hepatopancreas, the main site of absorption and digestion. The effect of changing food quality on gut retention time apparently varies with the quality of the food. Calow (1975b) found that the herbivorous limpet *Ancylus fluviatilis* increased its retention time for poor-quality food (the expected result), but the detritivorous snail *Planorbis contortus* did the opposite. It may be that whenever the food carrier is highly refractory, as in the case of lignin, it pays to process material rapidly for easily removed microbes rather than attempt to extract energy from nearly indigestible substrate.

In summary, deposit feeders are among the least understood of FFGs in running waters, partly for lack of analysis of feeding mechanisms, and partly because of shortcomings in understanding the sources and pathways of FPOM. Some taxa may shift opportunistically between this role and shredding (e.g., *Gammarus*), and others between the collecting of FPOM and grazing of easily removed periphyton (the "brusher" category discussed below). There is evidence to suggest that deposit feeding is common in early instars that will occupy other, more specialized guilds as they grow larger. Clearly, there is room for further research into this feeding role.

8.2.3 Herbivory

The *grazer–periphyton* and *piercer–macrophyte* linkages (Figure 8.8) are the principal pathways for the ingestion of living primary producers by invertebrates. The latter refers primarily to the microcaddis flies (Hydroptilidae), which pierce individual cells of algal filaments and imbibe cell fluids (Cummins and Klug 1979). Descriptions of the grazing pathway typically focus on attributes of the periphyton mat and the mode of invertebrate herbivory. The periphyton, comprised mainly of diatoms, green algae, and cyanobacteria, are found almost everywhere in running waters (Chapter 6). The extent of herbivory varies with algal growth form and differs among the major taxonomic groups for reasons that we shall consider shortly, but it appears that virtually all serve as food for some grazing animal.

Morphological specialization of grazing invertebrates includes the bladelike mandibles of glossosomatid caddis larvae, the rasping radula of snails, chewing mouthparts of some mayflies and brush-like structures of others, piercing

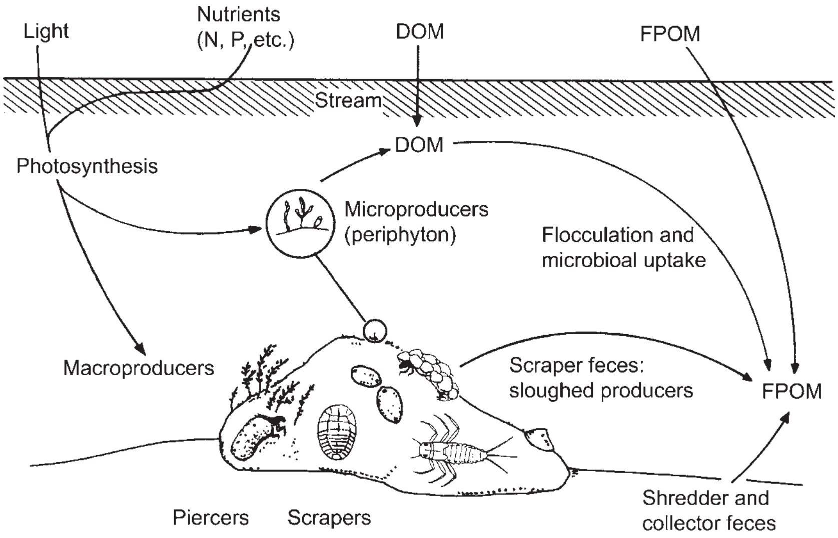

FIGURE 8.8 The grazer–periphyton and piercer–macrophyte linkages for a temperate stream. The periphyton-biofilm organic layer on substrate surfaces is scraped or browsed depending on the consumer's mode of feeding. Diatoms and other algae are important constituent of this basal resource, but consumers also may ingest detritus, microorganisms, and occasional very small invertebrates. Piercers such as caddis larvae (Hydroptilidae) imbibe cell fluids through the cell walls of macroalgae. (Reproduced from Cummins and Klug 1979.)

mandibles of hydroptilid caddis larvae, and so on. These are described as scrapers, grazers, and piercers, respectively. Other FFGs likely ingest plant matter occasionally. Collector-gatherers surely consume loose algae along with microbes and detritus (Lamberti and Moore 1984), and shredders benefit from the presence of an attached flora growing on the surface of fallen leaves (Mayer and Likens 1987). Drifting diatoms and algae also are captured by suspension feeders, especially those taxa possessing fine sieving devices (philopotamid caddis flies, some chironomid and black fly larvae), and even the relatively coarse meshes of most hydropsychids retain some diatom and algal cells. Indeed, within the North American insect fauna, consumption of algae has been noted in at least six orders and 38 families (Merritt and Cummins 2004). Moreover, the composition of an herbivore's diet changes with many factors, including age, season, food availability, and location (Lamberti and Moore 1984).

A detailed study of the functional morphology and feeding behavior of the mayfly *Stenonema interpunctatum*, which is usually classified as a scraper although it also is considered a gatherer, illustrates the difficulties of categorizing feeding roles. Using a flow-through chamber, video, scanning electron microscopy, and even constructing a moveable plastic model of its mouthparts, McShaffrey and McCafferty (1986) observed that several feeding modes were employed depending upon feeding conditions. For attached material such as algae and diatoms, a series of movements of the labium and maxillae comprised a brushing cycle. A collecting cycle occurred in the presence of loose detritus and involved similar feeding movements, but mouthparts were not pressed as tightly against the substratum. Moreover, in the presence of abundant suspended particles, *S. interpunctatum* radically altered its behavior, using the apical setae of extended maxillary palps for passive suspension feeding. Only the labial palps and tips of maxillary palps of *S. interpuntatum* can reach the substrate, and these are setose rather than sclerotized, so scraping is the one feeding mode that does not apply. McShaffrey and McCafferty (1986) prefer the term "brusher" for taxa that remove material from the substrate using setae, and suggest that "scraper" be used only for taxa with hardened structures that can remove adherent material.

Just as animals differ in their mode of feeding, members of the periphyton differ in a number of ways that affect their overall vulnerability to particular herbivores. Benthic algae vary markedly in growth form and mode of attachment as well as in overall size (Figure 6.1), and this must affect their availability to particular kinds of grazers. For example, field manipulations of grazer densities in a California stream established that the mayfly *Ameletus* with collector-gatherer mouthparts was most effective with loosely attached diatoms. In contrast, the stout, heavily sclerotized mandibles of the caddis *Neophylax* were effective against tightly adherent diatoms (Hill and Knight 1988).

Filamentous algae apparently are difficult for grazing insects to harvest or digest, and so they are consumed principally as new growths (Lamberti and Resh 1983, Dudley et al. 1986). To the snail *Lymnaea*, however, possessing both a radula for their harvest and a gizzard for their mechanical breakdown, filamentous green algae provide a very satisfactory diet (Calow 1970).

The assimilation efficiencies of herbivore–detritivores fed different diets are a useful measure of the wide range of nutritional value of various foods. Based on a review of 45 published values for 20 species of aquatic insects, assimilation efficiencies range from 70% to 95% on a diet of animal prey, 30% to 60% for a variety of algal and periphyton diets, and from 5% to 30% on a diet of detritus (Pandian and Marian 1986). Considerable variation can occur even for a single species feeding on periphyton. Assimilation efficiencies for the snail *Juga silicula* were as high as 70–80% when first added to laboratory streams, but values declined during the course of the study to as low as 40% (Lamberti et al. 1987). This coincided with a shift in composition of the periphyton from diatoms and unicellular green algae to filamentous green algae and cyanobacteria. The decline in assimilation efficiency could be the result of cell senescence and other changes in physiological condition, or a decline in nutritional value owing to successional changes in the periphyton assemblage.

The wide range of assimilation efficiencies observed with periphyton diets is at least partly due to their structural and biochemical characteristics. Variation in protein and lipid content and in cell wall thickness likely is responsible for differences among autotrophs in their nutritional value and palatability. A high C/N ratio signals a poor diet, indicating a high cellulose and lignin content and a low protein content; in general C/N ratios should be <17:1 for animal utilization. On this basis, members of the periphyton appear to be generally suitable (C/N ranges from 4 to 8:1), whereas aquatic vascular macrophytes appear to be nutritionally less adequate (C/N from 13 to 69:1) (Gregory 1983). Based upon a correspondence across sites between periphyton characteristics and gastropod growth, McMahon (1975) concluded that low C/N ratios and high organic content are indicative of a high-quality food resource. Variation in the N content of diets was an extremely effective predictor of assimilation efficiency for twenty taxa of aquatic insects reviewed by Pandian and Marian (1986).

Lipid content is another variable likely to influence the nutrition and development of herbivores. Most insects are unable to synthesize polyunsaturated fatty acids and sterols, indicating that the lipid content of their diets is important to food quality. Intense grazing by a snail and a larval caddisfly in laboratory streams altered the fatty acid composition of the periphyton, suggesting that grazing may have been responsive to this aspect of diet quality (Steinman et al. 1987). Cargill et al. (1985) showed that specific fatty acids were critical dietary components to a detritivorous caddis larva, *Clistoronia magnifica*.

Cyanobacteria are considered to be a poor food supply for freshwater plankton feeders (Wetzel 2001) and possibly for periphyton grazers as well. Cyanobacteria may have a high protein content, but other attributes, including a polymucosaccharide sheath rendering cell walls resistant to digestion, perhaps toxins, and a filamentous growth form all detract from their value as food. However, the evidence from lotic grazers is mixed. For example, in laboratory feeding trials the mayfly *Tricorythodes minutus* ate and assimilated two cyanobacteria, *Anabaena* and *Lyngbya* (McCullough et al. 1979), whereas *Asellus* and *Gammarus* would not consume *Phormidium* (Moore 1975). Orthoclad midges have suppressed blooms by *Phormidium* and *Oscillatoria* in outdoor channels (Eichenberger and Schlatter 1978). Because studies of cyanobacteria have used primarily filamentous forms rather than colonies or single cells, consumption of the latter is little known.

Herbivory generally is of minor importance to freshwater macrophytes. According to Wetzel (2001), less than 10% of macrophyte production is consumed live. The tough cell walls and high lignin content that provide structural support to macrophytes are effective barriers against their ingestion and digestion. Herbivorous taxa belonging to primary aquatic invertebrate groups usually are ineffective grazers of higher plants (Newman 1991). However, decapod crustaceans and certain insects of terrestrial origin can reduce the biomass of submersed and floating-leaved taxa. Several studies have found crayfish to significantly reduce the abundance of submersed macrophytes, although they have no apparent effect on emergent taxa, presumably because of the greater amount of support tissue (Feminella and Resh 1989). Crayfish also cause nonconsumptive loss by clipping shoots of submersed macrophytes, which then float away. In northern Wisconsin lakes, *Orconectes* spp. altered assemblage structure of submersed macrophytes, primarily because single-stemmed species were more vulnerable than rosulate growth forms (Lodge and Lorman 1987).

Intriguingly, the most dramatic effects of invertebrate grazing on living aquatic macrophytes involve herbivores derived mainly from terrestrial insect lineages. These include chrysomelid and curculionid beetles, aquatic and semiaquatic lepidopterans, and specialized dipterans (Newman 1991). At a site in the Ogeechee River, Georgia, infested with the water lily leaf beetle *Pyrrhalta nymphaeae* (Chrysomelidae), leaves of the water lily *Nuphur luteum* lasted only 17 days compared to more than 6 weeks at another site where the beetle was absent (Wallace and O'Hop 1985). Some macrophytes, including the water hyacinth *Eichornia crassipes* and the kariba weed *Salvinia molesta*, can become so abundant that they present serious weed control problems worldwide, particularly in the subtropics and tropics. A Brazilian beetle that feeds on kariba weed is one potential agent of biological control (Barrett 1989).

8.2.4 Predaceous invertebrates

The *predator–prey linkage* (Figure 8.9) is ubiquitous. All animals are prey at some stage of their life cycle, and predaceous invertebrates occur in all sizes, from protozoans that engulf other protozoans to insects and crustaceans capable of ingesting large invertebrates and small fish. Most predators engulf their prey whole or in pieces, but snipe flies (Diptera: Athericidae) and some hemipterans have piercing mouthparts (Cummins 1973). Other distinctions can be made between hunting by ambush versus searching (Peckarsky 1984), and whether prey are obtained from suspension, as in some hydropsychids, or strictly from the substratum, as in flatworms. Occasional predation probably is widespread, particularly the ingestion of micrometazoans, protozoans, and early life history stages of macroinvertebrates. Such unpremeditated carnivory may provide high-quality

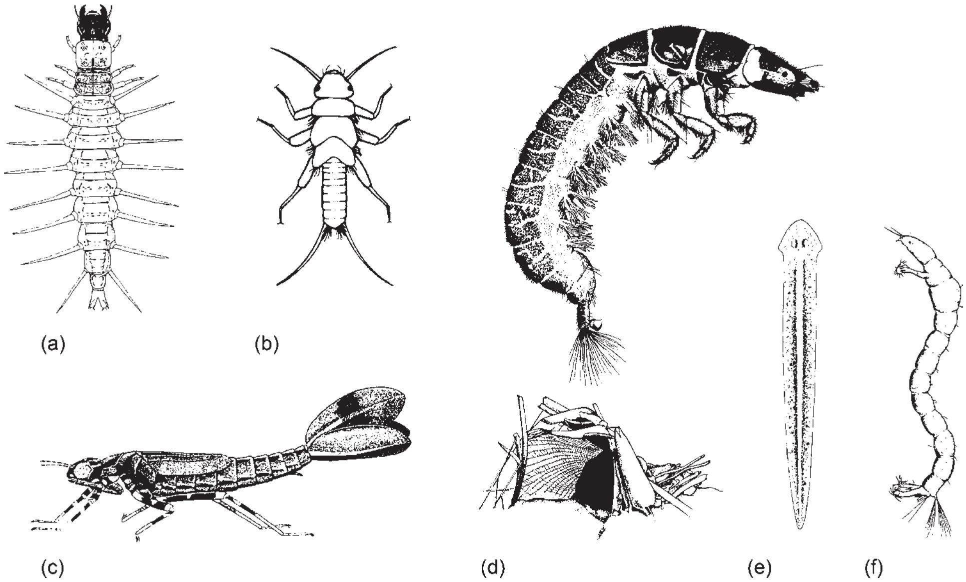

FIGURE 8.9 Examples of predaceous invertebrates, including those consuming large prey, illustrated by nymphs of (a) Megaloptera (Corydalidae) and (b) Plecoptera (Perlidae); those consuming prey of intermediate size, illustrated by (c) Odonata (Zygoptera) and (d) Trichoptera (Hydropsychidae); and those consuming small prey, illustrated by (e) Turbellaria (Tricladida) and (f) Chironomidae (Tanypodinae). (Figures a and d reproduced from Merritt and Cummins 2004; figures b, c, e, and f reproduced from Pennak 1989.)

protein needed by many invertebrates to complete their life cycles (Anderson 1976), and also may form an important link between microbial and macroconsumer food webs.

Mechanical detection is a widespread and varied modality for sensing prey. In many instances this means actual contact, for instance, with antennae and setal fringes of limbs as in the stonefly *Dinocras cephalotes* (Sjöström 1985). Vibrations in the water or of capture nets also serve as signals, as in the hemipteran *Notonecta* (Lang 1980), which captures prey on the water surface, and net-spinning caddis larvae that detect vibrations of prey in their nets (Tachet 1977). Visual cues likely are less important to invertebrate predators, because eyes are not well developed and many species dwell in crevices or are not active by day, but odonates, some heteropterans, and gyrinid beetles rely more on vision (Peckarsky 1984). Larval *Libellula depressa* (Odonata) were observed to strike at a mayfly nymph in response to either mechanical or visual cues, but mechanical cues were primary and did not require contact, and chemical cues apparently were ineffective (Rebora et al. 2004). Indeed, chemical detection of prey is important only in a few predaceous insects in the Hydrometridae and Dytiscidae, but it may be important in other invertebrates. Lake-dwelling triclads exhibit a chemosensory response to their isopod prey (Bellamy and Reynoldson 1974), and presumably stream-dwelling triclads do so also. The water mite *Unionicola crassipes* locates prey primarily by mechanoreception and vision, but it also becomes more sedentary in prey-conditioned water, suggesting that chemical detection promotes area-restricted search behaviors that presumably enhance encounter rates (Proctor and Pritchard 1990).

Sit-and-wait predators include those that simply remain motionless until the prey approaches within striking range, and those that trap their prey using nets (e.g., caddis larvae, Townsend and Hildrew 1979) or mucus trails (e.g., flatworms, Adams 1980). Odonates that usually ambush also will stalk prey (Johnson and Crowley 1980), perhaps influenced by hunger level. The caseless caddis larva *Rhyacophila nubila* captured agile mayfly nymphs from sheltered positions, whereas it captured sedentary black fly larvae upon random search (Otto 1993). Sjöström (1985) reported that *D. cephalotes* searched in darkness, but was primarily a sit-and-wait predator in very low light. Risk from its own predators is the most likely explanation, although ability of prey to escape may be an additional factor.

Predators often are undiscriminating in their diets, capturing whatever they encounter that is small enough to subdue. Aspects of the predator that bias it toward consuming more of some prey than others include sensory capabilities, foraging mode, and behavioral mechanism of prey capture. For prey, many aspects of body plan, life style, and behavior influence their vulnerability. These traits of predator and prey are not easily separated. From the many studies of the diet of predaceous invertebrates, usually based on gut analyses and behavioral observations, body size, prey availability, and prey vulnerability are of particular importance in determining what is eaten.

Size relationships between predators and their prey, as well as within a guild of invertebrate predators are of critical importance to food web relationships, a topic discussed in greater detail in Section 9.2.1.2. Typically, the average size of ingested prey increases with size of predator, as does the variety of prey items consumed. Predaceous stoneflies tend to ingest diatoms and other nonanimal items when very small. Diet changes gradually over development, often consisting primarily of chironomids in early instars, and then broadening to include a menu in which mayflies, simuliids, and trichopterans supplement and may eventually replace midge larvae as prey. Although some differences are reported among species and study locales, presumably reflecting differing availability of prey, any two stoneflies of about the same size, when in similar habitats, consume diets of similar species composition. By measuring head widths of ingested prey and converting those values to dry mass, Allan (1982a) showed a very similar positive relationship between prey size and predator size for several species of predaceous stoneflies and the two most common preys, *Baetis* and Chironomidae (Figure 8.10). With an increase in the size of prey ingested there usually is an increase in diet breadth as well. Small predators tend to have less diverse diets because they do not reach sufficient size to capture prey larger and more agile than midge larvae.

Analysis of gut contents typically reveals a good correlation between what is eaten and what is available. In a small and relatively species-poor stream in southern England, the caddis *Plectrocnemia conspersa* and the alderfly *Sialis fuliginosa* during summer consumed prey roughly in proportion to their abundance (Hildrew and Townsend 1976). Similarly, the rank order of prey taxa in the diet of large *Hesperoperla pacifica* was similar to the prey rank order in the benthos (Allan and Flecker 1988). There is some evidence that prey availability is such a decisive factor that it may override differences between predators in foraging mode. The net-spinning *P. conspersa* and the more mobile *S. fuliginosa* exhibited considerable overlap in habitat use and diet, although the former consumed more terrestrial items, large stoneflies, and small chironomids, which apparently were more easily trapped in the net of *P. conspersa* (Townsend and Hildrew 1979).

Lastly, field studies suggest that predators influence their diet through their choice of where to hunt, referred to as patch use. Predators appear to aggregate in patches of high prey

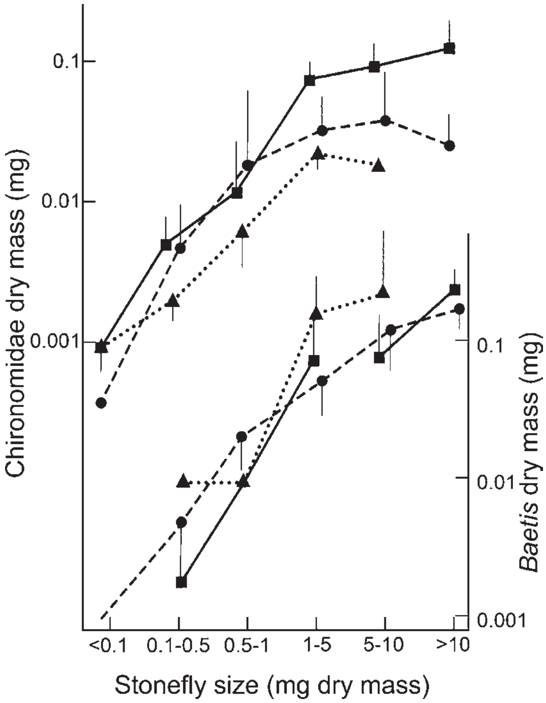

FIGURE 8.10 Average dry mass of prey found in the foreguts of three species of predaceous stoneflies, as a function of size groupings of predators. stoneflies of a particular size consumed prey of the same size for both prey species. Means and 95% confidence limits are shown for *Megarcys signata* (■), *Kogotus modestus* (▲), and *Hesperoperla pacifica* (●). (Reproduced from Allan 1982a.)

density. Individuals of *Notonecta hoffmanni* were observed to shift habitat use rapidly in the field (isolated pools of a California stream) and the laboratory in response to changes in prey availability (Sih 1982). The polycentropodid *P. conspersa* is more likely to place its nets where prey have recently been captured and to abandon sites after some time has elapsed since a previous capture (Hildrew and Townsend 1980). The observed aggregation of these predators and their prey in nature apparently is due to predators staying where capture rates are high and leaving when they are not. The leech *Glossiphonia complanata* foraging for snails in the laboratory spent more time than expected by chance in patches containing prey compared to empty patches, although it did not discriminate between high versus low prey patches (Brönmark and Malmqvist 1986).

In summary, the classification of invertebrates into functional feeding roles based on food-gathering mechanism and food type has proven to be an effective tool for understanding trophic relationships in fluvial ecosystems. Stream-dwelling invertebrates occupy all trophic positions and form important links between basal resources and top predators. Individual taxa often change their feeding role during their life cycles, and flexible feeding habits allow many to shift or blur the lines between FFGs. Nonetheless, the FFG classification of the invertebrate consumers of streams has demonstrated great utility for description and analysis. Much progress has been made over the last several decades toward understanding the various energy sources and how they are used. Characteristics of a particular river, including its size, hydrology, and the vegetation of the surrounding landscape significantly influence which pathways predominate. As long as one does not lose sight of the fact that FFGs are working conveniences, they serve as useful building blocks toward a broader synthesis in stream ecology.

8.3 Vertebrates in Lotic Food Webs

Although all vertebrate classes have representatives in running waters, fishes are the principal vertebrate component of most riverine food webs. In small headwater streams, salamanders and snakes may be important top predators; there are many species of fish-eating birds and some that consume aquatic invertebrates; a few mammals feed primarily or exclusively on aquatic prey, and a surprising diversity of mammals do so at least occasionally.

8.3.1 Fishes

A number of attempts have been made to construct feeding categories for stream fishes. In North America, most stream fishes are invertivores, some become piscivorous for much of their life cycle, and a few are herbivores (Allen 1969). Just as was true for early efforts to categorize invertebrates (most were herbivore–detritivores, some were predators), so simple a scheme is of limited value. Additional detail on where and how feeding occurs allows greater resolution of fish trophic categories (Table 8.3), and some of these categories can be subdivided further. Herbivorous fish with scraping mouthparts such as the stone roller *Campostoma anomalum* clearly have little in common with ooze feeders such as the bluntnose minnow *Pimephales notatus*. Some benthic invertebrate feeders utilize prey primarily from soft bottoms (the suckermouth minnow *Phenacobius mirabilis*), and others from stony bottoms (the greenside darter *Etheostoma blennioides*). Table 8.3 gives the percentage of fish species in each category from Horwitz' (1978) study of 15 river systems in the United States. All but one

TABLE 8.3 Trophic guilds of stream fishes, for temperate North America (modified from Horwitz 1978) and tropical South America (modified from Welcomme 1979).

Guild	*Description for temperate streams*	*Occurrence[a] by species (%)*	*Comments for tropical streams*
Piscivore	Consumes primarily fish and/or large invertebrates, but includes smaller invertebrates	16	Piscivores may consume entire fish or specialize on parts of fish
Benthic invertebrate feeder	Feeds on benthic invertebrates, primarily immature insects	33	Most common in small to midorder streams
Surface and water column feeder	Consume surface prey (mainly terrestrial and emerging insects) and drift (zooplankton and invertebrates of benthic origin)	11	Diverse surface foods occurring in forested headwaters and during seasonal flooding
Generalized invertebrate feeder	Feeds at all depths	11	Similar category
Planktivore	Midwater specialists upon phytoplankton and zooplankton	3	Seasonally important in larger rivers
Herbivore–detritivore	Bottom feeders ingesting periphyton and detritus; includes mud feeders with long intestinal tracts	7	Herbivory may be subdivided into microphytes and macrophytes, and detritus feeders separated from mud feeders
Omnivore	Ingest a wide range of animal and plant foods, and detritus	6	Similar category
Parasite	Ectoparasites (e.g., lampreys)	3	Ectoparasites (e.g., candirú catfishes)

[a] Percentages are based on the number of species, rather than the number of individuals, from the central United States only, based on Horwitz' (1978) study of 15 US river systems. An additional 9% of species could not be categorized, and one species (*Lepomis microlophus*) fed on snails

(the Powder River, Wyoming) were Midwestern rivers, so his results may best represent that region. Guild proportions were very similar across basins, except for the Powder River where detritivores were many and piscivores absent. Planktivores were absent from headwaters and piscivores increased downstream; otherwise the downstream increase in species richness was unrelated to changes in trophic representation. Combining the relevant categories from Horwitz' study, less than 20% of the species subsisted on a diet of plant and detrital material.

Herbivory is not common among the stream fishes of North America, where only about 55 of over 700 total fish species are primarily herbivorous. However, some introduced species, including the grass carp *Ctenopharyngodon idella*, illustrate that herbivorous fishes can be effective grazers of macrophytes, despite the limitations of a diet of living macrophyte tissue. Grass carp daily rations (in wet mass of macrophyte tissue) range from 50% to over 100% of their body mass per day, indicating that this feeding strategy is based on processing a high volume of material. Furthermore, the grass carp's preference among nine macrophyte species native to the Midwest was not correlated with measures of plant nutritive value. Instead, preferences appeared to reflect relative handling times, allowing fish to maximize "throughput" (Wiley et al. 1986). Grass carp also are known to have a low metabolic rate and assimilation efficiency relative to other fishes, and to require animal protein for proper growth.

Many primarily herbivorous fishes are really omnivores even though the majority of their diet is plant matter, because animal prey, detritus, and organic-rich sediments frequently are consumed as well. Quantitative evaluation of the diet of central stone roller minnows *C. anomalum* in a tallgrass prairie stream showed it to derive the majority of its growth from consumption of algae (47%), followed by amorphous detritus (30%), animal matter (21%), and leaves (2%) (Evans-White et al. 2003). In Río las Marías in the Andean foothills of Venezuela, the grazing armored catfish *Chaetostoma milesi* and the detritivore *Prochilodus mariae* both consume algae and detritus, and benefit from the organic fraction of consumed fine sediments (Flecker 1992a).

Detritivory usually is a minor feeding role for fish in temperate rivers, but in tropical rivers, especially the great rivers of South America, the ingestion of dead organic matter can support the bulk of fish biomass (Bowen 1983). Special adaptations include a muscular stomach to grind food and an intestine with greatly increased absorptive surface due to elongation (up to 20 times body length) or elaborate mucosal folding. Because of their high contribution to biomass, detritivorous fishes play an important role in food webs, linking C originating in detritus both to piscivorous fishes (Winemiller 2005) and human fishers (Barbarino Duque et al. 1998, Bowen 1983).

While some fish can be placed in a trophic guild without difficulty, others cannot, due to their morphological specializations, flexibility in feeding habits, and changes that occur over an individual's life cycle. Within the suckermouthed armored catfishes (Loricariidae), *Rhinelepis aspera* feeds on fine-grained detritus using suction to obtain food, and possesses long gill rakers, rudimentary labial and pharyngeal teeth, a thin stomach wall, and a long intestine (Delariva and Agostinho 2001). In contrast, *Megalancistrus aculeatus* and *Hypostomus microstomus* feed on coarser material including periphyton by scraping the substrate and have large, spatulate teeth, short gill rakers, a well-developed stomach, and a shorter intestine. The feeding biology of sunfishes (Centrarchidae) illustrates how specific functional features can underlie differences in feeding performance and diet among taxa, including the jaw opening and closing systems, size of the mouth, and size of muscles used in prey-crushing behaviors (Wainwright 1996). Piscivores tend to have larger mouth gapes (Mittelbach and Persson 1998), and molluscivores have crushing teeth that can vary in their effectiveness against hard- versus soft-bodied prey (Huckins 1997). Body shape also influences prey choice through habitat use and swimming ability. Among young fish from the Sinnamary River, French Guiana, disciform taxa fed mainly on aquatic insect larvae and terrestrial insects, most anguilliform taxa ate insect larvae, and those with an intermediate morphotype had varied diets ranging from plant debris to fish (Merigoux and Ponton 1998).

Ecomorphological analyses of entire assemblages have documented a strong relationship between the ecological role of fishes and their anatomical features. Gatz (1979) examined 56 morphological features of 44 species seined from North Carolina piedmont streams, calculated 3,080 pair-wise correlation coefficients among characters, and then used factor analysis to look for associations among characters. The first four factors together accounted for 60% of the variance in the correlation matrix. Factor 1 separated "lie-in-wait" biting predators from cruising suction feeders; factor 2 reflected the differences in body shape and proportions associated with habitat use; factor 3 separated a benthic from midwater lifestyle; and factor 4 separated small insectivores with short guts from other fishes. Ecological correlates of these factors indicate that morphology does indeed influence or reflect diet and habitat preferences. Fishes with flat, deep bodies were associated with slow water habitats. Fishes with ventral mouths obtained relatively more food from the bottom; those with terminal or anterior mouths did not. Fishes that dwell on or near the bottom in fast water regions had reduced swim bladder volume, and relative gut length was greatest in mud feeders, to list some principal findings. Ecomorphological analyses of tropical fish assemblages also have successfully related food and habitat partitioning to differences in body plan, discussed further in Section 9.3.1.3.

In addition to the morphological specializations just described, the sensory systems of fishes are strongly attuned to environmental constraints on food acquisition. River water varies in clarity, perhaps nowhere more evidently than in the Amazon basin. Whitewater streams are heavily colored by their alluvial loads, while blackwaters carry little silt but are darkly stained with dissolved material. Typical Secchi disk readings are <0.2 m in the former, 1–1.5 m in the latter (Muntz 1982). Clearwater rivers carry comparatively little silt or dissolved organics, and light penetration often equals or exceeds 4 m. These are markedly different visual environments. Absorbance of short-wavelength light is relatively great in fresh water, and more so as light penetration is reduced. Levine and MacNichol (1979) examined 43 species of mostly tropical freshwater fishes, and divided them into four groups on the basis of visual pigments. Species with strongly "short-wave-shifted" visual pigments were primarily diurnal, and fed from the surface or in shallow waters. Several species exhibiting the typical behavioral and morphological characteristics of catfishes lay at the other extreme. Their visual pigments were the most long-wave sensitive; in addition, they were primarily benthic and probably foraged either nocturnally or in very turbid waters. Rodríguez and Lewis (1997) determined that transparency was a very good predictor of fish species composition in floodplain lakes of the Orinoco River. In turbid lakes, fishes with sensory adaptation to low light like catfishes and knifefishes were dominant, whereas visually oriented characiforms, cichlids, and clupeomorphs were typical of clear lakes.

Extension of the guild structure for temperate zone fishes to the tropics is at best very tentative. Large tropical rivers that have not been regulated by reservoirs have extensive lateral floodplains where much fish production occurs in seasonally inundated habitat (Welcomme 1979). Allochthonous inputs are of great importance in these systems; consequently there is a greater role for mud and detritus feeding (which often supports the greatest biomass of fish), and for predation (which often dominates species richness). The extensive flooded forests of the Amazon make available a wide variety of food items including seeds, nuts, fruits, flowers, leaves, monkey feces, numerous terrestrial invertebrates, and the occasional vertebrate (Goulding 1980). Diversity of resources obviously contributes to diet diversity, and special feeding adaptations further increase the variety of feeding roles. Large characins such as the tambaqui (*Colossoma*) have evolved broad, multicusped molariform teeth in order to crush hard nuts. A number of unrelated taxa eat particular parts of other living fishes, including scales, skin, fins, gill filaments, and eyes, as well as whole chunks of the body (Roberts 1972, Sazima 1983). Morphological specialization in these carnivores includes sharp, forward-directed cutting teeth, and behavioral specialization such as aggressive mimicry.

Despite considerable specialization of dentition, jaw shape, body form, and alimentary tract, many tropical fishes nonetheless display considerable flexibility in their diet, due largely to changes in habitat and food availability driven by seasonal fluctuations in water level. In the Apure and Arauca rivers, two tributaries of the Orinoco River, the catfish *Pseudoplatystoma hemioliopterus* is primarily piscivorous, while in the Amazon basin, fruits and seeds have been found in their stomachs (Barbarino and Winemiller 2003). Goulding (1980) reported that piranhas ingested mostly seeds and fruits during the flooded period. Seasonal comparisons in a small Panamanian stream (Zaret and Rand 1971) revealed greater diet overlap in the wet compared to the dry season. Reduced food levels in the dry season evidently led to greater habitat and food specialization in that study, and Winemiller (1991) also reported strong food and/or habitat specialization among predatory haplochromine cichlids in the Upper Zambezi river basin during the annual period of falling water levels.

A number of tropical species have evolved long-distance migrations to best exploit the higher primary and secondary production that accompany wet-season flooding. *Semaprochilodus*, an algivorous and detritivorous fish of South America, migrates during the period of high water from less productive blackwater rivers to the more productive floodplains of the Orinoco and Amazon to feed and spawn. Early in the dry season the juveniles migrate upstream into the blackwater rivers where they are consumed by piscivores like *Cichla temensis* (Winemiller and Jepsen 2004). The migratory movements of *Semaprochilodus* thus constitute a longitudinal energy subsidy, transferring C accrued in the more productive floodplain systems into less productive blackwater rivers.

To a greater degree than is seen in temperate zone studies, the proportional representation of guild categories in tropical rivers varies among sites. In the Río Machado, a large, nutrient-poor clearwater tributary of the southern Amazon with extensive inundation forest, autochthonous plant food was sparse or absent and thus grazing on periphyton, plankton feeding, and consumption of aquatic herbaceous vegetation were unimportant (Goulding 1980). Quite a different result was obtained in a dry-season study of feeding guild structure in nine small (1–6 m wide) Panamanian streams lying mostly in mature forest, but including some disturbed land (Angermeier and Karr 1983). Seven feeding guilds incorporating 26 fish species were identified by cluster analysis of computed diet overlap. Mud feeders and planktivores were absent and algivores were well represented, in marked contrast to the Río Machado and quite reasonable for small streams with primarily coarse substrate and well-defined channels. The distribution of guild biomass varied with habitat and stream characteristics, including a trend toward fewer aquatic invertivores and more algivores with increasing stream size. Still further downstream, one finds the floodplain fauna with its preponderance of mud-eaters. Inundation forests support a diverse assemblage of fruit and seed feeders, but these ecosystems are uncommon outside South America, perhaps because of past human modification of inundation forests in other parts of the world.

Fish body size has an influence upon diet but it is difficult to generalize about diet from size alone, or to distinguish between temperate and tropical faunas. Often a greater proportion of large species are piscivorous, as illustrated by the trophic composition of the fish species of various inland waters of West Africa (Figure 8.11). However, the largest freshwater fishes include representatives of all trophic categories. The Mekong giant catfish (*Pangasianodon gigas*), believed to be the world's largest purely freshwater species at 300 kg, is a detritivore, as are the giant sturgeon (such as *Huso dauricus*, with a maximum reported weight of 1,000 kg in inland seas). The giant arapaima (*Arapaima gigas*) of South America is a piscivore that reaches 200 kg, and other large-bodied species include the omnivorous carp of India (e.g., *Catla catla*), and the herbivorous tambaqui (*Colossoma macropomum*) of South America.

A study of body size and trophic position in a diverse tropical food web in a savannah tributary of the Orinoco River, Venezuela, illustrates the complexities and limitations of a size-based analysis (Layman et al. 2005). Because primary consumers (algivores and detritivores) exhibit a wide size range, predatory fishes of all body sizes were able to exploit taxa low on the food web, resulting in relatively short, size-structured food chains for individual components of the overall web. However, no relationship was found between body size and trophic position across the range of body sizes for the 31 predaceous species in this system, due to the wide range of body sizes of the primary consumer fish taxa.

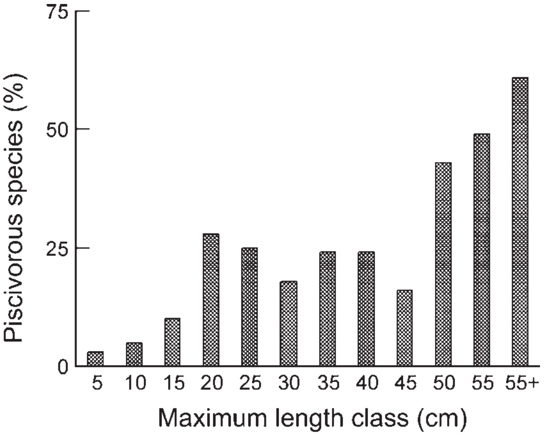

FIGURE 8.11 The percentages of fish from West African rivers that are piscivorous in a given maximum length class. (Reproduced from Allan et al. 2005a, based on analyses by RL Welcomme.)

In sum, the categorization of fishes into feeding guilds provides useful insights into trophic structure, but requires similar caution as when categorizing invertebrate FFGs. Diet changes with age because of growth in size, and with season because of shifts in availability of habitat and food types. Even a single individual at a particular time and place may fall into more than one feeding category. In practice, guilds are a useful way to summarize the broad similarities in the trophic ecology of taxa that have similar feeding roles, as long as their use does not obscure the individual differences and great flexibility of which fish are capable. Because of differences in resource availability between temperate and tropical regions, their fish guilds also differ, particularly in the greater roles of detritivory and ooze feeding in the tropics. Moreover, guild structure appears less uniform from place to place among river-dwelling fishes of tropical rivers, compared to temperate zone studies.

8.3.2 Other vertebrates

Amphibians, reptiles, birds, and mammals are all represented in lotic food webs. The taxa most likely to have a significant impact on riverine food webs probably are the salamanders of headwater streams, and fish-eating snakes, birds, and crocodiles in larger rivers, but perhaps this reflects lack of knowledge concerning other groups. Salamanders can attain large size, including *Megalobatrachus* of the Orient, *Cryptobranchus* (the hellbender), and *Necturus* (the mud puppy) of Eastern North America, and *Dicamptodon ensatus* of the Pacific Northwest of North America (Hynes 1970, Nickerson and Mays 1973). They are carnivores of invertebrates, other amphibians, and fish. Small salamanders may be the principal vertebrate predators in headwater streams. Petranka (1984) concluded that the larval two-lined salamander *Eurycea bislineata* was an opportunistic generalist, consuming a variety of insect larvae and crustaceans. In cave streams, however, *Eurycea* may be a detritivore rather than a predator based on stable isotope analyses (Simon et al. 2003).

The larvae of some frogs and toads feed on algae in small streams, and a few possess powerful suckers that provide attachment and allow leech-like maneuverability (Hynes 1970). Tadpoles of the web-footed frog, *Rana palmipes*, widely distributed in the Neotropics, are epibenthic consumers that feed on algae and sediments and can grow on sediments alone (Flecker et al. 1999).

Reptiles that feed in rivers include the Crocodylia, many families of snakes but especially the Colubridae (water snakes), and the Chelonia (turtles). The former two groups are predators of fish and invertebrates; the latter are omnivores of sluggish streams and rivers and consume substantial amounts of invertebrates and fish. Size of prey relative to size of predator is a common constraint, and many predators increase the size and breadth of their diet as they grow. An aquatic population of the Oregon garter snake *Thamnophis atratus* fed on small prey along the stream margin as juveniles, but as adults they consumed a wider variety of prey types and sizes, especially concentrating on larvae of the Pacific giant salamander in midstream substrates (Lind and Welsh 1994). Fish are the dietary mainstay of the alligator snapping turtle *Macrochelys temminckii*, the largest of North American turtles, which possesses a unique lingual lure to attract its prey (Harrel and Stringer 1997). Nonetheless, they consume a wide mix of plant and animal matter. Even young crocodiles feed primarily on invertebrates until they reach a length of about 2 m, when they become predatory on a wide range of aquatic and terrestrial vertebrates (Corbet 1959, 1960), as do American alligators, which consume fish, turtles, muskrats, and rabbits, among other prey. Hynes (1970) remarks that, considering the abundance of crocodiles along tropical rivers where exploitation has not reduced their numbers, they are likely to have a major impact on lower trophic levels. In the Big Cypress Swamp of Florida, the American alligator *Alligator mississippiensis* is unusually abundant, and based on a model of indirect trophic effects, it appears to benefit invertebrates, frogs, mice, and rats through its predation on snakes and turtles (Bondavalli and Ulanowitz 1999).

At least 11 orders of birds make use of rivers and streams as feeding habitat (Hynes 1970). Many are fish predators but some feed directly on invertebrates (e.g., the Cinclidae or dippers, Ormerod 1985). Diving ducks also consume significant amounts of invertebrates, especially mollusks, although submerged aquatic vegetation is their primary food (Perry and Uhler 1982), and ducks can be important consumers of macrophytes (Lodge 1991). There are many piscivorous birds, but at present the weight of evidence suggests that they do not have a major impact on fish populations except when fish are easily captured, such as during low water conditions (Draulans 1988). However, some studies of bird predation report a substantial effect on population size or on the foraging behavior of the prey species. Steinmetz et al. (2003) altered the abundance of Great Blue Herons (*Ardea herodias*) and Belted Kingfishers (*Ceryle alcyon*) along an Illinois prairie stream by suspending plastic bird netting along an exclusion reach and adding kingfisher perches along an augmentation reach. The mean sizes of two abundant prey, striped shiners, and central stone rollers, decreased under normal and elevated predation but increased in the reduced predation reach, in accord with preferred prey sizes of the two predators, apparently due to a combination of direct mortality and prey emigration. Armored catfish in Panamanian streams experience significant predation risk from fishing birds (Power 1984a, b), and this causes larger individuals to avoid shallow waters. Because these fish are effective herbivores, the depth distribution of periphyton inversely mirrors the distribution of fish.

A diversity of mammals feed within running water. Taxa ranging from shrews to racoons to bears occasionally or frequently consume invertebrates and fish. Others such as the river otter *Lutra canadensis* are fully aquatic and feed almost entirely on aquatic resources. The duckbill platypus *Ornithorhynchus anatinus*, a nocturnal hunter in Australian rivers, possesses electroreceptors capable of detecting the muscle activity of invertebrate prey (Scheich et al. 1986). Very large river-dwelling mammals include the plant-eating manatees of South America and West Africa (Campbell and Irvine 1977), and dolphins, which feed on invertebrates and fish. River dolphins are top predators and those from the Amazon have been found to eat at least 50 fish species from 19 families, including individuals up to 0.8 m in length (Best and Da Silva 1989); in addition, they occasionally consume mollusks, crustaceans, and turtles.

Seasonal fluxes of anadromous fishes into rivers provide nourishment for a great many mammal species (Willson and Halupka 1995). Spawning salmon or their fry have been shown to provide critical sources of food for martens during years of low rodent abundance (Ben-David et al. 1997), influence the body mass and litter size of North American brown bears (Hilderbrand et al. 1999), and even be significant components of the diet of wolves (Szepanski et al. 1999).

Although different vertebrate predators are capable of a variety of hunting tactics, most are morphologically constrained to hunt primarily by wading, diving, or swimming. Wading birds typically fish in water no deeper than 20–30 cm. Leg length and striking distance must limit their success at greater depths. Diving and skimming predators such as kingfishers and bats usually fish very close to the surface, although kingfisher dives to a depth of 40 cm are not unknown (Power 1984b) and mergansers fish at depths of one meter or more. Swimming predators typically fish at greater depth, either to minimize their own risk of predation or, especially if they are of large body size, to have more room to maneuver. The need to capture and swallow prey generally results in a rough correspondence between prey size and predator size, even in species able to extend their gapes or rend prey into pieces. The combination of a predator's depth range and size range may significantly affect the size and depth distribution of fishes in streams, and perhaps affect other members of the biota as well (Power 1984b). Indeed, many vertebrate predators may have their impact on riverine communities by influencing the foraging location of their prey. As we shall see in subsequent chapters, the consequences can ramify widely through the food web.

8.4 Secondary Production

Secondary production includes new biomass produced by microbial and animal growth and reproduction. In lotic ecosystems, animal production is due primarily to the meiofauna, macroinvertebrates, and fish. It represents the production of new biomass over some time period, often a year, due to growth and recruitment and accounting for losses to mortality, and commonly is expressed in mass per area per time (Benke 1993). The ratio of production to biomass (P/B), called the turnover rate (in units of time), is a measure of the productivity of some population or assemblage. High P/B ratios usually are associated with fast life cycles and rapid individual growth rates. High production may be due to a high P/B ratio, high biomass or both, but usually is due to high individual growth rates and short life spans resulting in rapid population turnover (Huryn and Wallace 2000).

The magnitude of secondary production can be calculated for a population of a particular species in a stream reach, for the most common taxa, and for an entire assemblage (Benke 1993). The measurement of secondary production requires estimation of biomass per unit area, also referred to as standing stock, and of growth rate. Typically one uses wet mass for fishes and either dry mass or ash-free dry mass (AFDM) for invertebrates. In species with cohort population structure, usually seen when reproduction occurs annually, growth rate can be obtained by measuring the average mass of individuals sampled frequently, often monthly. When growth rates are more rapid or cohorts overlap it may be necessary to measure growth rates in the laboratory, usually across a range of temperatures and at different stages of the life cycle. Production is the product of mass-specific growth rate and population biomass, so factors influencing either growth rates (primarily temperature and food availability) or population biomass (habitat suitability, discharge fluctuations, resource supply, and predators) can affect production.

Studies of secondary production by macroinvertebrates are undertaken to obtain a better understanding of energy flow through populations and to investigate the trophic base that supports the population. When secondary production is estimated for an entire assemblage, it can then be compared with estimates of primary production and production of fishes to examine energy produced and consumed at each level. Benke (1993) and Huryn and Wallace (2000) provide excellent reviews of the more than 2,000 estimates of stream secondary production worldwide. Conversion to common units is achieved by assuming that dry mass = 0.2 × wet mass and 1.11 × AFDM. Studies from small streams greatly outnumber those from larger rivers, few are from tropical latitudes, and annual production values vary greatly, from approximately 1 to 10^3 g m^{-2} $year^{-1}$ dry mass. The highest values on record are from dense aggregations of filter-feeding black flies in lake outlet streams with favorable temperatures and an abundant plankton supply (Wotton 1988); however, any estimates >100 g m^{-2} $year^{-1}$ are exceptional, and most are considerably lower (Huryn and Wallace 2000). Figure 8.12 shows that most estimates for individual species are below 10 g m^{-2} $year^{-1}$, many are <1, and highest estimates are from filter-feeding invertebrates.

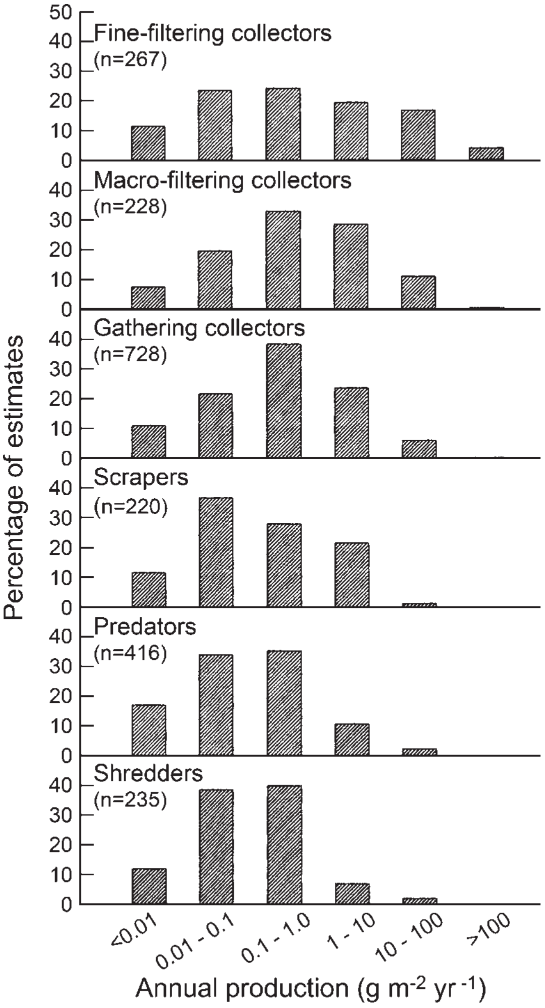

FIGURE 8.12 The range of production estimates for various functional groups of stream invertebrates. (Reproduced from Benke 1993.)

Estimates of whole stream secondary production are relatively few and highly variable, making it difficult to generalize. The highest value from an unaltered stream, Sycamore Creek in the Sonoran desert of Arizona, was 135 g m^{-2} $year^{-1}$ (Fisher and Gray 1983). In contrast, annual production was 4.1 g m^{-2} $year^{-1}$ for the shaded Hubbard Brook in New England (Fisher and Likens 1973). Extremely high secondary production has been recorded from some anthropogenically enriched systems, e.g., 268 g m^{-2} $year^{-1}$ for a river in Wales (Lazim and Learner 1986), and 612 g m^{-2} $year^{-1}$ in the New River below a dam (Voshell 1985 cited in Huryn and Wallace 2000). In the summary of 58 studies of production for entire macroinvertebrate communities, Benke (1993) found that 40% reported levels of <10 g m^{-2} $year^{-1}$, 78% reported levels of <50 g m^{-2} $year^{-1}$, but only three studies reported levels less than ~ 3 g m^{-2} $year^{-1}$.

The majority of annual P/B ratios tend to fall between 1 and 10, with occasional estimates throughout the 10–100 range, and a few higher yet. Among functional groups, the highest production estimates were from filtering collectors, and both shredders and predators tended toward lower values (Benke 1993). Over 75% of P/B estimates for predators were <10, presumably because of their relatively large size and long development. Over 90% of shredder P/B estimates were <10, and large body size and poor food quality are the likely explanations. Small consumers with a high-quality food supply have been recorded to achieve very high P/B ratios. Benke (1998) estimated turnover rates for two larval chironomids dwelling on snags in the Ogeechee River to be 158 (*Rheocricotopus*, a filtering-collector) and 258 (*Polypedilum*, a gathering collector). The turnover rate for *Polypedium* is the highest reported for a metazoan and indicates that its biomass is being replaced almost daily. In Sycamore Creek, Arizona, the annual production by all Chironomidae was 58 g m^{-2} $year^{-1}$ and the P/B ratio for this group was 121.5 (Jackson and Fisher 1986).

Further evidence of the influence of life span can be seen from the comparison of cohort (life span) P/B ratios, which usually range between 2 and 8, versus annual P/B ratios, which range from <1 in species that may require 2 years or more to mature, to >100 in species with many generations annually (Huryn and Wallace 2000). The freshwater mussel *Unio*, with a life span of at least one decade, has an annual P/B < 0.1 (Negus 1966). High production tends to be the consequence of high growth rates more than of high biomass.

Estimation of secondary production coupled with examination of diet can provide valuable insight into energy flux through individual species. Annual secondary production by filter-feeding caddis larvae (*Cheumatopsyche* spp. *Hydropsyche rossi*, and *Chimarra moselyi*) occupying snag habitat in the Ogeechee River, Georgia, was 43.5-63.9 g m^{-2} of snag surface (Benke and Wallace 1997). Production by *Chimarra* peaked during summer, whereas *Hydropsyche* production was greatest from late summer through winter, and *Cheumatopsyche* showed no defined pattern. The omnivorous *Cheumatopsyche* and *Hydropsyche* derived 51% and 64% of their production from animal food and 41% and 24% from amorphous detritus, respectively. The production of *C. moselyi* was primarily based on amorphous detritus (91%). The contribution of detritus to production was higher in the Ogeechee than in another study conducted in the Tallulah River (Benke and Wallace 1980), apparently because of greater bacterial biomass associated with FPOM and a higher density of drifting invertebrates in the Ogeechee.

A number of environmental factors affect growth and thus secondary production. Temperature is the most important variable affecting growth, which often at least doubles for each 10°C increase within tolerance limits of the species. A midge larvae studied in a warm-water river in Georgia showed some decline in daily growth rate at temperatures above 25°C, whereas a mayfly and black fly did not (Figure 5.18). The highest growth rates reported for stream insects are from warmwater streams in Georgia and Arizona (Huryn and Wallace 2000).

Food quantity and quality are major determinants of secondary production. The highest production values observed are from densely packed populations of filter feeders that have a rich food supply from a lake outlet (Wotton 1988). Shredders, scrapers, and predators are much more likely to be limited by available resources (Figure 8.12). However, despite its low quality, allochthonous detritus is important to invertebrate secondary production, as can be seen from a leaf litter exclusion study in headwater streams of Coweeta Hydrologic Laboratory. After 4 years, total secondary production in mixed substrate habitats (cobble, pebble, and sand–silt) had decreased by 78% compared to pretreatment values, demonstrating a strong impact of the exclusion of terrestrial detritus (Wallace et al. 1999). However, secondary production of invertebrates living on moss-covered bedrock was not affected. These were filterers, collector-gatherers, and predators, so were less dependent on coarse detritus and likely derived their production from transported FPOM. In a shaded, second-order stream and an open canopy, fifth-order stream in Hubbard Brook Experimental Forest, Hall et al. (2000) found that invertebrate secondary production was low in both rivers compared with other systems. Detritus supported a high fraction of production in both (63% in the second-order stream and 50% in the fifth-order stream) and animals were the second most important source (27% and 22%, respectively). The contribution of algae was higher in the fifth-order stream (22%) than in the smaller stream (4%). Although the shaded and open stream reaches differed in the contributions of allochthonous versus autochthonous energy sources as expected, the effect was relatively small.

A comparison of snag, sand, and mud benthic habitats in the Satilla, a subtropical blackwater river, demonstrates that secondary production can vary greatly among habitats (Benke et al. 1984). Consumer production was far higher in the snag habitat, where filterer-collectors were most abundant, and much lower in sand and mud substrates dominated by collector-gatherers (Figure 8.13). Biomass was much higher on snags (20–50 times greater than on sand, 5–10

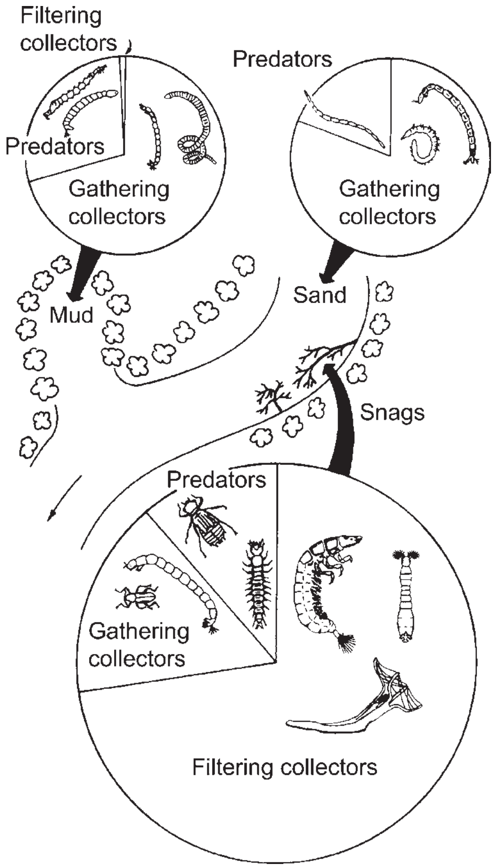

FIGURE 8.13 Relative production of invertebrates in snag, sandy, and mud habitats in the Satilla River, Georgia. Relative production on habitat area basis is indicated by the size of the circles. (Reproduced from Benke et al. 1984.)

times greater than on mud); however, production on snags was only 3–4 times higher than in sand and mud habitats, suggesting that turnover rates of their primary consumers, mostly chironomids and oligochaetes, were higher in the benthic habitats.

Few studies have estimated invertebrate secondary production in tropical streams. In Costa Rica, Ramirez and Pringle (1998) estimated a very low secondary production by benthic insects (364 mg AFDM m^{-2} $year^{-1}$) compared to estimates in subtropical and temperate systems. However, P/B ratios were between 5 and 103, suggesting that biomass turnover was high. High flows, resource limitation, and predation by shrimp and fishes likely explain the low insect production in this river. In a Hong Kong stream, production was higher than in the Costa Rica stream, but values still to were low compared to other systems (Dudgeon 1999).

Most studies of invertebrate secondary production neglect the meiofauna, and their contribution may be substantial. In a study of the entire metazoan benthos larger than 42 μm in an acidic stream in England, total production (5.2 g m^{-2} $year^{-1}$) was modest, probably due to the acidic conditions (Stead et al. 2005). Although permanent meiofauna represented only 3% of the total biomass, they contributed 15% of the total production. The average P/B of the permanent meiofauna was 38, much higher than the value of 7.6 for the metazoan community. When production was estimated based on size, the permanent and temporary meiofauna (small oligochaetes and early instars of insects) contributed 51% of the total. Clearly, exclusion of the meiofauna can lead to serious underestimates of secondary production.

The study of fish production has a long history of quantitatively rigorous analysis, following the pioneering work of Ricker (1946) and others. From the perspective of stream ecosystem production, a famous study by Allen (1951) in the Horokiwi stream, New Zealand, sparked decades of study into what became known as Allen's Paradox. Production by brown trout, which was estimated reasonably accurately, greatly exceeded the biomass and assumed production by invertebrates, which at that time was an approximate value. Suggested answers included a hidden role for the hyporheic and meiofauna, higher P/B ratios than were thought to be common, and terrestrial subsidies. However, even as the accounting improved, the consumption by fish seemed to at least press the limits of secondary production by invertebrates (Allan 1983), raising doubts that a reasonable surplus of prey survived to maintain their populations (Huryn 1996). Huryn was able to account for the food demands of brown trout in another New Zealand stream, but only by including all compartments of the stream ecosystem. Surficial invertebrates provided most of the food consumed, but the full accounting included hyporheic and terrestrial invertebrates, and cannibalism upon young trout (Figure 8.14). Intriguingly, there was still no "leftover" invertebrate production, and Huryn suggested that uncertainty in estimates might explain how sufficient individuals survive for population replacement. Because Huryn's study indicated that trout consume 80% or more of invertebrate production, he inferred that top-down control of benthic prey populations must have a strong influence in his system, and probably in similar systems as well.

A long-term study of trout populations in a Minnesota stream illustrates the value of biomass and production estimates in interpreting population dynamics (Waters 1999). In a stream initially populated only by brook trout, a 21-year-long study documented how floods, sedimentation, and invasion by brown trout reduced brook trout standing crop from 184 to 4 kg ha^{-1}, and production from 171 to 9 kg ha^{-1} $year^{-1}$. By the end of the study, brown trout production was 322 kg ha^{-1} $year^{-1}$, and so the species replacement resulted in trout production that was markedly higher than observed previously.

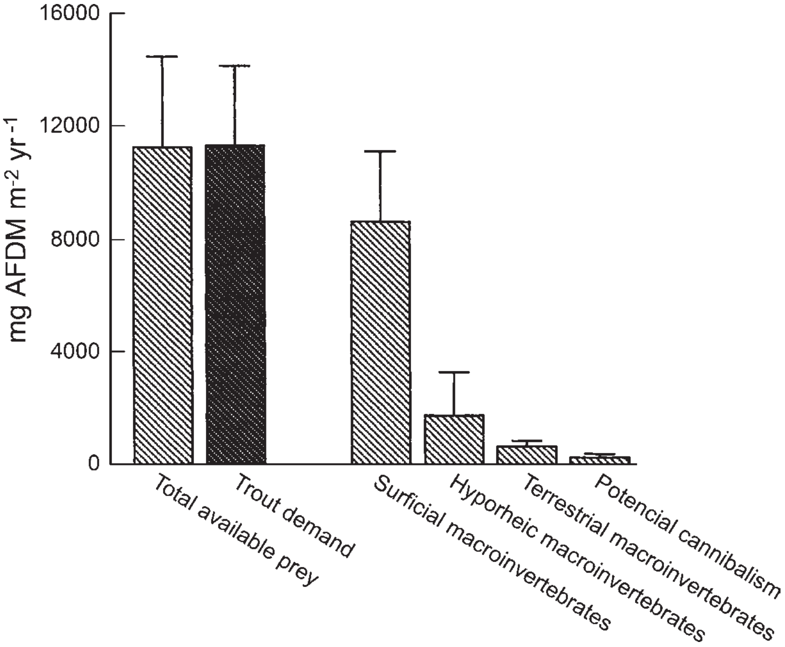

FIGURE 8.14 Total prey available for consumption by trout as well as prey available from various sources, in units of annual production. Trout demand was estimated using known values for its ecological efficiency. Error bars are 95% confidence intervals. (Reproduced from Huryn 1996.)

8.5 Summary

Trophic roles in lotic ecosystems are a reflection of the variety of basal resources, including various primary producers and categories of dead organic matter, the complicated role of microorganisms, and the diverse morphological and physiological mechanisms for the ingestion and assimilation of food. For invertebrates and fishes, the concepts of FFG and guild greatly aid our assessment of feeding roles by adding the "where" and the "how" to the "what" of resource consumption. Recent advances in microbial ecology have greatly improved our understanding of the ways that bacteria and fungi act as consumers of POM and DOM and synergistically within biofilms, and at the same time are, in essence, basal resources to many consumers.

Production by bacteria and fungi converts POM and DOM into microbial tissue available not only to the meiofauna, but to macroinvertebrates as well. The permanent and temporary meiofauna are suspension feeders or browsers feeding on bacteria and biofilm-coated FPOM. Because of the small size of the meiofauna, it has been speculated that microbial production, especially by bacteria and in biofilms, would have to pass through many food chain links before reaching macroinvertebrates, and so much energy would be dissipated with each step that little energy would reach higher trophic levels. Under this scenario, the microbial food web is a sink for C transfer, although still important in remineralizing C and nutrients. However, bacterial production has been shown to reach virtually all consumers including fish, almost certainly due to the consumption of biofilms associated with larger particles. Bacteria associated with surfaces and within organic sediments are the most likely candidates for this pathway, although some bacterial ingestion in association with suspended POM may occur in larger rivers.

The FFGs of macroinvertebrates, categorized according to food sources and mechanism of food acquisition, reflect the four most important food resources found in streams: periphyton, CPOM, FPOM, and animal prey. Grazers ingest periphyton, shredders feed on CPOM, collectors feed on FPOM either from the water column or the streambed, and predators consume prey. Most suitable for late instars, FFGs provide insight into the relative importance of various basal resources. Further feeding specialization is seen to varying degrees within each of these feeding groups. Shredders vary in how they feed on CPOM, such that leaves may be skeletalized in a characteristic fashion, and also in their digestive capabilities, where crustaceans and mollusks tend to be more specialized than insects. Grazers include scrapers whose specialized mouthparts permit the removal of tightly attached algae close to the substrate, while browsers have mouthparts better suited to brushing the loose overstory of algae. A few have piercing mouthparts that allow them to imbibe cell fluids. Filter feeders have evolved elaborate food-capturing devices such as fans, nets, and setae, resulting in specialization by particle size and habitat. Detritus feeding by collector-gatherers is a common feeding mode and probably widespread in early instars; however, specialized adaptations for this feeding role have received less emphasis and perhaps are few. Invertebrate predators posess various adaptations to detect their prey, of which mechanical detection seems to be common, and can be separated into searching versus ambush hunting styles. The relationship between prey and predator body size strongly affects which prey are consumed, so that prey size and diversity typically increase with predator body size.

The guilds of fishes categorize feeding roles through a combination of what is eaten and where it is consumed, such as midwater versus benthic invertivores. Relatively few fishes are herbivorous in the temperate zone, and so most members of an assemblage fall into various categories of invertivores, or are piscivores. A great deal of functional specialization can be observed in fish mouthparts, digestive capabilities, and sensory modalities for detecting prey. Fishes in the tropics show high species and high functional diversity, and include many more specialists in the consumption of algae, mud, and ooze. Fish body size has an important but complicated influence on fish feeding roles. Although piscivores tend to be larger on average than their prey, the largest freshwater fishes include detritivores as well as piscivores. At least in tropical rivers, evidence suggests that predatory fishes are found in all sizes and so often are at the apex of relatively short food chains. All classes of vertebrates are represented in fluvial food webs. Salamanders may act as top predators in fishless headwaters, reptiles and birds can be important predators in some circumstances, and a surprising diversity of mammals including terrestrial taxa make opportunistic use of aquatic production, and of migrating fish in particular.

Secondary production quantifies the elaboration of new biomass through growth and reproduction, after accounting for mortality, per some unit of area and time. High secondary production is due to high biomass or high population growth rates that result in high rates of biomass replacement, and so depends on temperature, resources, and all of the factors that affect the success of populations. By combining estimates of secondary production with diet studies, it is possible to connect the magnitude of consumer production to the primary or secondary production that sustains it. In the case of trout streams, it appears that consumption at the top of the chain is capable of removing all of the production below, suggesting top-down control of lower trophic levels.

Chapter nine

Species interactions

The assemblage of species within a stream reach forms a network of linkages and interactions that vary in strength and the number of species affected. The basal resources of algae and detritus, with associated microorganisms, sustain higher consumers including herbivores, predators, and parasites. The availability of resources can limit the abundance of consumers (called bottom-up control), and consumers can regulate the abundance of their prey at lower trophic levels (called top-down control). Species often compete for the same limiting resources such as food or space, and successful competitors are able to retain their place in the assemblage while less aggressive or efficient species may be excluded. The interactions of grazers with algae, predators with their animal prey, and among competing species constitute the primary linkages that collectively bind species together within food webs. This chapter focuses on the ecological consequences and complexity of such linkages, and Chapter 10 explores the forces that ultimately determine which species are found together and thus the structure of lotic communities.

9.1 Herbivory

Primary producers, including algae, cyanobacteria, bryophytes, and vascular plants, are important basal resources in lotic food webs. As discussed in Chapter 6, macrophytes are subject to comparatively little grazing pressure before entering the detrital pool, and phytoplankton play a relatively minor role in most free-flowing rivers. Grazing on benthic algae by invertebrates, some fishes, and a few amphibian larvae is the most important pathway of herbivory in streams, and has received by far the most study. Benthic algae vary in their distribution, growth form, and nutritional value, and grazers differ in their means of scraping and browsing this food supply (Section 8.2.3). Thus, which algae are consumed reflects their vulnerability to particular grazers, and possibly aspects of preference as well. Grazers can have a number of impacts on algae, reducing their abundance, altering assemblage composition, and even stimulating algal growth and overall productivity through the removal of senescent cells and the recycling of nutrients (Feminella and Hawkins 1995, Steinman 1996).

9.1.1 Grazer responses to food supply

Algae are patchily distributed, from the smallest scale of the surface of an individual substrate, to an intermediate scale such as from stone to stone, through larger scales such as open versus canopied sections of streams. Although some herbivores might feed essentially at random, an ability to perceive and respond to this patchiness ought to be advantageous. Richards and Minshall (1988) studied grazer distribution at small scales in an alpine stream, using natural stones that were selected based on visual assessment of periphyton abundance and in some instances scraped to produce patches of various widths. Stones were replaced in the stream under glass viewing boxes, and insect presence was then determined by photography. Within 1–2 days, *Baetis* mayflies were concentrated in patches rich in periphyton.

A similar response of grazers to periphyton can be seen at larger spatial scales. Fuller et al. (1986) shaded a 20 m long riffle with black plastic, reducing chlorophyll *a* levels after 4 weeks to $<0.1\,\mu\text{g cm}^{-2}$, compared to values from 1 to $6\,\mu\text{g cm}^{-2}$ in unshaded sections. *Simulium* larvae increased slightly, and several taxa showed no apparent change, but *Baetis* was much rarer in the shaded section than in open controls. Removal of one half of the shaded plastic resulted in chlorophyll *a* levels similar to the open stream after only 11 days, as well as much greater *Baetis* densities. Body size was smaller for those mayflies that remained in the shaded section, indicative of reduced food availability, and also a rather surprising reluctance to depart for greener pastures. Unaffected taxa (*Simulium*, several crustaceans) presumably relied on other food sources. A similar experiment in a New Zealand stream (Towns 1981) failed to influence any of the fauna, and was taken as evidence that biofilms and associated microorganisms are the most important energy sources in some circumstances.

At an even larger spatial scale, of stream sections or entire streams, grazing animals have been shown to respond to variation in resource availability. In a small stream draining an area that had recently been clearcut, *Baetis* production was roughly 18 times higher than at a reference site, and on stable substrates the difference was even greater (Wallace and Gurtz 1986). Mayfly guts contained mainly diatoms, and estimates of gut fullness from the open canopy stream were up to double those from the forested stream. Although algal cell densities varied little among sites, periphyton production (based on *Baetis* production and projected food consumption) was estimated to be nearly 30 times greater at the open site. Subsequent forest regrowth resulted in canopy closure, and after 6 years *Baetis* was much rarer and periphyton production had dropped tenfold. Because clear-cutting affected the entire stream, recruitment rather than redistribution is the presumed mechanism. In fact, the response of *Baetis* was much greater than that of other mayflies, indicating that its short generation time allowed rapid increase in population size to take advantage of the newly available resources.

Grazers can concentrate in food-rich locations through behavioral mechanisms at small and even relatively large scales, and such non-random foraging has been established in both vertebrate and invertebrate grazers of periphyton. In laboratory microcosms containing rocks with algae from a nearby stream, *Baetis* distributions were unselective when algal biomass was homogeneously distributed, but clustered on high-food rocks when it was heterogeneously distributed (Alvarez and Peckarsky 2005). Detailed analyses of foraging in the caddis larvae *Dicosmoecus* (Hart 1981) and the mayfly nymph *Baetis* (Kohler 1984) document that these insects spend much more time in periphyton-rich patches than would be expected under a model of random movement. When individual *Dicosmoecus* entered an area with abundant periphyton, gathering movements of the forelegs and the rate of mandibular scraping both increased. In addition, overall movement rate slowed, and individuals tended to turn back upon reaching a patch boundary. As a result, time spent in rich patches was 2–3 times what would be expected by chance alone.

The ability to perceive spatial heterogeneity in food supply and respond by simple movement rules that tend to concentrate foraging in regions of high reward is termed area-restricted search. When the periphyton attached to an artificial substrate were scraped to create a checkerboard design that covered only 20% of the substrate surface, *Baetis* spent up to 80% of its time in food patches (Kohler 1984). By comparing the area searched to the smallest area that circumscribed the sequence of movements, Kohler determined that these mayflies searched food-rich patches very thoroughly. Moreover, search behavior upon departure from a patch was influenced by patch quality. Search intensity was much greater just after departing a high quality patch, as evidenced by high thoroughness and low movement rates in comparison to movements following departure from patches of lower quality (Figure 9.1).

Whenever highly mobile herbivores concentrate where algal resources are rich, crowding can reduce the rate of return for an individual grazer to approximately what it would experience in a less productive but less crowded region. A likely consequence is for the abundance and biomass of grazers to increase proportionately with algal productivity, but for foraging gain per individual to be roughly constant. Power (1983) observed just this pattern in the distribution of armored catfish among pools in a Panamanian stream. Shaded pools were less productive and supported a lower abundance and biomass of herbivorous fish compared to open pools. However, individual growth rates were similar across this resource gradient (Figure 9.2). Movements of individuals among pools in a manner similar to the finer scale foraging behaviors of *Baetis* and *Dicosmoecus* presumably result in this pattern, referred to as the ideal-free distribution.

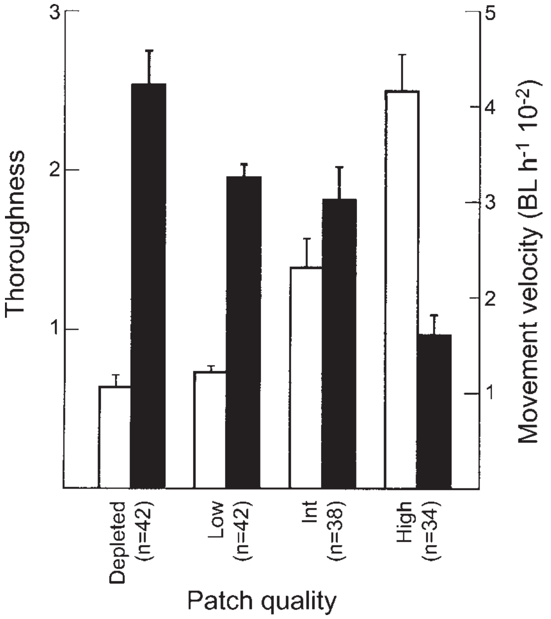

FIGURE 9.1 The influence of patch quality (periphyton cell density) on *Baetis* search behavior immediately after leaving a patch. Thoroughness of searching (open bars) increased and movement rate (solid bars) decreased with increasing patch quality. BL is body length. (Reproduced from Kohler 1984.)

In sum, grazing animals respond to locations of high periphyton abundance, both by shifts in distribution and, if conditions persist, by population recruitment. These concentrations of grazers can either reduce or enhance variation in the distribution and abundance of periphyton, and as we shall see in the next section, influence the composition and physiognomic structure of the periphyton assemblage.

9.1.2 Grazer effects on periphyton

Herbivores affect the periphyton by direct consumption, by physical disruption of the algal mats, and through indirect pathways, especially by nutrient regeneration. Grazing studies commonly report a reduction in periphyton biomass, compositional changes including a reduction in the overstory component, and marked differences in effects depending on the identity of the grazer (Steinman 1996). In addition to these structural changes, grazing can induce functional changes including more vigorous cell growth and enhanced nutrient availability, although these responses vary greatly with context. The preceding section considered evidence that the distribution of periphyton influences that of herbivores – the "bottom-up" effect of resources on consumers. We now turn to the "top-down" influence of herbivory on algae. Whether bottom-up or top-down control prevails depends upon

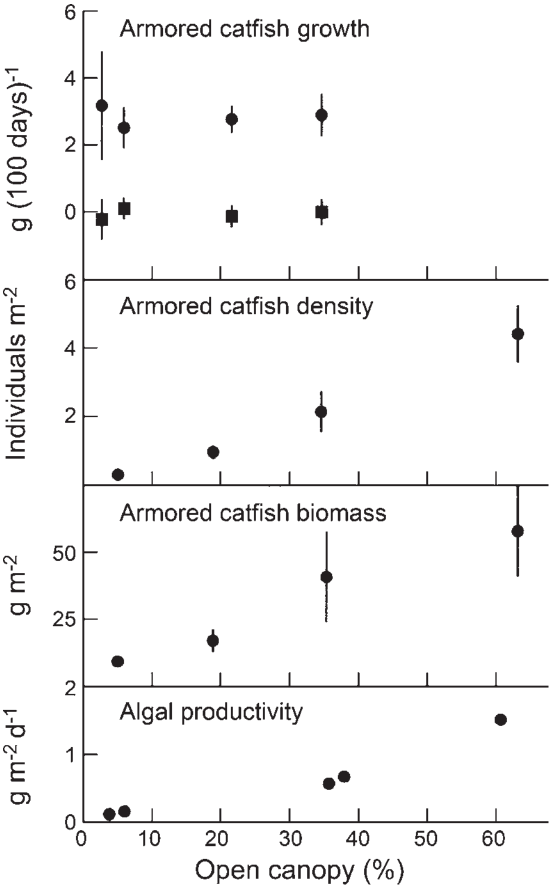

FIGURE 9.2 Evidence that the loricariid catfish *Ancistrus* conforms to an ideal-free distribution. Algal productivity increases in relation to openness of canopy. Density and biomass of catfish increase proportionately with algal productivity, but growth rate (●, rainy season; ■, dry season) is constant. Two standard errors are shown. (Reproduced from Power 1983.)

time, place, and environmental circumstances, and these two patterns are not mutually exclusive.

The interaction between grazers and periphyton has been studied using a variety of experimental approaches, including laboratory streams and field experiments (Lamberti et al. 2006). The former have the advantage of experimental control, allowing manipulation of grazer densities and species, the point in time within algal succession when grazers are introduced, and environmental variables such as light and nutrients. Field experiments offer less experimental control but more natural conditions. One approach has been to position tiles colonized with benthic algae on raised platforms, thus restricting access by all grazers in some instances, or at least of those with poor swimming and dispersal ability. Enclosures placed on the streambed allow even greater control and can easily be placed in sunny versus shaded environments or stocked with different species and size classes, although altered flows and increased sedimentation can result in unwanted side effects. Small squares or hoops supplied with electric current often are effective in excluding larger herbivores including fishes, tadpoles, and shrimp, and avoid the undesirable side effects of cages.

9.1.2.1 Structural responses

Reduction in algal biomass due to herbivory has been recorded with many different grazers, including snails, shrimp, caddisfly, mayfly, and midge larvae, tadpoles, and fish (Steinman 1996). Snails and caddisfly larvae have proven to be highly effective grazers of periphyton in a number of studies, and share the traits of being individually large, relatively slow-moving, and well equipped with scraping mandibles or a radula. Periphyton biomass increased some 5- to 20-fold relative to control substrates when *Helicopsyche* was excluded using tiles raised above the bed of a California stream (Lamberti and Resh 1983). Barriers of petroleum jelly effectively excluded *Glossosoma* from stone surfaces in a Montana stream, resulting in a fivefold increase in algal cell counts (McAuliffe 1984a). Because more mobile grazers including mayflies and midges were unaffected by the manipulation in these two studies, the outcome suggests that these grazers were ineffectual. Lamberti et al. (1987) compared the mayfly *Centroptilum elsa*, the caddis *Dicosmoecus gilvipes*, and the snail *Juga silicula*, which they characterized as a browser, scraper, and rasper, respectively.

Laboratory streams were inoculated with algal scrapings, consumers were added at approximately natural densities 9 days later, and development of the periphyton mat was monitored for 48 days. The effect of the mayfly was slight and confined to small (<2 cm diameter) patches, but *Juga* had a substantial impact and *Dicosmoecus* even more so. However, other studies have found that grazing mayflies are able to limit benthic algae. An experiment that enclosed the mayfly *Ameletus* at realistic densities in Plexiglas chambers containing natural streambed material resulted in marked reductions in periphyton standing crops, even at densities of 0.5× ambient (Hill and Knight 1987, Figure 9.3). It is also possible that entire guilds of herbivorous invertebrates have a significant effect in the aggregate, but this may be difficult to establish from studies of individual species. When all herbivorous invertebrates in a 50 m^2 reach of a Colorado mountain stream were reduced by daily electroshocking with a portable apparatus typically used to collect fish, algal biomass increased substantially in comparison to a reference stream (Taylor et al. 2002).

Where herbivorous fish are plentiful, they have been found to exert considerable control over benthic primary producers. Exclusion of the stoneroller minnow *Campostoma* (due to the presence of a piscivorous fish) resulted in growth of filamentous algae, whereas introduced *Campostoma* caused rapid declines in algal biomass (Power and Matthews 1983). Tropical streams often contain numerous species of grazing fish, as well as algivorous insects, mollusks, crustaceans, and larval amphibians.

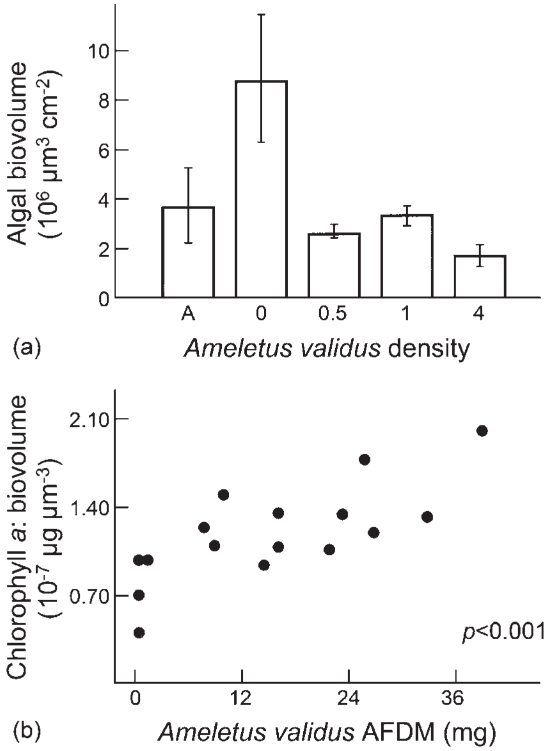

FIGURE 9.3 The effect of density of the mayfly *Ameletus* on periphyton standing crop and quality. (a) Periphyton abundance under various grazing conditions. A: ambient densities on streambed; 0: cages with zero density; 0.5, 1, and 4: cages with 0.5×, 1×, and 4× natural densities, respectively. Results were similar for chlorophyll *a* and AFDW. Note that even low densities of grazers reduced algal biovolume. (b) The ratio of chlorophyll *a* per unit biovolume increased significantly with *Ameletus* biomass. (Reproduced from Hill and Knight 1987.)

Heavy grazing pressure has the potential not only to reduce the total biomass of periphyton, but also to alter the structural and taxonomic composition of the assemblage. Benthic algae exhibit a variety of growth forms that include prostrate and low-profile species, upright and stalked species, and filamentous growth forms (Figure 6.1); furthermore, different grazers are best adapted to consume one or more layers. Many species of mayflies are most effective at browsing the loosely attached, outer layers of the periphyton mat, whereas the scraping and rasping mouthparts of caddis larvae and snails allow them to consume tightly attached algae. Filamentous algae appear to escape most invertebrate grazers due to their size and texture, although probably they are consumed in their early growth stages (Dudley and D'Antonio 1991). However, algal filaments can be very vulnerable to grazing fishes such as the stoneroller in temperate streams and a variety of herbivorous fishes in tropical streams.

One effect apparent in virtually all experimental exclusions of herbivorous invertebrates is a reduction in large, loose, or overstory components of the benthic algal assemblage and an increase in the relative proportion of small, tightly adherent cells (Steinman 1996). Increases in filamentous green and blue-green algae also may occur, as well as changes in particular species. Steinman et al. (1987) provide a particularly detailed account of changes in the algal assemblage in laboratory streams in response to four densities of *Juga* and *Dicosmoecus*. Ungrazed streams developed thick periphyton mats during the 32-day study. Rosettes of *Synedra* and aggregates of *Characium* became established first, then the assemblage became more heterogeneous as patches of other diatoms developed (*Scenedesmus*, *Achnanthes*, *Nitzschia*), followed by the filamentous green alga *Stigeoclonium tenue* and the blue-green alga *Phormidium uncinatum*. Grazing caused severe reductions in *Characium*, whose dense aggregations apparently made it vulnerable, and in *Scenedesmus*. In contrast, *Achnanthes lanceolata* and *S. tenue* increased in representation under herbivory, the former because it is adnate, the latter because its prostrate basal cells are little grazed and possibly benefit from removal of overstory cells.

Which components of the periphyton mat are most affected by herbivory can vary with the species of grazer and their feeding mode. The snail and the caddisfly just described caused broadly similar changes to benthic algal assemblages. However, it also is possible for two herbivores to have quite different effects, as Hill and Knight (1987, 1988) demonstrated in their comparison of the caddis *Neophylax* and the mayfly *Ameletus*. Loose and adnate layers were sampled separately and *Ameletus* affected principally the former, causing declines in motile diatoms including *Surirella spiralis* and several species of *Nitzschia*. *Neophylax* affected both layers but its major impact was through reducing the abundance of a particularly large, adnate diatom that comprised the bulk of total periphyton biovolume.

9.1.2.2 Functional responses

Primary production on an areal basis usually declines in response to grazing, for the straightforward reason that less biomass is present (Steinman 1996). However, grazing can stimulate area-specific primary production under some circumstances. Possible explanations include taxonomic shifts, nutrient release by grazers, and reduced shading of the understory due to removal of the overstory. An increase in area- or biomass-specific primary production due to grazing is plausible because the removal of senescent cells should leave a greater fraction of vigorous cells, which have enhanced access to light and nutrients. Thus, while an increase in herbivory is likely to cause a decline in periphyton biomass, cell-specific photosynthetic rates may increase. As a result, area- and biomass-specific primary production may be greatest under intermediate grazing pressure (Figure 9.4). In laboratory stream studies, McIntire and Phinney (1965) found that highest rates of photosynthesis were attained at low biomass, which they attributed to less shading and senescence. As a cautionary note, however, this effect may be exaggerated in laboratory streams, where initial colonization and rapid growth, followed by senescence and sloughing, are especially pronounced. Also using laboratory streams, Lamberti et al. (1989) observed stimulation of net primary production by grazing at low and intermediate but not high light levels, and for periphyton assemblages that had developed over months rather than weeks, which they attributed to taxonomic shifts, nutrient release by grazers, and benefits to the understory due to removal of the overstory. As attractive as this idea is, the evidence from a number of studies is inconclusive, at least in part due to difficulties in quantifying cell and biomass-specific rates (Steinman 1996).

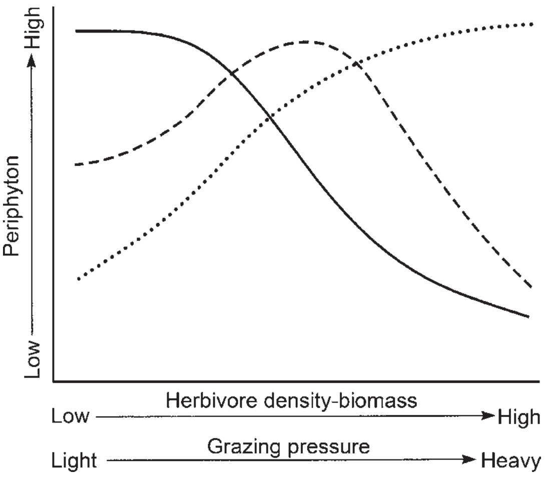

FIGURE 9.4 Theoretical expectation of the relationship between periphyton attributes and the intensity of herbivory. A decline of periphyton biomass with increasing herbivory appears well supported by evidence, and a few studies also document higher photosynthetic rates per unit biomass with increased grazing. The peak in gross primary production at intermediate levels of herbivory is largely speculative. (Reproduced from Lamberti and Moore 1984.)

Herbivory on periphyton can alter rates of nutrient cycling, either reducing demand for nutrients because of lowered biomass, or increasing demand by stimulating the growth rates of grazed populations, and by altering mat characteristics and thus diffusion rates. Because levels of an enzyme produced by algae in response to phosphorus (P) limitation were lower in grazed than ungrazed assemblages, Rosemond et al. (1993) inferred that grazing reduced algal biomass to a level where the available nutrients were largely sufficient to meet algal demand. A much greater biomass of filamentous diatoms and cyanobacteria accumulated in experimental streams when snails were excluded versus when present, with the result that P recycling was high within the ungrazed mat whereas P uptake from the water column was high under strong grazing pressure (Mulholland et al. 1994). The implication is that nutrient limitation may often increase as periphyton biomass increases, and that the dominant sources of nutrients may shift as periphyton mats accrue.

Because primary producers and animal consumers, particularly herbivores, require nitrogen (N) and P to meet their growth needs, ratios of C/N/P in inorganic form and in producer and consumer biomass provide insight into nutrient constraints extending across trophic levels. Autotrophs grown under nutrient limiting conditions develop high C to nutrient ratios in their biomass, potentially resulting in nutrient constraints on consumer growth rates and affecting the rates and ratios of nutrients excreted and thus recycled back to the primary producers. The potential influence of nutrient constraints on trophic interactions is the subject area of ecological stoichiometry, discussed further in Section 11.3.3.3.

9.1.3 Disturbance and herbivory

The interaction between herbivores and periphyton is generally considered to be strongest under favorable environmental conditions and diminished when environmental conditionals are extreme or highly variable. Most field studies of grazing have been conducted under low flow conditions and thus do not adequately represent interactions during the more physically stressful conditions associated with environmental extremes that can occur seasonally or episodically (Feminella and Hawkins 1995). Such extremes are commonly referred to as disturbances, and are often thought of as abiotic but can also include biotic factors such as invasive species. Many of the best documented examples involve extremes of current.

Grazing may result in an algal assemblage that is less vulnerable to scouring by floods, presumably by reducing mat buildup. When the periphyton in laboratory streams subjected to different grazing pressure by the snail *Elimia clavaeformis* experienced a common scour disturbance, most structural characteristics of the periphyton displayed significantly higher resistance to the disturbance in streams with snails than in streams without snails (Mulholland et al. 1991). Experimental reduction of grazers at locations of differing current velocity revealed an interaction between grazing and current in a Colorado stream (Opsahl et al. 2003). After 45 days, electrified tiles had significantly fewer grazers and more than twice the algal biomass compared with controls, but greater algal abundance on tiles in slow currents suggested that grazers differed in their ability to regulate algae across the current velocity gradient.

9.1.4 Top-down and bottom-up effects on periphyton

A large ecological literature explores the relative importance of top-down and bottom-up controls in food chains (Power 1992a). From a bottom-up perspective, higher productivity driven by nutrient enrichment potentially can propagate along food chains, increasing productivity of consumers and possibly lengthening food chains by supporting the addition of another trophic level. Top-down effects of predators typically reduce abundances of their prey, which benefits the next trophic level down the food chain. This pattern is widely observed when predators reduce grazers, leading to an increase of algae. When such effects extend over multiple trophic levels they are called trophic cascades, and because some species may be more strongly affected and others less so, the indirect ramifications can be complex.

Members of the periphyton are subject to a combination of top-down control through grazing and bottom-up control through nutrient availability. Both can dominate in a given ecosystem, and can act separately or synergistically. For instance, high grazing pressure can counteract nutrient limitation by reducing the thickness of the periphyton mat, thereby enhancing water circulation and nutrient uptake, and by recycling nutrients through excretion. In turn, nutrient enrichment may allow periphyton to accommodate higher grazing pressure. In some instances herbivory completely overrides any influence of nutrients. Grazing by the algivorous minnow *Campostoma* was sufficiently strong that algae were similarly reduced in fertilized and unfertilized stream pools (Stewart 1987). Grazing by snails in a headwater stream in Tennessee likewise reduced algae to a thin, grazer-resistant layer regardless of nutrient addition (Hill 1992). Several syntheses of the substantial literature on grazer–periphyton interactions agree that top-down regulation of stream periphyton is common, although almost all studies were conducted under benign environmental conditions (Feminella and Hawkins 1995, Steinman 1996). A meta-analysis[1] of 85 studies that quantified the size of effects associated with grazer access and nutrient supply on periphyton biomass found large effects of both factors, indicating that top-down and bottom-up effects each can be strong (Hillebrand 2002). Grazer effects generally were stronger, which Hillebrand attributed to their immediacy, whereas nutrient stimulation of periphyton growth acts over a longer time period.

An interaction between grazing and nutrient supply would be expected if some algae are more vulnerable to grazing or more responsive to nutrients. By manipulating the density of the snail *Gonoibasis* in enclosures placed in pools of a Kentucky stream, McCormick and Stevenson (1991) showed that a diatom overstory was susceptible to grazing but not strongly affected by nutrients, whereas *Stigeocloneum*, an understory alga that was more resistant to grazing, was highly responsive to nutrient enrichment only in the presence of grazing. Greater nutrient availability may have been the result of increased diffusion due to the removal of overstory algae or excretion by the snails. From simultaneous

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[1] A meta-analysis is a synthesis of prior studies that makes quantitative comparisons by treating individual studies as data points in subsequent statistical analysis. Direction and size of effect classified by experimental conditions and environmental variables typically are assessed.

manipulations of snail densities and N and P concentrations, Rosemond et al. (1993) demonstrated that nutrients had positive effects and herbivory had negative effects on algal biomass (chlorophyll *a*, ash-free dry mass, total algal biovolume) and primary productivity (area- and chlorophyll-specific). Grazing favored chlorophytes and cyanobacteria, which were overgrown by diatoms when herbivores were removed, and N and P both appeared to be at limiting concentrations. Periphyton responded strongly to the combined influence of grazing and nutrients, indicating that both top-down and bottom-up controls were acting on the periphyton (Figure 9.5). In addition, nutrient addition stimulated snail growth, implying that bottom-up nutrient enrichment could influence consumer trophic levels. The interactive effects of nutrients and grazers were also apparent in a tropical stream where the limiting effects of N and grazing fishes both were strong (Flecker et al. 2002). Grazers had greater overall effects than nutrients on biomass and composition of the algae, but the periphyton response to N addition was more pronounced in the presence of grazers. Algal productivity appears to have been stimulated by grazing, possibly due to the dislodgement of sediments that otherwise inhibited rates of diffusion to the periphyton.

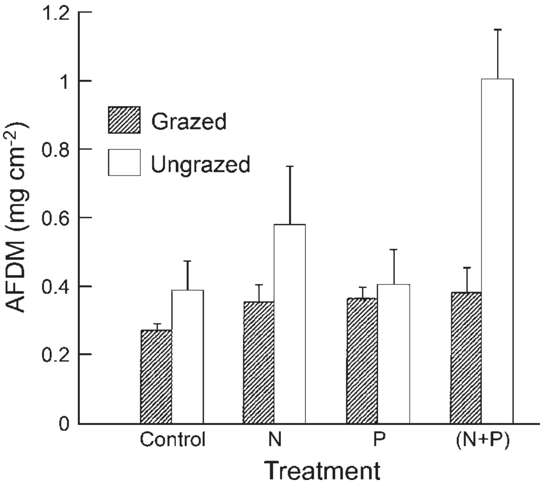

FIGURE 9.5 Ash-free dry mass of periphyton on tiles at week 7 of an experiment in stream-side channels at Walker Branch, Tennessee. Control = ambient streamwater; N, P, and N + P are nutrient additions; grazed channels included the snail *Elimia clavaeformis* at natural densities. Error bars are 1 standard error. (Reproduced from Rosemond et al. 1993.)

Environmental conditions can interact with nutrient supply and grazer abundance to determine the extent of top-down versus bottom-up control of periphyton. Light, nutrients, and grazing all exerted strong control over periphyton biomass and productivity in a woodland stream in Tennessee, but the relative importance of these factors shifted seasonally. Light was limiting to periphyton biomass in summer and autumn but not in spring, nutrients were more limiting in seasons in which light levels were higher, and herbivory was influential during all seasons (Rosemond et al. 2000).

In summary, evidence from laboratory and field experiments demonstrates that grazing not only reduces total periphyton biomass but also alters structural and functional characteristics of the assemblage. Direct consumption, physical disruption, and regeneration of nutrients can each be important. As we broaden our perspective to include all of the environmental variables that affect periphyton, including seasonal and episodic disturbance as well as the predators and parasites that can regulate grazer abundance, it becomes increasingly apparent that biological assemblages are complex entities subject to multiple, interacting controls.

9.2 Predation

Predation is ubiquitous. All heterotrophic organisms are prey for others at some stage of their life cycles, and many species encounter predation risk throughout their lives. The potential effects of predation are diverse, and include reduction in abundance or even the elimination of a species from a region, restrictions on habitat use and foraging efficiency that affect growth rates and reduce fitness, and adaptation via natural selection to persistent predation risk. Top predators can cause a potential cascade of interactions through the trophic web, directly affecting prey by reducing their abundance and changing their foraging behavior, and indirectly influencing additional species to which the prey are linked as food or competitors. Furthermore, changes in energy pathways and species composition may have consequences for nutrient utilization and regeneration. We first consider the predator–prey linkage as an interaction between individuals that has effects on populations, directly through consumption and mortality, and indirectly through behavioral and morphological adaptations that may entail some fitness cost to the prey in order to survive. We then examine how predation can trigger trophic cascades that have consequences for the entire ecosystem.

9.2.1 The predator–prey interaction

All predators show some degree of preference, feeding mainly on certain species of prey. Aspects of the predator that bias it toward consuming more of some prey than others include sensory capabilities, foraging mode, and behavioral mechanism of prey capture. For prey, many aspects of life style and body plan influence their vulnerability. These traits of predator and prey were introduced in Sections 8.2.4 and 8.3, and here we elaborate on the many ways that prey abundance, size, morphology, and behavior shape the interactions between individual predators and prey.

9.2.1.1 Vertebrate predators

Prey abundance and size are both strong predictors of prey consumption of fishes. The number of prey eaten increases with prey abundance for all types of predators, at a decelerating rate due to the time limitation imposed by the handling and ingestion of individual food items. This relationship is known as a functional response curve. Whenever more than one type of prey is present, gut analyses generally find that prey that are abundant in the environment are also common in the diet (Allan 1981). However, the correspondence often is not 1:1, indicating some degree of preference. Prey choice can be strongly influenced by contrast, motion, and size, all of which serve to make certain prey more conspicuous. Many studies have established that predation intensity increases with prey size (Metz 1974, Allan 1978). Larger prey items are expected to be preferred because they offer a greater energy reward and simply because they are more readily detected.

Feeding behavior often changes with experience and learning in vertebrate predators. Ringler (1979) found that brown trout preferred large prey (the mealworm *Tenebrio molitor*) over small (the brine shrimp *Artemia salina*); however, this preference developed gradually over 4–6 days and the least preferred prey never was completely excluded from the diet (Figure 9.6). Changes in fish predatory behavior due to experience result in higher rates of predation. Searching often improves via greater reactive distances, higher swimming speeds, and greater path efficiency, while attack latency may decrease and capture success may increase (Dill 1983). The result is a tendency to specialize on the prey that the predator has consumed most frequently in its recent feeding history, with an accompanying increase in foraging efficiency. Hunger can influence predation rate by modifying any of several aspects of predatory behavior. As hunger decreases, searching also decreases owing to changes in movement speed and reactive distance. In addition, the probability that an attack will follow an encounter declines, and handling time increases (Ware 1972). Capture rate consequently varies with hunger level.

Environmental variables, especially those that affect prey visibility, can significantly modify predation rates. Although visually dependent predators can feed under quite dim light, prey capture success declines with falling light levels. A light

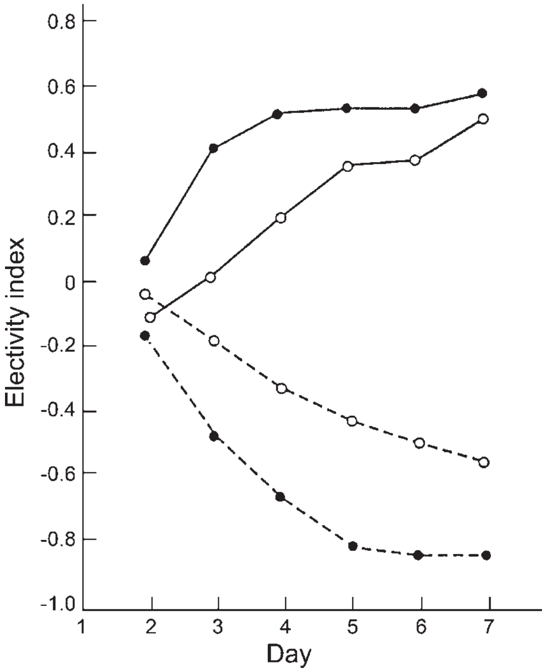

FIGURE 9.6 The size preference for large prey of drift-feeding brown trout in a laboratory stream. Wild trout were maintained on a diet of brine shrimp. In this experiment, brine shrimp (dashed lines) only were provided on day 1, and the larger mealworms (solid lines) were added on day 2. Drift rates were 5 (open circles, low) and 10 (solid circles high) per minute. "Electivity" is a measure of preference based on prey consumed in relation to prey available. (Reproduced from Ringler 1979.)

intensity of 0.1 lux, corresponding to late dusk or a full moon, often is the lower threshold for effective visual location of prey (Hyatt 1979). Even within the range we consider daylight, however, gradation in light level can be influential. Wilzbach et al. (1986) compared the feeding of cutthroat trout in pools from forested sections of streams with pools from open (logged) sections. Prey were captured at higher rates in open pools, and artificial shading lowered the capture rate to that observed in shaded pools. Under varying light conditions corresponding to twilight, moonlight, and overcast night conditions, the foraging efficiency of young Atlantic salmon in the laboratory was unaffected by current velocity until light levels fell below 0.1 lux, at which point the fish were more efficient at prey capture in slower currents (Metcalfe et al. 1997). When provided a choice of foraging location, juvenile salmon shifted toward slower velocity positions as light level was reduced. Habitat characteristics can also influence prey availability and ease of prey capture. The capture rate of epibenthic prey declines with increasing complexity of the substrate; for example, sculpins feeding in the laboratory were able to capture prey more readily from a sandy bottom than from a more heterogeneous cobble habitat (Brusven and Rose 1981).

9.2.1.2 Invertebrate predators

Relative body size of species within a food web strongly influences trophic relationships, influencing resource partitioning, diet breadth, and predator–prey interactions (Warren and Lawton 1987, Chase 1999). Larger species may outgrow predation risk, entering a "size refuge" at some stage of their life cycle, whereas smaller species may never reach a size where they escape predation. Although these statements may apply to all predator–prey interactions they are especially true within invertebrate systems, as is illustrated by the extensive mutual predation and cannibalism seen within the predator guild of Broadstone Stream, UK (Woodward and Hildrew 2002a). The six species (three predaceous midges, a caddisfly, an alderfly, and a dragonfly) exhibited marked size differences, but relative size relationships changed seasonally due to growth (Figure 9.7). Small predators had the narrowest diets, and niche overlap was greater when sizes overlapped strongly and was reduced as predator size diverged (Figure 9.8). The largest predator, *Cordulegaster boltonii*, was preyed upon only by larger conspecifics, and the smallest, *Zavrelimyia barbatipes*, was eaten by all five of the larger species and by conspecifics. The direction of intraguild predation could be reversed whenever early instars of large species

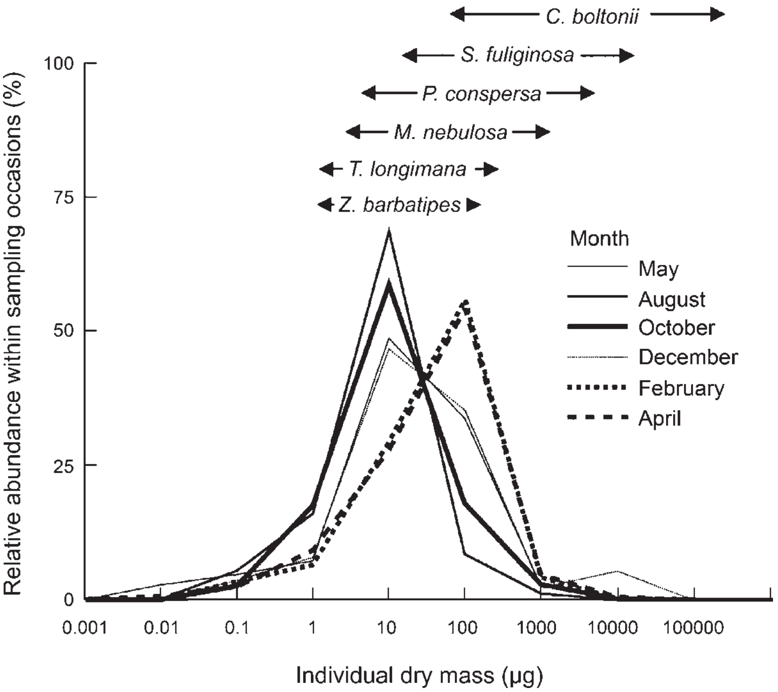

FIGURE 9.7 Relative abundance size-spectra of benthic macroinvertebrates in the Broadstone Stream, UK, on six sampling occasions in 1996–1997. The double-headed arrows indicate the size ranges of the six predator species. From largest to smallest the predators include the dragonfly *Cordulegaster boltonii*, the alderfly *Sialis fuliginosa*, the caddisfly *Plectrocnemia conspersa*, and three tanypod midges *Macropelopia nebulosa*, *Trissopelopia longimana*, and *Zavrelimyia barbatipes*. (Reproduced from Woodward and Hildrew 2002a.)

coexisted with late instars of small species. In this system, clearly, food web structure was influenced mainly by body size relationships, although encounter probabilities and foraging mode also were influential.

Predator foraging mode affects prey vulnerability, interacting with aspects of prey movement to influence localized encounter rates and departures. Mobile prey are likely to flee if able to detect the approach of large, actively searching predators, and so predator impact may be greatest with least mobile prey. This is a complication for cage experiments, which have the potential to overestimate predator impact when predator and prey are confined, and to underestimate whenever prey can escape or enter from the surrounding environment (Wooster and Sih 1995). For sit-and-wait predators, prey mobility may increase their mortality as a consequence of increased encounter rates. In the Broadstone Stream, predation by the dragonfly *C. boltonii*, a sit-and-wait predator, fell most heavily on mobile mayflies, which were not greatly depleted due to high prey exchange rates, but their losses were indeed attributable to consumption rather than flight (Woodward and Hildrew 2002b). In the same system, the net-spinning caddis *Plectrocnemia conspersa* was also reported to have the greatest impact on mobile prey (Lancaster et al. 1991). Prey abundance, movement by crawling or drifting, and speed of prey movement and predator attack likely are additional variables affecting encounter rate and capture success with sit-and-wait predators.

The foraging behavior of predaceous invertebrates does not appear to be much influenced by

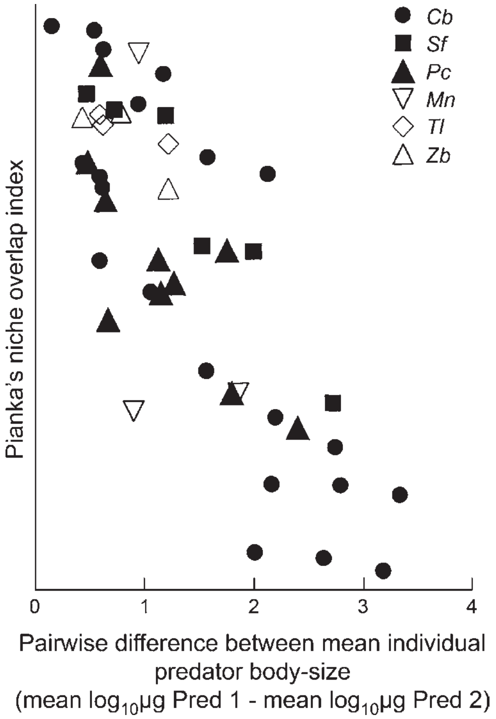

FIGURE 9.8 Pair-wise dietary overlap among invertebrate predators as a function of differences in individual predator body size using mean log dry mass of pairs of predators among size classes within each species. See Figure 9.7 for species codes. (Reproduced from Woodward and Hildrew 2002a.)

prey availability or prior experience, although it has been suggested that predators aggregate in areas of high prey density (Townsend and Hildrew 1978, Malmqvist and Sjöström 1980). However, Peckarsky and Dodson (1980) found that predaceous stoneflies were no more likely to colonize cages containing high prey densities than cages with few prey. Peckarsky (1985) argued that the absence of any aggregative behavior in these predators is explained by the ephemeral nature of prey patches, since highly mobile potential victims like *Baetis* can rapidly disperse. Hunger level did influence which prey were consumed by the stonefly *Hesperoperla pacifica* offered a choice between the soft-bodied, agile-swimming mayfly *Baetis bicaudatus*, and the slow and clumsy *Ephemerella altana*, which has a spiney and rigid exoskeleton (Molles and Pietruszka 1983). Starved stoneflies ate mostly *E. altana*, while satiated stoneflies ate both prey in about equal numbers. When freshly killed prey were offered to starved predators, however, a preference for *Baetis* was evident. The proposed explanation was that starved predators attacked both prey equally, but with increasing satiation began to restrict their attack only to *Baetis*.

Habitat complexity and the availability of refuges can markedly alter predation rates. Refuges may be absolute, rendering the prey unavailable, but more commonly they serve to reduce the likelihood of encounter and capture. In laboratory trials with two invertebrate predators, four invertebrate prey, and various substrate conditions, Fuller and Rand (1990) showed that all variables affected prey capture rates. *Baetis* was more vulnerable than the other prey (an ephemerellid mayfly, a black fly larva, and several hydropsychids), probably because its mobility led to high encounter rates. The predators, a stonefly and an alderfly, differed in their predation rates on various substrates due to differences in their sensing of prey with their antennae and pursuit success. The substrates, which included sand, gravel mixed with pebbles, and artificial turf, resulted in differential capture success via its effects on encounter rates and by facilitating the construction of stronger retreats in some caddis. Although the particular outcomes may be influenced by specifics of the experimental design, such effects of habitat complexity on prey capture probably are common.

9.2.2 Prey defenses

Exposure to risk of predation is a common consequence of foraging and other activities, and thus individuals will benefit from adaptations that minimize predation risk while maintaining energy intake. Predator avoidance takes many forms (Harvell 1990) and often reflects the need to balance foraging opportunities with survival (Sih 1987). Some avoidance mechanisms operate regardless of the physical proximity of predator and prey and serve to reduce the likelihood of initiation of an attack, whereas others function to foil attack and capture. Antipredatory traits can be fixed, such as protective armor or invariant nocturnal activity, or induced by the presence of the predator, such as fleeing after tactile or visual contact, or perceiving the "scent of death" when waterborne chemicals reveal a predator's presence (Kats and Dill 1998). Flexible predator avoidance requires some ability to assess risk and make an escape, and so fixed responses may be favored when those conditions are not met (Dill 1987) or the cost in lost foraging opportunity is modest (Dixon and Baker 1988). Because predation can rarely be entirely ignored or eliminated, threat-sensitive predator avoidance behaviors should be a widespread solution to the trade-off between foraging and avoiding being eaten (Lima and Dill 1990).

Many examples attest to the prevalence of antipredator adaptations among aquatic organisms. Cooper (1984) found that adult water striders (Gerridae) occupied all areas of stream pools when trout were absent, but only the margins of pools that contained trout. When trout were removed from some pools and transferred to others lacking trout, gerrid distribution adjusted accordingly. Similarly, juvenile crayfish *Orconectes propinquus*, the preferred prey of fish such as smallmouth bass, avoid open, sandy substrates where larger and less vulnerable crayfish are abundant (Stein and Magnuson 1976). Many stream fishes avoid habitats that pose high risk coupled with high reward, and instead forage in less profitable patches where risk of predation is less (Cerri and Fraser 1983, Power 1984a).

Peckarsky (1996) describes alternative predator avoidance syndromes by mayfly species that she relates to a continuum of mobility and predation risk. Predaceous stoneflies in Rocky Mountain trout streams consume the swimming mayfly *Baetis* in high frequency, the surface-clinging heptageniids *Epeorus* and *Cinygmula* with lower frequency, and the benthic crawler *Ephemerella* least of all. The agile *Baetis* quickly departs when encountered, using the water column as an escape route and sacrificing foraging opportunity in doing so, whereas the heptageniids are less prone to drift in response to encounters. *Ephemerella* has a spiny and rigid exoskeleton and arches its body in an apparent defensive reaction on contact with a predaceous stonefly, and this rather than escape provides its main defense.

9.2.3 Effects of predation on prey populations

Size classes and species of fishes that are vulnerable to piscivores frequently show an inverse relationship between predator and prey abundances or exhibit nonoverlapping distribution patterns. Surveys of fish assemblages at 86 pool sites in tropical streams in Trinidad provided cases where the widely distributed killifish *Rivulus hartii* occurred alone, as well as in various combinations with other species (Gilliam et al. 1993). Its distribution was largely complementary to the piscivorous fish *Hoplias malabaricus*, and its abundance at sites with other species was only about one third of that predicted from expectations based on *Rivulus*-only pools. Similar efforts to document negative statistical associations of invertebrate populations with natural variation in predation have met with varying success. The sampling of three streams of differing acidity in southern England demonstrated an inverse correlation between fish and predaceous invertebrates (Hildrew et al. 1984). Reice and Edwards (1986) found no differences in invertebrate abundances in stream sections below waterfalls, where trout were present, and above waterfalls, where trout were absent. In a comparison of 18 trout streams and six troutless streams in central Finland, *Baetis* densities were fivefold higher in troutless streams, midge larvae showed a nonsignificant trend toward greater abundance in trout streams, and cased caddis larvae did not differ (Meissner and Muotka 2006).

Several studies comparing total prey consumption by trout to prey biomass and production have concluded that predators consumed essentially all of the available prey production (Allan 1983, Huryn 1996, Section 8.4). Although the demonstration that all of the energy produced at one trophic level is consumed by the trophic level above is not definitive evidence of either bottom-up or top-down control, it certainly indicates that consumption by predators is the principal fate of the trophic level in question. Estimated prey consumption by stoneflies, the most abundant invertebrate predators present at several sites in a Rocky Mountain stream, was roughly half that attributed to trout, suggesting that the influence of invertebrate predators was markedly less than that of fish (Allan 1981, 1983). On the other hand, when fish are absent it seems plausible that invertebrate predators consume all secondary production at lower trophic levels. Indeed, predaceous invertebrates consumed nearly all detritivore production in a coastal stream (Smith and Smock 1992), and consumption by invertebrate predators was also high in small, fishless streams in the southeastern United States (Hall et al. 2000).

Manipulations of fish abundance using small cages and by fencing off and removing fishes from large stream reaches have demonstrated effects on invertebrate abundance in some studies, and no change in others. Placing small wire baskets filled with substrate with or without tops to prevent or allow entry of fish in streams in North Carolina, Reice (1983) reported little or no change in benthic macroinvertebrate populations. Using a field enclosure design, Flecker (1984) documented a reduction in numbers of some benthic invertebrates in response to a guild of invertivores, primarily sculpins (*Cottus*) and dace (*Rhinichthys*). Baskets of substrate were placed in enclosures containing 0, 3, 6, or 12 sculpins, while open cages were used as an additional treatment permitting free access by fish and therefore natural levels of predation. Chironomidae and the stonefly *Leuctra* showed a significant reduction in abundance with increasing intensity of fish predation, while other insect taxa were unaffected. Enclosure of small creek chub *Semotilus atromaculatus* within $0.5\,m^2$ areas of a warm-water, soft-sediment stream reduced total invertebrate abundance (Gilliam et al. 1989). Oligochaetes and isopods were strongly affected while midge larvae and clams showed no response. When trout were reduced to about 10% of their initial abundance in a 1 km reach of a Rocky Mountain trout stream, no change in macroinvertebrate populations was detected, possibly because of high replenishment of prey by drift into the experimental reach (Allan 1982b). In addition, trout often feed selectively on infalling terrestrial invertebrates, and when these are sufficiently abundant the predation pressure on benthic invertebrates may be lessened (Nakano et al. 1999). Exclusion of trout from 100 m reaches of a small stream in Finland resulted in significant benefits to large prey, particularly predaceous invertebrates and cased caddis, but *Baetis* mayflies and chironomid larvae were unaffected (Meissner and Muotka 2006).

9.2.3.1 Nonconsumptive effects of predation

Predator avoidance adaptations typically result in lost foraging opportunity, reduced growth rate, adult body size, and fecundity, and thus an overall reduction in fitness. When *Baetis* was reared in laboratory microcosms containing predaceous stoneflies with glued mouthparts, nonlethal contact resulted in reduced gut fullness and smaller size at maturity relative to microcosms without stoneflies (Peckarsky et al. 1993). In the study by Cooper (1984) described earlier, female gerrids from trout pools weighed less than those from pools without trout, suggesting that lost feeding opportunity translated into reduced growth. Juvenile coho salmon *Oncorhynchus kisutch* feed on stream drift by making short excursions from a holding position. Using houseflies as prey and a model of a rainbow trout as threat, Dill and Fraser (1984) asked whether risk reduced foraging and whether the reduction was proportional to risk. Exposure to the model trout reduced reaction and attack distances and shortened attack time compared to young salmon foraging in the absence of threat. When the investigators varied the frequency with which they presented the model before the salmon, thereby varying the level of risk, attack distance varied proportionally (Figure 9.9). Moreover, the responsiveness of young coho to the model was reduced by higher hunger levels and the presence of a competitor. Such behavioral flexibility evidently allows juvenile salmon to make complex adjustments in their foraging.

Baetis also shows evidence of an inducible life history shift in the presence of trout, resulting in faster maturation to escape the stream environment but causing it to mature at smaller body size, which translates into reduced fecundity. Mayflies reared in laboratory microcosms with trout odor matured at smaller size relative to individuals reared without exposure to trout odor (Peckarsky and McIntosh 1998). This effect was supported by comparisons of streams that contained or lacked brook trout, and induced when water from containers with brook trout was added into previously fishless streams (Peckarsky et al. 2002).

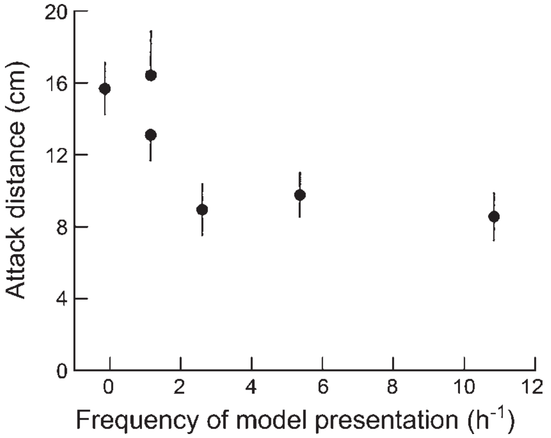

FIGURE 9.9 Attack distance of Coho salmon responding to medium-sized flies, as a function of frequency of presentation of a model rainbow trout. Values are means ±1 standard error. (Reproduced from Dill and Fraser 1984.)

Many aquatic invertebrates use the current as a means of dispersal, and the number of individuals in the water column can be surprisingly large. The strong nocturnal periodicity of drift fascinated and perplexed early workers, who documented that numbers captured in suspended nets during the day were very low, but increased by one to several orders of magnitude at nightfall and remained high but variable until dawn (Müller 1963, Brittain and Eikeland 1988). The finding that nocturnal periodicity varied among size classes and taxa in accordance with predation risk, so that less vulnerable taxa were nearly aperiodic and more vulnerable taxa were strongly nocturnal, made it apparent that nocturnal drift was an adaptation to reduce predation (Allan 1978). In rivers of the Venezuelan Andes, the night to day drift ratio for a number of mayfly taxa increased dramatically along a gradient of increasing predation intensity, providing further support for the view that predation risk governs drift periodicity (Figure 9.10).

Whether benthic invertebrates enter the drift actively, in search of food-rich locations and perhaps to escape predators, or are passively swept from the substrate, is not fully resolved. Because high food levels reduced drift in laboratory studies, and the absence of food resulted in at least modest levels of day drift, Kohler (1985) concluded that the relationship between food availability and food demands influenced drift entry, subject to constraints mainly due to predation risk.

In streams where fish are predictably present, nocturnal periodicity may be a fixed response,

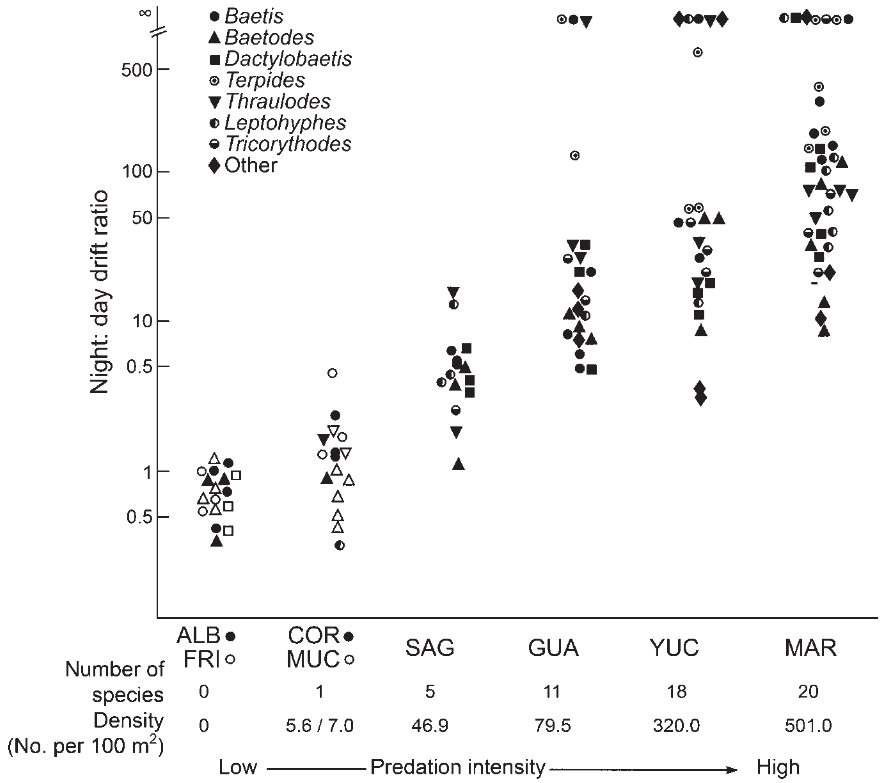

FIGURE 9.10 Night to day drift ratio of mayfly drift densities from a series of streams in the Venezuelan Andes representing a gradient from low to high predation. Note that drift is greater by day in high elevation streams lacking drift-feeding fish (Río Albarregas [ALB] and Quebrada La Fria [FRI]) compared to nearby streams containing introduced trout (Quebrada Coromoto [COR] and Mucunutan [MUC]). Other rivers are Río Saguas (SAG), Río Guache (GUA), Río la Yuca (YUC) and Río las Marías. (Reproduced from Flecker 1992b.)

which is consistent with laboratory studies that usually find an innate nocturnal pattern to drift. However, in headwater streams and other circumstances where fish presence or absence is less predictable, an induced response to chemical cues signaling fish presence would be adaptive. This is supported by a study of Rocky Mountain streams where rapid, size-specific changes in drift periodicity occurred in response to the addition of water that contained brook trout in a region where drift was aperiodic in fishless streams but nocturnal in streams containing brook trout (McIntosh et al. 2002). Addition of predator odor to stream-side channels (McIntosh et al. 1999) and to a reach of a fishless stream (McIntosh and Peckarsky 2004) caused mayflies to become nocturnal.

9.2.3.2 Experimental scale

The degree to which prey appear to be influenced by predators, and whether the effect is due to direct consumption or behavioral avoidance, can be influenced by the spatial scale and other details of the experiment (Cooper et al. 1990, Englund 1997). Because many stream invertebrates are highly mobile, experiments at the patch scale may provide only a partial image of predator effects. Enclosures and exclosures that allow free movement of most individuals (typically just the predator density is manipulated) and do not seriously restrict the flow of water are desirable because they are more natural. Cages tend to be small, on the order of 0.1 to perhaps hundreds of square meters, although some ambitious efforts have manipulated fish densities at larger scales. When prey are free to depart, patch-scale studies often detect behavioral responses rather than predator consumption, whereas closed systems may allow the predator excessive opportunity to deplete prey. Because movements and behaviors decrease in their influence as spatial scale increases, the consequence of a reduced perimeter to area ratio, large-scale experiments can more accurately detect direct consumption effects on mortality rates and population processes. Using models to investigate how treatment impacts should vary with spatial scale in predation experiments, Englund (1997) concluded that the area-specific migration rate must be <1–5% per day for an enclosed population to behave in a representative fashion; for most systems that requires an area that is impractically large. Meissner and Muotka (2006) addressed the issue of scale through a study of brown trout predation using small-scale field experiments, a larger-scale survey of fish and fishless streams in northern Finland, and a meta-analysis of over 20 published studies. Salmonids had their greatest impact on larger prey and this was consistent across the three analyses, which the authors interpreted as evidence that effects were through direct consumption rather than behavioral responses.

It is difficult to perform large-scale manipulations of the density of invertebrate predators, and so all experimental studies have been small-scale enclosure or exclosure experiments. From a meta-analysis of studies of predation on stream macroinvertebrates, Wooster (1994) concluded that the impact of invertebrate predators was greater than vertebrate predators. However, fish enclosures were larger and used larger mesh than did invertebrate enclosures, and there was a significant inverse relationship between effect size and enclosure size. Thus one cannot rule out the possibility that the experimental scale of invertebrate predation studies contributes to the finding of relatively strong effects on prey abundance. Indeed, because total prey consumption generally is greater for fish than for invertebrate predators, it seems more plausible that the latter have a smaller effect on prey abundances, and results obtained using small cages are best suited to identifying mechanisms of preference and avoidance rather than population effects.

9.2.3 Trophic cascades

When a predator at or near the top of the trophic web has a pronounced effect on the abundance or distribution of its prey, the potential exists for the influence of that predator to extend beyond its immediate prey and ramify throughout the food web. In systems where algal-grazing fish are abundant, the amount and distribution of algae can be determined by the activities of piscivorous birds (Power 1984b) or fish (Power and Matthews 1983). In small, Midwestern US streams during low flow, pools separated by shallow riffles typically exhibit a striking complementarity between an algivorous minnow (*Campostoma anomalum*) and piscivorous bass (*Micropterus*). In addition, algal abundance varies inversely with the number of minnows. When a bass-free pool was divided longitudinally and *Campostoma* added to one side, algal standing crop was markedly lower on the side containing minnows. Addition of bass to *Campostoma* pools immediately resulted in these minnows restricting their grazing to shallower regions, and so algae were heavily grazed along pool margins but abundant in deeper waters (Power et al. 1985).

A number of variables, including the identity of species in the assemblage and environmental factors, can determine whether top-down predation has strong effects on the entire assemblage.

The presence of steelhead trout induced a trophic cascade among the biota associated with boulder–bedrock substrates in pools of a northern California river during summer base flow (Power 1990, 1992b). By suppressing densities of damselfly nymphs and other small predators, fish released algivorous chironomids from predation (Figure 9.11). In the presence of fish, chironomid grazing reduced filamentous green algae to low, prostrate webs, whereas an upright algal turf developed when fish were excluded. These effects were documented during the summer low-flow period when large pools become nearly lentic; during winter, scouring flows are an alternative mechanism that reduces algal densities.

Strong top-down effects on the benthic food web are unlikely to occur whenever the top predator exerts modest predation pressure on intermediate trophic levels. This appears to be true for trout when the infall of terrestrial invertebrates provides an abundant alternative prey. In a forested stream in Japan, Nakano et al. (1999) used a combination of greenhouse-type covers to manipulate terrestrial insect infall and instream cages to manipulate fish distributions to show that rainbow trout induced a trophic cascade when terrestrial inputs were low, whereas high invertebrate infall suppressed the cascade. Despite strong effects of trout predation on some invertebrates, Meissner and Muotka (2006) did not observe any response of periphyton, possibly because the food web was largely detritus-based, and perhaps because trout had no effect on grazing *Baetis* and may have benefited midge larvae.

There is some evidence that the strength of a trophic cascade depends on which species of predator is present. A more pronounced reduction in benthic invertebrates within fish enclosures occurred in the presence of the bullhead sculpin *Cottus gobio* than with brown trout (Dahl 1998). These sculpins were benthic feeders that reduced the abundance of a variety of macroinvertebrates, whereas trout fed mainly on drift and had only a moderate impact on a baetid mayfly. Because 80% of trout diet consisted of terrestrial invertebrates, the different effect of the two fishes may reflect differences in their ability to utilize terrestrial inputs. Introduced trout in New Zealand streams have brought about a fascinatingly complex series of changes in stream food webs. Although clearly an unnatural event, studies of the impacts of invasive trout provide convincing evidence of its complex, system-wide influence (Huryn 1996, Townsend 2003). The native fishes, vaguely trout-like members of the family Galaxiidae, are competitively displaced by brown trout, invertebrate abundances are reduced, and, in a trophic cascade, algal blooms result from reduced grazing pressure. Trout have a marked influence at the ecosystem level, as streams with trout have substantially greater primary production, invertebrate secondary production, and fish production, and they export surplus algal production. Native galaxiids occupy the same trophic role as trout, but have at best weak effects, causing a "trophic trickle" rather than a cascade.

In summary, predation in stream ecosystems unquestionably exerts a direct influence upon prey populations. Predator foraging mode and prey vulnerability result in differential predation rates that constitute a strong force driving adaptations to minimize predation risk. In some circumstances predators clearly are able to exclude prey species from certain habitats or markedly reduce their abundance. The immediate effects are lost foraging opportunity and reduced growth rates, or direct mortality, which affects some size classes and species more than others. Because the prey themselves are consumers of other animal or plant resources, the potential exists for predation to create top-down trophic cascades and indirectly affect other species in the food web. In fact, some of the most dramatic effects of predation in lotic ecosystems are revealed in far-reaching cascades, offering convincing evidence that predation is a strong force shaping biological communities.

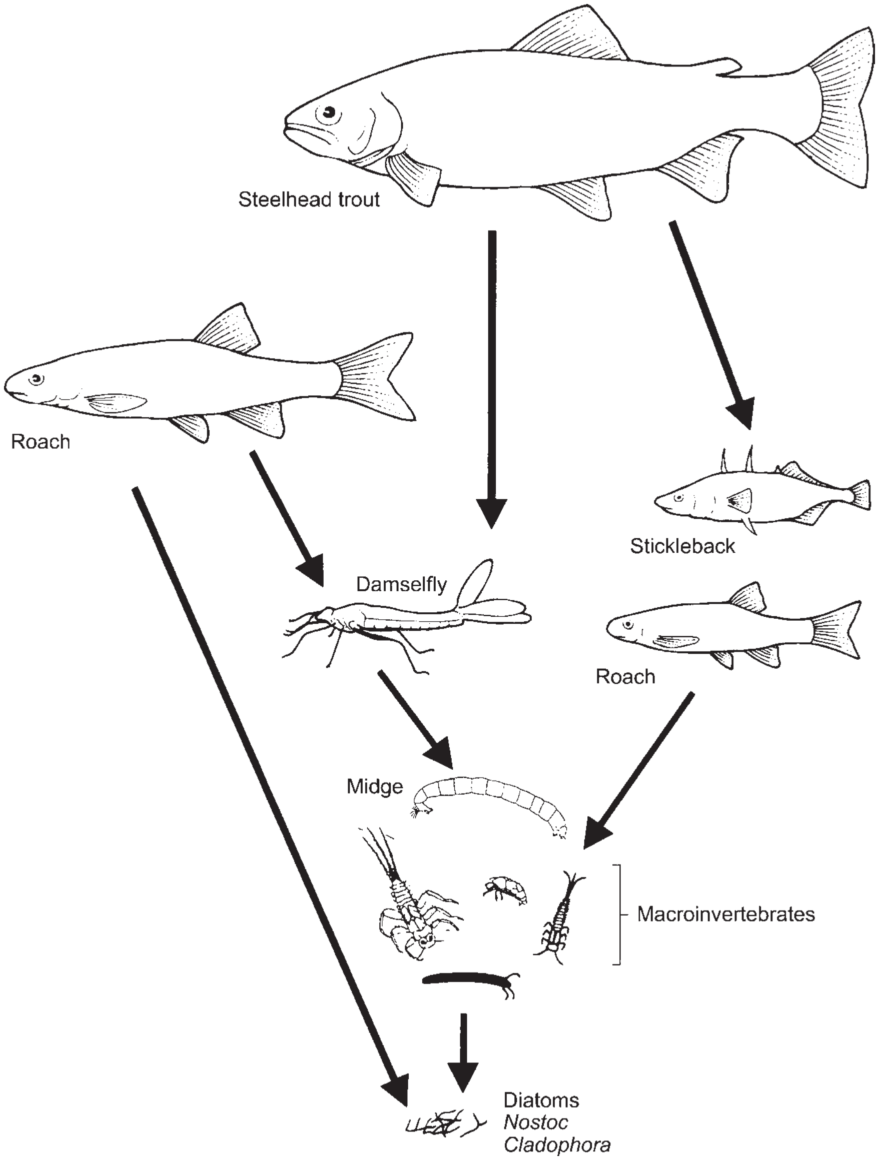

FIGURE 9.11 Trophic relations of dominant biota in and around algal turfs on boulder–bedrock substrates in pools of a California river during the summer low-flow period. Fishes include steelhead trout (*Oncorhynchus mykiss*), two size classes of the roach (*Hesperoleucas symmetricus*), and the stickleback (*Gasterosteus aculeatus*). Lestid damselflies fed on midge larvae and a number of other aquatic insects. In turn, these insects grazed a periphyton turf consisting of filamentous green algae (*Cladophora*), diatoms, and the cyanobacterium *Nostoc*. (Based on Power 1990.)

9.3 Competition

Competition occurs when members of the same or different species utilize shared resources that are in limited supply, thereby reducing one another's individual fitness and population abundance through the depletion of those resources. This definition encompasses two mechanisms of competitive interaction. Exploitation competition involves the depletion of resources such that another individual is disadvantaged. Interference competition is a direct interaction, usually of an aggressive nature, for instance when one individual excludes another from a preferred habitat. Competition has long been viewed as a challenge to species coexistence, requiring sufficient differences between species to prevent competitive exclusion. Thus niche specialization becomes a key consideration in community assembly, a topic we return to in Chapter 10. Competition has been demonstrated in many different settings, however, and when it occurs it often is asymmetrical, with one species able to exclude a second species, which persists by occupying habitats or using resources largely unutilized by the superior species (Begon et al. 2005). Competition may be less evident a force than predation and herbivory, perhaps because it acts more gradually (Gurevich 2002). In addition, competition may often be diffuse, emanating from many species rather than just a pair-wise interaction.

A rigorous demonstration of competition generally requires evidence of an adverse effect of numbers of one population upon the abundance, growth, or survival of individuals of another population under reasonably natural conditions, and also some insight into the mechanism. However, many studies simply document some overlap in resource use, from which competition is inferred, and some differences, from which niche partitioning is inferred. Although such studies must be viewed as weak evidence, they make up a large portion of the literature on competition. Thus we shall first consider the evidence in support of resource partitioning, and then look to other lines of evidence including experimental and natural comparisons. Finally, since unrestrained competition ultimately should result in the elimination of all but the best competitors, it is necessary to ask how commonly this occurs. Physical disturbance, floods in particular, appear to be important in counteracting strong competition in a number of instances.

9.3.1 Resource partitioning

Resource overlap typically is evaluated based on similarities between individuals along three major axes: food, habitat, and time (season or time of day) when the organism is active. The evidence from many studies of resource partitioning encompassing a variety of taxa in both aquatic and terrestrial settings indicates that habitat segregation occurs more commonly than dietary segregation, which in turn is more common than temporal segregation (Schoener 1974). Schoener also reported a tendency for trophic separation to be of relatively greater importance among aquatic organisms. Evidence of food specialization usually comes from inspection of gut contents; thus it matters a great deal whether food items fall into easily distinguished categories. Not surprisingly, food partitioning is reported more commonly from studies of grazers and predators than of detritivores. Resource partitioning between two species often involves multiple axes, and so similarity in resource use along just one axis provides an incomplete picture. Fish and invertebrates both have been studied extensively from a resource partitioning perspective, but the literature for aquatic plants and benthic algae is scant.

9.3.1.1 Algae

Few studies explicitly address competition between species of algae in lotic ecosystems. It is well established that algal abundance in artificial streams changes in response to adjustments in nutrient, light, or current regime, and also undergoes succession under a particular environmental regime. Many field studies describe shifts in algal dominance associated with changing environmental conditions. The tendency for filamentous green algae to dominate under high light levels is suggestive of a competitive advantage, while their scarcity under low light regimes may be due to the reduced pigment diversity of chlorophytes relative to other common stream algae (Steinman and McIntire 1987). Such patterns might be viewed as evidence of the potential for competition, but they can be equally well explained by a model in which species with independent and nonoverlapping requirements replace one another along environmental gradients over space and time.

The longitudinal distribution of *Achnanthes deflexa* and a species of *Chlorella* in the effluent plume of a sewage outfall is indicative of a competitive interaction (Klotz et al. 1976). Together these two taxa comprised nearly 90% of the epilithic algae at all sites studied; *Chlorella* was most abundant nearest the outfall, while *A. deflexa* increased with distance. When cultured alone, *A. deflexa* grew well at high concentrations of effluent, but in mixed culture *Chlorella* dominated at higher effluent concentrations and *A. deflexa* at lower concentrations, corresponding to their field distribution. Additional studies ruled out any extracellular inhibitor, leading Klotz et al. to conclude that the competitive superiority of *Chlorella* under high nutrient conditions was due to a combination of nutrient depletion and occupation of space.

The response of different members of the periphyton to nutrient addition is also suggestive of competitive effects. In comparing the influence of nutrient availability in the water column versus nutrient diffusing substrates, Pringle (1990) observed the diatoms *Navicula* and *Nitzschia* to dominate the overstory and interfere with the establishment of understory taxa *Achnanthes* and *Cocconeis*. The development and succession of diatom assemblages on glass slides suspended in two reservoirs exhibited species replacement and overgrowth by taxa of high physical stature, an indication of competitive interactions (Hoagland et al. 1982). Considering the diversity of periphyton species and variety of growth forms (Figure 6.1), and the likely competition for substrate space and access to light, future studies of individual algal species may be expected to provide stronger evidence of the importance of competitive interactions within assemblages of benthic algae.

9.3.1.2 Invertebrates

Many studies document habitat partitioning among stream-dwelling invertebrates. Temporal separation of life cycles over seasons is frequent among the univoltine insects of temperate streams, and differences in diet are reported principally in animals that consume easily categorized food items.

The distribution and abundance of filter-feeding caddisfly larvae provide an attractive system for the study of resource partitioning, as they utilize the common resource of fine particulate organic matter (FPOM), require space to attach their nets, and have seemingly ample opportunity for resource partitioning via differences in the mesh size of capture nets and location of attachment. Indeed, differences in food particle size consumed (Wallace et al. 1977), microhabitat distribution (Hildrew and Edington 1979), longitudinal distribution (Lowe and Hauer 1999), and life cycle (Mackay 1977) have each been demonstrated. The instars of a species also differ in habitat use, and their preferred current velocity typically increases over their development (Osborne and Herricks 1987). On the other hand, it does not appear that either food or space commonly is limiting to co-occurring caddis larvae. After estimating the size fraction captured by six filter-feeding caddis larvae as well as total availability of organic particles, Georgian and Wallace (1981) found no evidence that food was limiting or that resource partitioning occurred. The size fractions captured showed very high overlap, and amounted to only about 0.1% of available FPOM.

Although it remains unclear whether competitive interactions among species of filter-feeding caddis larvae frequently limit their distribution and abundance, this guild nonetheless illustrates resource partitioning along multiple dimensions. Some species clearly differ in net dimensions, current, and other microhabitat preferences, and in temperature adaptations that determine larger-scale spatial segregation. Detailed analysis of microhabitat use by filter-feeding caddis larvae in lake outlet streams in northern Finland revealed differences among instars and species, particularly in their association with moss and Froude number (Muotka 1990). *Polycentropus falvomaculatus* was a microhabitat generalist but three species of *Hydropsyche* (*H. augustipennis*, *H. pellucidula*, and *H. saxonica*) were more specialized. It has been suggested that larger species with their larger mesh sizes are suited to higher current velocities and also to the capture of larger food items, and smaller mesh sizes might function best in slow currents (Alstad 1987), but Muotka (1990) found only partial agreement with this expectation, and in one study the species with the smallest mesh net was most abundant at the highest velocities (Wallace et al. 1977).

Although temporal segregation is apparently less common than habitat or diet partitioning across diverse taxa (Schoener 1974), numerous examples from temperate running waters illustrate a distinct seasonal succession among closely related taxa. Co-occurring species of stoneflies in the genus *Leuctra* and family Nemouridae in small streams of the English Lake District display staggered life cycles that minimize the temporal overlap in their resource demands (Elliott 1987b, 1988). The periods of maximum larval growth were sufficiently out of phase among five species of riffle-dwelling *Ephemerella* mayflies to ensure at least tenfold size differences on any given date between the most closely related species (Figure 5.14). Highly synchronized, non-overlapping life cycles among presumed competitors are not always the rule, however. Of six leptophlebeid mayflies in a New Zealand stream, only two had reasonably well-defined growth periods, and overlap of life histories was pronounced (Towns 1983). As with resource partitioning along microhabitat and food axes, temporal specialization likely is offset by the advantages of flexible habits and life cycles.

To evaluate whether temporal partitioning should be attributed to competition, Tokeshi (1986) developed a null model of expected overlap by assuming that species' life cycles were distributed independently of one another throughout the year, with the constraint that most growth should occur during favorable seasons. For nine species of chironomid larvae living epiphytically on spiked water milfoil and consuming a similar diet of diatoms, actual overlap of life cycles was greater than expected by chance alone. Since this result is the opposite of that expected in temporal partitioning, it appears that all nine species were tracking seasonal peaks in resource abundance. Competition, if it occurred, was not manifested in temporal partitioning.

9.3.1.3 Fishes

Resource partitioning within fish assemblages has received a great deal of study, and as with macroinvertebrates, extensive segregation can be documented along the axes of diet, habitat, and time. In a review of some 116 such studies conducted primarily with salmonids of cool streams or small, warm-water fishes of temperate regions, Ross (1986) found that segregation along habitat and food axes was about equally frequent while temporal separation was less important. However, even among similar faunas the importance of space, food, and time axes varied considerably. Although the resource partitioning perspective is upheld in many studies, other researchers report greater overlap and attribute co-occurrence to a combination of individual specializations and the importance of environmental variation in mitigating competitive interactions.

Studies of darters and minnows in North America provide examples of low overlap in species' distributions or in microhabitat and feeding position at a single locale. Eight species of cyprinids that co-occurred in a Mississippi stream showed considerable microhabitat segregation with respect to vertical position in the water column and association with aquatic vegetation (Baker and Ross 1981). Only two species failed to separate on these two axes, and one was the only nocturnal feeder in the assemblage. Direct observation by snorkeling in streams of West Virginia found evidence of habitat partitioning by depth, substrate size, and water velocity for 10 darter species. *Percina* typically occurred in the water column, whereas species of *Etheostoma* were benthic and segregated by occurring under, between, and on top of rocks (Welsh and Perry 1998). Moyle and Senanyake's (1984) study of an even more diverse group of fish in a small rain forest stream describes a highly structured assemblage with minimal overlap based on fish morphology, habitat use, and diet.

The extent of resource overlap versus partitioning is likely to vary with food availability owing to opportunistic feeding when certain prey are very abundant. Seasonal changes in diet overlap are well illustrated by Winemiller's (1989) study of nine species of piscivorous fish that were abundant in a lowland stream and marsh habitat in western Venezuela. Members of this guild exhibited substantial resource partitioning in food type, food size, and habitat. Of the possible 72 species combinations among the nine piscivores, only one pair of fin-nipping piranhas exhibited substantial overlap on all three niche dimensions. For the most part, diet overlap of pairs of piscivore species within their feeding guild was low (Figure 9.12). Highest overlap occurred during the wet season when prey were abundant and lowest overlap occurred during the transition season when prey were least available. Thus, despite the opportunities for competition in this species-rich tropical system, food resource partitioning was widespread. Winemiller (1991) concluded that the higher species diversity of tropical fish assemblages relative to temperate assemblages was paralleled by higher ecomorphological diversity, which facilitates niche partitioning and reduces competition.

Some studies of habitat partitioning among stream fishes have reported segregation between groups of species occupying distinct microhabitat guilds but considerable remaining overlap at the species level. In an observational field study of six minnows in an Ozark stream, using the habitat variables of water depth, current, substrate, vertical and lateral position of the fish, and their use of pools, riffles, and glides, Gorman (1988) found a clear separation between species occupying higher versus lower water column position but considerable overlap among species within those two categories. The fishes of Coweeta Creek, North Carolina, were separable into three microhabitat guilds: benthic, lower, and mid-water column, but differences in microhabitat use between species within these guilds were not easily distinguished (Grossman et al. 1998). This is interpreted as evidence that environmental variation is more influential than resource availability in limiting population densities of stream fishes, as several authors have argued (Baltz and Moyle 1993, Gorman 1988). In this view it is advantageous that fishes exhibit flexibility and overlap in their use of resources, and assemblage structure reflects the combined influence of environmental variation, particularly in hydrology, together with differences among species in their individual ecology.

Further evidence of competitive interactions among stream fishes can be found in the many examples of novel species combinations that

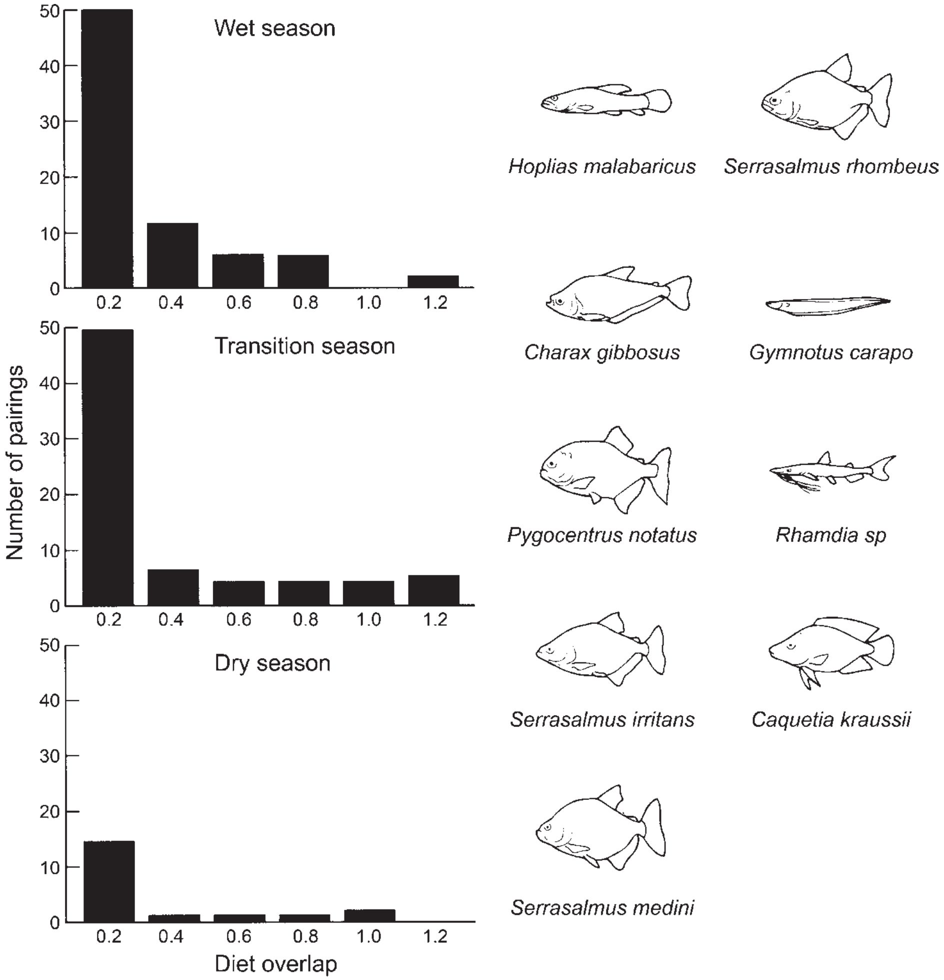

FIGURE 9.12 Frequency histograms of dietary overlap exhibited by each of nine piscivorous fish during different seasons at a lowland creek-and-marsh site in Venezuela. Wet season lasts from May to August, transition season from September to December, and dry season from January to April. Diet overlap was computed from pair-wise comparisons of ingested prey after converting prey abundance to volume as an approximation of biomass. Dry season data are less extensive because not all species were present and many had empty guts. Over half of overlap estimates were <0.10. (Reproduced from Winemiller 1989.)

result from invasions, range expansions, and intentional introductions. The distributional patterns of salmon and trout afford many opportunities for evaluating competition because fishermen and managers have thrown together ecologically similar species which, until 50 or 100 years ago, had nonoverlapping ranges. So, for example, European brown trout are replacing brook trout through much of their native range in Appalachian and Midwestern US streams, restricting the latter to headwater reaches (Fausch and White 1981). Moreover, interspecific aggression among salmonid species is well known, thus lending plausibility to the view that competition is important in species replacements. Fausch and White (1981) recorded the daytime positions of brook trout in the presence of brown trout, which is the behaviorally dominant species, and then removed brown trout from a section of a Michigan stream. Brook trout subsequently shifted to resting positions that afforded more favorable water velocity characteristics and greater shade, and this habitat shift was greatest in the larger individuals. In laboratory streams, native brook trout consumed less food, lost weight, and contracted fungal infections in the presence of hatchery brown trout (DeWald and Wilzbach 1992).

In closing, the extensive literature on resource partitioning clearly demonstrates that species differ in their habitat use, food capture abilities, and timing of activity or growth. These are in effect descriptions of the specializations that constitute a species' niche. Such differences constitute weak evidence of competition, as they do not resolve whether species adversely affect one another, or whether these examples of niche segregation reflect ecological specializations acquired and fixed over the species' evolutionary history, referred to as the "ghost of competition past" (Connell 1980). It is for these reasons that recent work has focused on more rigorous tests, typically involving experiments under fairly natural conditions, and we now consider such studies.

9.3.2 Experimental studies of competition

Competitive interactions can be manipulated in the laboratory or in the field, conditional on the ingenuity of the investigator to construct an experiment that allows realistic interactions and reveals the mechanisms involved. Laboratory experiments usually offer the greatest experimental control and can be particularly useful in demonstrating the potential for competition and in identifying mechanisms. Field experiments at least in principle offer greater realism, although they too have artifacts and their outcomes may be influenced by the relatively small scale and short timeframe of the typical field study. Investigators often have used a combination of laboratory and field experiments, and in some cases have exploited natural comparisons or unusual environmental events to provide evidence of competitive effects at large scale and under natural conditions.

Both laboratory and field studies have shown interference competition and aggressive displacement of one species by another. Baltz et al. (1982) found riffle sculpin to be most abundant in the upper reaches of a small California stream, while speckled dace dominated riffles downstream, and the two species were inversely related over the 12.5 km section. Laboratory studies demonstrated that dace avoided areas occupied by sculpins, but also tolerated warmer temperatures, which presumably explains the downstream prevalence of dace.

Interference competition is well documented in space-limited taxa of invertebrates. Large size almost invariably conveys an advantage, and the loser may be injured or cannibalized. In the latter instance the line blurs between competition and predation. Larvae of a netwinged midge (*Blepharicera*) and black flies (Simuliidae) compete for space on stone surfaces in swift-flowing small streams, even though the former feed on attached periphyton and the latter are primarily suspension feeders. Their densities were inversely correlated in a California stream, and behavioral observations of interactions revealed that larval black flies "nipped" at *Blepharicera* within reach, disrupting their feeding (Dudley et al. 1990). *Blepharicera* spent significantly less time feeding in the presence of black fly larvae, compared to when the investigators removed all simuliids within a 5 cm radius. Aggressive competitors such as caddis larvae affect other species by multiple mechanisms including interference, predation, behavioral avoidance, and by modifying flow patterns (Hemphill 1988). Small-scale density manipulations of *Hydropsyche siltalai* illustrate the multiple pathways of its influence in a lake outlet stream in north Sweden (Englund 1993). The presence of *H. siltalai*, a net-spinning filter feeder that aggressively monopolizes space, resulted in reduced numbers of the mayfly *Ephemerella ignita* and the black fly *Simulium truncatum*, and increases in the free-living, predatory caddis *Rhyacophila nubila* and chironomid larvae. Direct mortality due to predation was the primary cause of declines, although hydropsychid nets likely also interfere with the attachment and feeding of simuiliid larvae. Increased abundances of *R. nubila* and chironomid larvae is somewhat surprising since they also are consumed by *H. siltalai*, but apparently hydropsychid nets enhanced food availability to these taxa, and so the presence of *H. siltalai* resulted in a positive facilitation.

Strong competitive interactions involving stream macroinvertebrates have been demonstrated with sessile or slow-moving grazers, due to a combination of exploitation and interference competition. Snails of the family Pleuroceridae appear to be competitive dominants in those headwater streams where they reach high abundances. Both *Juga silicula* in the northwestern United States and *Elimia clavaeformis* in the southeast have been reported to reach high densities and to make up >90% of the invertebrate biomass (Hawkins and Furnish 1987, Hill 1992). Snails can graze periphyton to very low levels, and because of their large size, individual snails also may harm other species by "bulldozing" over substrate surfaces. The interaction between *Elimia clavaeformis* and the caddis *Neophylax etnieri* in a headwater stream in Tennessee makes a strong case that the snails' influence is via exploitative competition (Hill 1992). High dietary overlap determined from gut analysis suggested that these two grazers were competing for periphyton. Both species substantially increased their growth rates and condition (ash-free dry mass per unit wet mass) when transferred from the stream to a high quality diet in the laboratory, suggesting food limitation in nature. In a natural experiment, Hill examined periphyton abundance and *Neophylax* condition in six streams lacking *Elimia*, and in six streams where the snail was abundant. Periphyton biomass was three times greater and caddis larvae at diapause roughly twice as large in the absence of snails (Figure 9.13).

The caddis larva *Glossosoma* has been shown to be an effective grazer of periphyton and competitor with other macroinvertebrates in several studies. Its slow rate of movement and efficient grazing reduce periphyton to low levels, it is able to maintain high population densities at

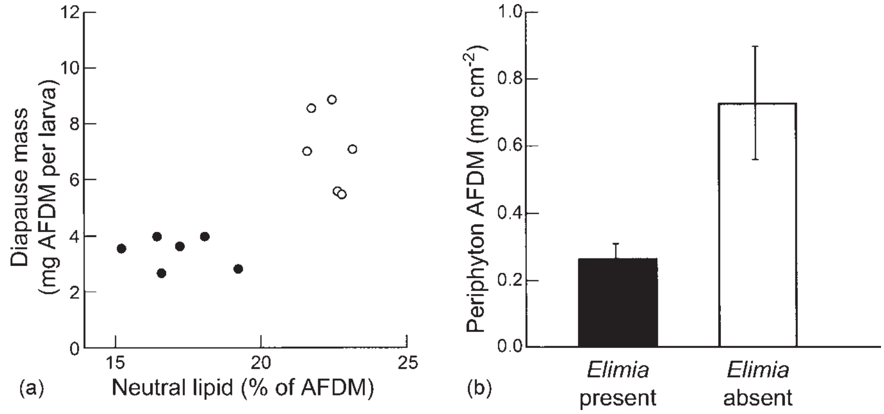

FIGURE 9.13 Comparison of six streams in the southwestern United States lacking the snail *Elimia clavaeformis* versus six streams where the snail was extremely abundant. (a) Average mass of diapausing larvae of the caddis *Neophylax* was higher in the absence of snails. (b) Periphyton mass also was higher in the absence of snails. (Reproduced from Hill 1992.)

relatively low resource levels, and its stone case deters predation. By erecting barriers of petroleum jelly in a Montana stream, McAuliffe (1984a, b) was able to achieve approximately a fivefold reduction in *Glossosoma* densities, which resulted in a twofold increase in algal cell density. Mobile grazers such as *Baetis* were significantly more abundant in areas where *Glossosoma* was excluded. At normal densities *Glossosoma* appears to be able to reduce algal densities to levels where *Baetis* experiences resource limitation, and thus exploitation rather than interference is the primary mechanism. A 10-month exclusion experiment in a Michigan springbrook of very constant flow provides additional evidence of the community-wide effects of *Glossosoma*. Periphyton biomass increased substantially, as did the densities of most grazers (Kohler 1992).

The majority of studies that document competition amongst benthic invertebrates in streams involve space-requiring filter feeders and slow, efficient grazers such as snails and *Glossosoma*. Systems dominated by highly mobile grazers of periphyton are common, and the extent to which these species compete with one another is less well known. However, laboratory studies demonstrate that depression of resource levels can limit food available to others of the same species. When *Baetis tricaudatus* and *Glossosoma nigrior* were allowed to compete for periphyton in laboratory stream channels, both strongly reduced periphyton abundances, suggesting that exploitative competition in nature was likely. *Baetis* had a greater impact on *Glossosoma* than the converse, and effects were seen mainly in terms of growth (Kohler 1992). When Hill and Knight (1987) manipulated numbers of the mayfly *Ameletus validus* in field enclosures, algal standing crop and the growth of *A. validus* both declined as its density increased.

Collectively these studies demonstrate that competitive interactions indeed take place among macroinvertebrate assemblages of streams, but the extent and magnitude of competitive effects in natural systems are not well resolved. However, observations that accompanied the collapse of *Glossosoma nigrior* populations in Michigan trout streams due to outbreaks of the microsporidian *Cougourdella* provide impressive documentation of the ecosystem-wide influence of a dominant grazer (Kohler and Wiley 1997). The pathogen-induced decline of *Glossosoma* resulted in marked increases in the biomass of periphyton (Figure 9.14) and in the abundance of most grazers and filter feeders (Figure 9.15). Remarkably, these changes dovetailed with results from Kohler's (1992) prior laboratory and field experiments in a stable, spring-fed stream where *Glossosoma* was the dominant grazer. Long-term exclusion of *Glossosoma* resulted in increases in periphyton biomass and in the abundance and growth of a number of other species of grazers including midge larvae, indicating that the caddis larva might influence other members of the assemblage through diffuse competition. Two sessile filter feeders, the black fly *Simulium* and the midge *Rheotanytarsus*, also increased in the *Glossosoma* exclusion, which may reflect interference competition from physical encounters with the more robust *Glossosoma*. Inspection of Figure 9.15 leaves little doubt that, in this system, competition from a dominant grazer has dramatic, system-wide consequences. It also is instructive that although all responses were in accord with results from previous, smaller-scale experiments, those studies underestimated the extent and magnitude of *Glossosoma*'s influence.

Finally, as with herbivory and predation, environmental factors influence the outcome of competitive interactions. Dense aggregations of hydropsychid larvae in lake outlet streams, maintained by the outflow of plankton, set the stage for strong interspecific effects. Flow disturbance can reduce the numbers of strong competitors, permitting entry by other species that disperse and colonize more rapidly. The interaction between *Glossosoma* and *Baetis* was suppressed in the presence of sculpins in a Japanese stream

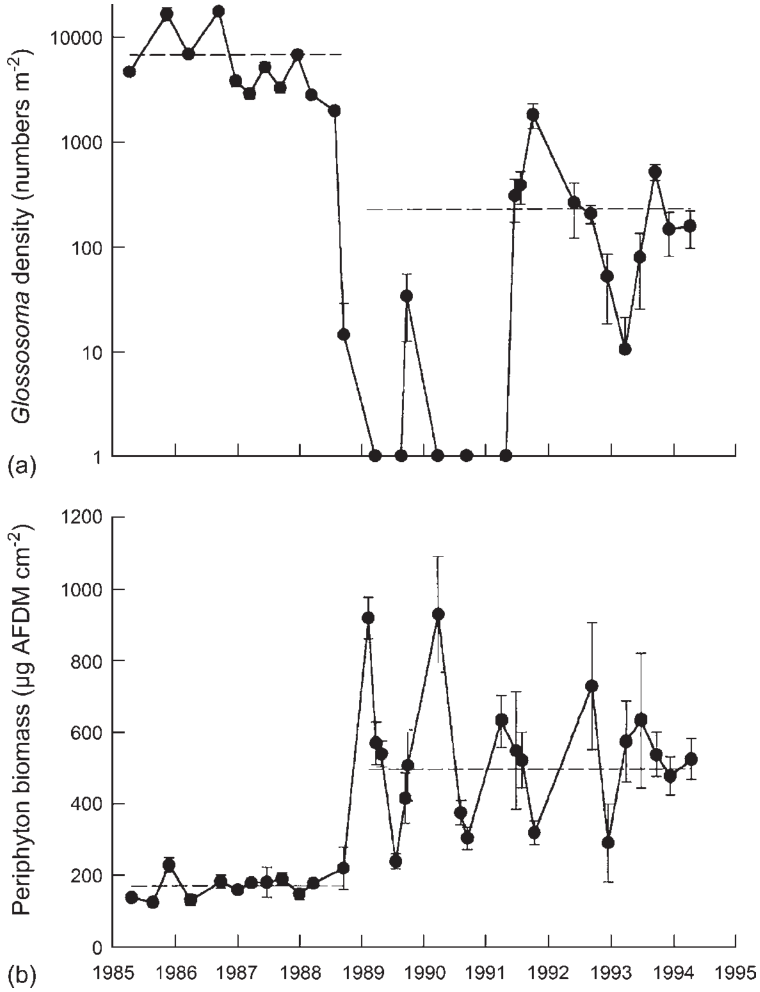

FIGURE 9.14 Density of *Glossosoma nigrior* (a) and biomass of periphyton (b) in Spring Brook, Michigan. Horizontal dashed lines are the overall mean density or biomass for the periods before and after *Glossosoma*'s collapse in 1988. Values are means + 1 SE. (Reproduced from Kohler and Wiley 1997.)

(Kuhara et al. 1999). For all of the above reasons, it is likely that the influence of competition within stream communities will vary among locations, over seasons, and between different species assemblages.

9.4 Summary

Species are interconnected through the proximate food chain linkages of herbivory, predation, and competition. The supply of resources is potentially limiting to consumers, and an abundance of consumers may in turn deplete resource levels. The importance of these bottom-up and top-down effects is seen in foraging and risk-avoidance adaptations, in the size of populations, and sometimes in trophic cascades and indirect effects on species several steps removed from the initial interaction. Consumers of the same resource are competitors whenever resource

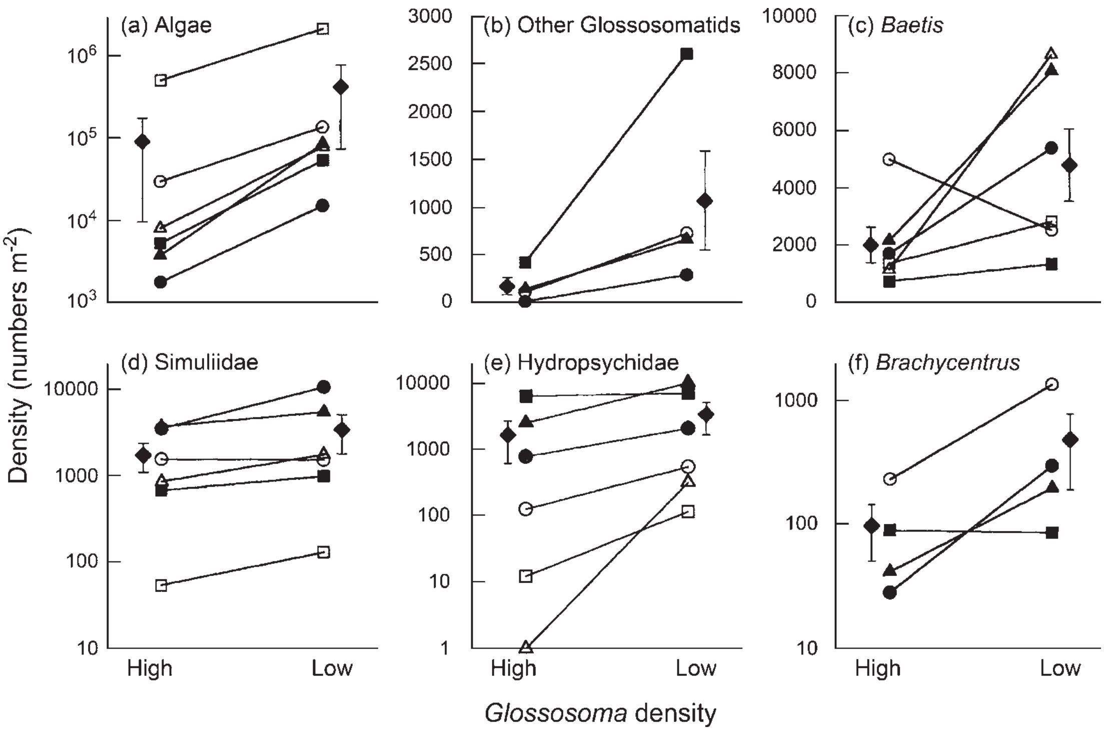

FIGURE 9.15 Mean abundances of periphyton (as algal cells cm^{-2}) (a), periphyton-grazing insects (b, c) and filter feeders (d–f) as a function of *Glossosoma* density (high, low = prior to or during recurrent pathogen outbreaks, respectively) in six streams from southwest and northern lower Michigan. Invertebrate densities are expressed as number of individuals per square meter. Symbols denote the six streams. (Reproduced from Kohler and Wiley 1997.)

sharing is mutually detrimental, but various mechanisms of resource partitioning may sufficiently reduce overlap to permit coexistence. The strength of species interactions is most evident when the abiotic environment is moderate, and may be reduced or undetected whenever environmental variation is extreme.

The study of herbivory in stream ecosystems has focused mainly on the grazing of benthic algae by invertebrates, some fishes, and a few amphibian larvae. Benthic algae vary in their distribution, growth form, and nutritional value, and grazers differ in their means of scraping and browsing this food supply. Grazers have numerous impacts on algae, reducing their abundance, altering assemblage composition, and even stimulating algal growth and overall productivity through the removal of senescent cells and the recycling of nutrients. Strong effects of herbivory in streams have been documented with a number of invertebrates, including snails and some caddisfly and mayfly larvae, and in fishes such as the stoneroller in North America and armored catfishes in the Neotropics. Under the usually moderate environments in which most grazing studies are carried out, top-down control of algae by grazing appears to be at least as strong as bottom-up control by nutrient supply. Disturbance, particularly due to extremes of flow, can alter the grazer–algal dynamic by reducing grazer abundance, and heavy grazing pressure can reduce algal biomass to a level where it is less vulnerable to scouring during high flows.

Predation affects all organisms at some stage of the life cycle, and many species encounter predation risk throughout their lives. It affects individuals and populations directly through consumption and mortality and also can result in behavioral and morphological adaptations that may entail some fitness cost to the prey. The many fascinating examples of the foraging behavior of predators and risk-avoidance tactics of prey attest to the importance of this interaction to both parties. Prey species depart from risky environments, restrict the time of day and location of foraging, and evolve morphologies that may exact a cost in growth or subsequent reproduction. Because the prey are themselves consumers of other resources, these responses help us to understand how the indirect effects of top predators can extend throughout the food web. Top predators have often but not invariably been demonstrated to limit the abundance of prey populations, to confine the prey's distribution to habitats where the predator is absent or ineffective, and in some instances to trigger an elaborate cascade of interactions with consequences for whole ecosystems. Habitat conditions, the identity of the top predator, the magnitude of external subsidies, and environmental disturbance can act as switches that turn a cascade into a trickle, or the reverse.

Competition between consumers for a shared resource either through its mutual exploitation or by aggressive interference depends on the extent of niche overlap versus niche segregation. Estimates of overlap in diet, habitat, or temporal activity of groups of species that share a common resource are often used to infer competition. Field observations such as the different mesh sizes and locations of the nets of hydropsychid caddis larvae or use of stream habitat and time of day for foraging by stream fishes suggest how interactions within groups of potentially competing species can be ameliorated through the partitioning of diet, space, or time. The large literature on resource partitioning among stream-dwelling invertebrates and fishes provides much insight into the specialization of individual species, but because the extent to which resources actually are limiting often is unknown, this is weak evidence for the importance of competition. Experimental studies with invertebrates have documented numerous cases of aggressive interference, mainly involving space limitation, and in some cases the interaction is as much predation as competition. Evidence to date may reflect challenges of experimental design and scale, as is suggested by the system-wide effects that followed the decline of an abundant grazing caddis affected by a parasite outbreak. It seems that competition can be an important interaction in stream assemblages, but the extent of its influence is not well understood.

Chapter ten

Lotic communities

The forces that shape community structure are those that determine which and how many species occur together, which species are common and which are rare, and the interactions amongst them. Thus, the topic of community structure involves a synthesis of all the environmental factors and ecological interactions influencing an assemblage of co-occurring species. For communities to exhibit predictable structure requires that their assembly is the outcome of nonrandom processes that result in repeatable patterns, rather than chance and dispersal. This leads us to expect that the same species, in roughly the same abundances, will be found in the same locale as long as environmental conditions do not change greatly, and that similar communities should occur wherever environmental circumstances are comparable.

Explanations for patterns in species diversity and community structure frequently are based on niche-based models (MacArthur 1972, Chase and Leibold 2003), in which the presence and abundance of individual species is a reflection of their fit to habitat conditions and success in interspecific interactions, the subjects of Chapters 5 and 9, respectively. In stable or moderate environments, biological interactions are considered to be particularly influential in the assembly and maintenance of communities. However, many environments experience periodic disturbances, and stream ecosystems are no exception. Environmental disturbances such as floods and droughts, when sufficiently extreme or frequent, are likely to prevent biotic interactions from acting with the strength and regularity required to result in consistent community patterns. Very harsh environments or frequent disturbances may severely restrict the number of species that can survive those conditions and thus reduce diversity, whereas a moderate level of disturbance may enhance diversity by counteracting the tendency of a few superior species to win out. As a counterpoint to niche models, neutral models (Hubbell 2001) treat species as ecologically equivalent and substitutable, to be replaced from a regional species pool whenever a chance local extinction depletes site diversity. The recolonization of a lost population requires dispersal, and so distance, life-history traits, and other factors such as terrain can determine whether dispersal limits the opportunities for a particular species to reestablish.

Studies of local assemblages often assume that communities are determined solely by environmental conditions and species interactions at the local scale, without regard for such larger scale processes as dispersal, speciation, and historical biogeography. However, regional species pools and factors that influence dispersal at large spatial scales influence local diversity and assemblage structure by determining the pool of species that are available to colonize a location (Ricklefs and Schluter 1993). Thus, regional and historical factors determine diversity at large spatial scale, which in turn has an influence upon local diversity through the action of environmental factors acting at progressively smaller scales, often visualized as a hierarchical series of filters. Consideration of regional diversity also reminds us that the long-term persistence of a species usually does not depend solely upon its survival in any one local community. Separate populations of a species may exhibit different trends in different locales, with the consequence that dispersal permits a long-term regularity on a larger scale that is not apparent by detailed investigation on a finer scale. Such a perspective lessens the need for equilibrium-enhancing interactions, because regional processes of immigration and emigration may contribute some of the buffering against extinction that otherwise must be attributed to biotic factors.

Food webs depict the network of vertical and horizontal linkages extending from basal resources to top consumers in a single, integrated visualization of a biological community. Although the number of connecting links can be very large, a modest number of species often contributes the majority of the biomass and are responsible for most energy flow. Some species have complementary or overlapping roles, but at least in some cases certain species appear to be functionally irreplaceable. Thus, the potential loss of a species from intact, functioning communities due to overharvest, habitat degradation or other human actions raises the specter that simplified biological communities will be less efficient or productive than is observed in their unaltered state.

10.1 Regional Patterns in Species Diversity

Local biological diversity is the outcome of regional species richness interacting with the local environmental conditions and ecological processes that govern the subset of species at a location. Later in this chapter we will explore in depth several hypotheses that attempt to explain local diversity, but we begin with patterns in regional diversity and the factors that operate at the largest spatial scales, because these determine the species pool from which local communities are assembled. As an example of the relevance of this perspective, variation in regional diversity was the single most consistent predictor of local fish diversity across some 320 sites from 61 streams distributed throughout the State of Virginia (Angermeier and Winston 1998). Variation in regional species richness itself is difficult to fully explain, but speciation, differences in the ability of individual species to disperse, and historical dispersal opportunities clearly influence the regional species pool, and these in turn are influenced by overall productivity, habitat diversity, and biological interactions (Rosenzweig 1995). Here, we review patterns in large-scale species richness that are likely to influence the regional species pool and thus indirectly affect local assemblages.

10.1.1 Species–area relationships

The number of species generally increases with the area sampled, as has been well documented using collections from such discrete units as islands (MacArthur and Wilson 1967) and lakes (Barbour and Brown 1974). The relationship typically is log-linear, according to the equation:

$$S = cA^{z} \tag{10.1}$$

where S is the species richness, A is the area of habitat, and c and z are parameters determined from the data. The slope parameter z quantifies the rate of increase in number of species with area surveyed, and frequently falls between 0.2 and 0.4. Several studies document that Equation 10.1 applies to rivers, although estimates of z vary widely. Freshwater mussels fall well within the expected range, with $z = 0.32$ (Figure 10.1).

The principal mechanism underlying the species–area relationship probably is that larger rivers harbor greater habitat diversity due to their

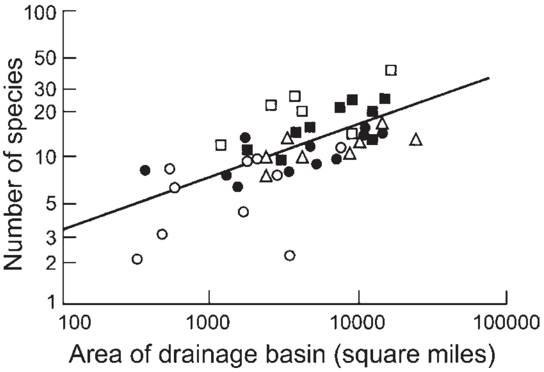

FIGURE 10.1 Species–area relationship for freshwater mussels (Unionidae) from 49 rivers draining the North American Atlantic coast between southern Canada and the eastern Gulf of Mexico. (Reproduced from Sepkoski and Rex 1974.)

more extensive habitat area. In addition, a larger habitat volume will contain more individuals, which is likely to result in the inclusion of more species. Finally, many species that occur in larger rivers appear unable to live in small streams. This is indicated by studies of species distributions, which typically show more addition than replacement as one proceeds downstream along a river's length (Illies and Botosaneanu 1963, Horwitz 1978), and by a positive relationship between fish size and river size (Hynes 1970).

10.1.2 Latitudinal gradients

An increase in numbers of species as one proceeds from high latitudes toward the tropics is one of the most general of geographic patterns of species richness, and it unquestionably is true for the fishes of running waters. Despite the inadequate state of taxonomic knowledge, well over 3,000 species of freshwater fish are estimated to occur in tropical South America, primarily in riverine habitats (Moyle and Cech 2006). This greatly exceeds the roughly 700 species found in the lakes and rivers of temperate North America and 250 species of Europe. Species richness is highly correlated with basin area for rivers worldwide, and stronger statistical relationships are observed when analyzed separately by continent (Amarasinghe and Welcomme 2002). The exponent of the species–area relationship always is greater in tropical than temperate regions (0.25 for Europe, 0.26 for Asia, 0.49 for Africa, and 0.51 for South America), demonstrating a trend toward a more rapid increase in species richness with increasing river size at low latitudes.

Surprisingly, no one has yet established convincingly that a similar latitudinal trend exists in numbers of invertebrate species, and it has been suggested that the biota of streams might be an exception to the general trend toward more species in the tropics (Patrick 1966). Whether stream insects contradict (Flowers 1991) or support (Stout and Vandermeer 1975, Jacobson et al. 1997) this pattern remains controversial. For a very large data set of mayflies, stoneflies, and caddisflies, Vinson and Hawkins (2003) found no simple latitudinal gradient other than a decline in diversity at very high latitudes, and instead noted taxon-specific peaks and troughs at particular latitudes. Some of this variation likely is due to incomplete sampling, and some to areas of radiation and spread. Because tropical studies are few and taxonomic knowledge is limited, the absence of a latitudinal trend in the invertebrate diversity of streams is far from established. It is interesting to speculate that the spectacular diversity of tropical fishes, many of which are insectivores, could represent a constraint on insect diversity in tropical streams.

10.1.3 History

Geographically distant regions typically have their own distinctive flora and fauna, attesting to chance differences in the establishment and diversification of particular taxa and the local interplay of environmental and biological forces that direct evolutionary change. As a consequence, when comparing ecological communities from different regions one cannot know in advance whether species from different taxonomic groups will display sufficient ecological similarity that assemblage structure will converge, or whether peculiarities of evolutionary history will result in differences. For example, our ability to appreciate the rich literature on the ecology of New Zealand streams is enhanced by the knowledge that many of its taxa are endemic, the mayfly *Deleatidium* is ubiquitous but *Baetis* is absent, shredders are rare, and one important group of shredders, caddisflies in the family Limnephilidae, also is absent (Winterbourn 1995).

Because ichthyologists have been collecting and describing the fishes of North America and Europe for several hundred years, the fish species and their distribution are well known (Hocutt and Wiley 1986). The European fish fauna is less diverse than North America, and regions within North America differ greatly. All of Canada and Alaska contain some 180 species of fish, considerably fewer than the rich Mississippi basin where most of the major adaptive radiations in North America have occurred. The Tennessee and Cumberland Rivers drainage realm alone includes some 250 species of fishes (Starnes and Etnier 1986). Species richness declines from east to west across the United States (Moyle and Cech 2006), due in part to major differences in extinction rates during the Pleistocene. As a consequence, the western United States contains only about one fourth as many fish species as does the east.

Comparison of species–area relationships for the fish faunas of Europe and North America provides further evidence that evolutionary and biogeographic history can have a profound influence on regional diversity (Figure 10.2). Postglacial recolonization was more restricted in Europe relative to North America because drainage divides in Europe tend to run from east to west and reestablishment from Iberia and the Adriatic was restricted by mountain ranges, therefore glaciated areas were recolonized largely from the Danube Basin. This likely limited both southward retreat and subsequent northward recolonization for the European fauna, whereas the North American fauna had a much larger area free from glaciation and easier routes for recolonization (Mahon 1984, Oberdorff et al. 1997). In both Europe and North America, the fish faunas of glaciated regions are species-poor in comparison with unglaciated regions, and contain species that are larger, more migratory, and give less parental care compared with the unglaciated regions of the Mississippi and Missouri basins (Moyle and Herbold 1987, Griffiths 2006).

Comparative studies of taxonomically related fish groups clearly show that history and biogeography can influence the taxonomic and ecological diversity of a region. The Nida River in south-central Poland and the Grand River in Ontario, Canada, are two river systems that exhibit similar gradients from the headwaters downstream and occupy similar climates. Thus, they might be expected to support about the same number of species, filling roughly similar ecological roles. There are in fact many

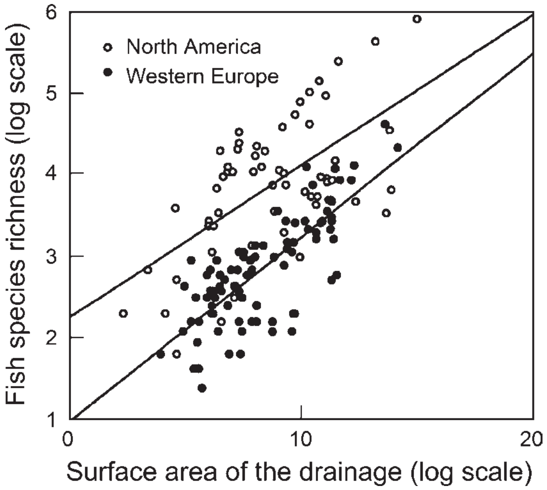

FIGURE 10.2 Fish species richness as a function of drainage basin area for West European and North American rivers. Lines represent best fit using a power function. (Reproduced from Oberdorff et al. 1997.)

similarities (Figure 10.3), due largely to the abundance of cyprinids in both, and comparable species in the Esocidae, Cottidae, and Gasterosteidae (Mahon 1984). There also are prominent differences, including the diversity in North America of Centrarchidae and Ictaluridae, and radiation within the genera *Notropis* and *Etheostoma*. The Grand River drainage contains more species overall, especially in smaller streams. In addition, more species in the Grand River are specialized stream dwellers, whereas the Nida includes a greater proportion of large species that are only occasional stream dwellers. Explanations for such differences always are speculative. Mahon (1984) suggests that the success of the lentic specialists (Centrarchidae and possibly Ictaluridae) in North America closed out the migratory option typical of the larger cyprinids of Europe, and favored species that formed resident populations in small streams. This may help to explain the greater North American diversity of smaller species.

Geographic diversity patterns in the Ephemeroptera, Plecoptera, and Trichoptera, the best studied of the macroinvertebrates found in streams, differ among biogeographic realms based on an analysis of genus-level local diversity from 495 locales around the world (Vinson and Hawkins 2003). Ephemeroptera richness was highest in the Africotropical realm and lowest in the Antarctic (New Zealand) realm, Plecoptera richness was highest in the Nearctic realm, and Trichoptera richness was highest in the Australian realm and lowest in the Africotropical realm. Given that the initial evolution of these taxa occurred prior to the splitting of the Pangean supercontinent, such disparate patterns among aquatic insects suggest either different centers of radiation or differential success in surviving subsequent environmental changes. In any case, these patterns provide important context when comparing studies of stream assemblages carried out in different biogeographic realms with potentially very different regional species pools.

10.2 Local Diversity

The number of species found at a site varies with the diversity of the regional species pool and with local conditions. In general, we expect to find a larger number of co-occurring species wherever habitat heterogeneity is greater, and this is supported by the many studies that demonstrate a positive correlation between measures of habitat complexity and numbers of species at a site (Section 5.2.3). A complete survey of all the species within a local assemblage is an extremely challenging task. Such studies are unusual partly because the taxonomic knowledge of many groups is inadequate, and partly because the exhaustive compilation of a species list is rarely a priority. It is more usual to find either a detailed study of a single taxon, or an ecological investigation where the focus is on the more common species, while taxa that are difficult to identify are lumped, often at the family or genus levels. Nonetheless, it is apparent that species richness is affected by a number of variables. The estimated number of species always depends upon the size of the sample collected: the more individuals examined, the more species one is likely to find, invariably through the addition of rare or occasional species. More species are found in large rivers than small streams, apparently because the spatial area and habitat diversity are greater in larger systems, as discussed above. Historical differences between regions in rates of speciation and rates of extinction will influence the size of the species pool, and hence have an impact on local diversity.

The importance of sample size is nicely illustrated by a study of macroinvertebrates collected from individual stones in a large reach of rapids (20–40 m wide, ~1 km in length) of the river Lestijoki, Finland (Kuusela 1979). The number of individuals per stone was positively correlated with the number of species per stone (Figure 10.4a). In addition, the cumulative number of species increased with the logarithm of the cumulative number of stones sampled, i.e.,

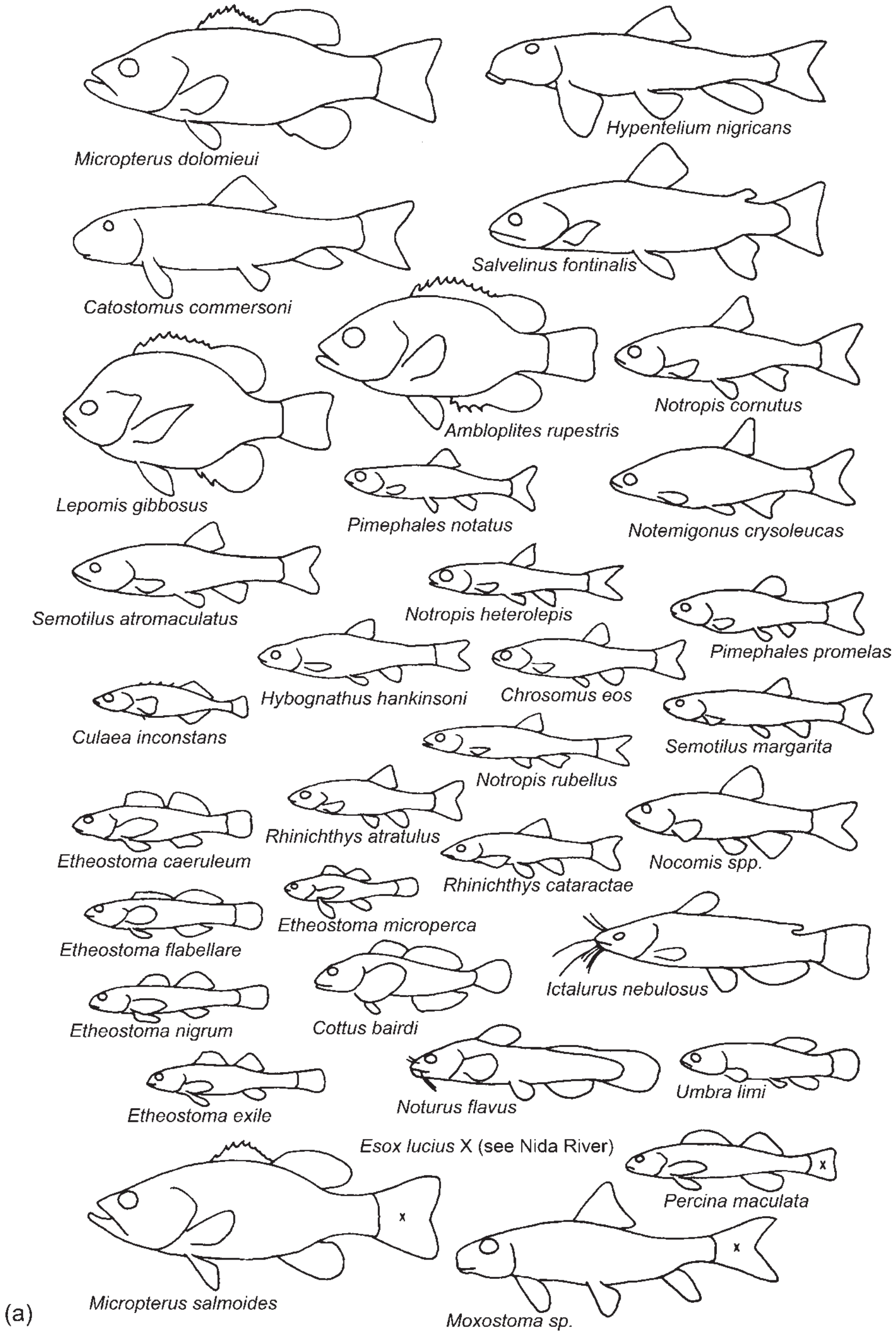

FIGURE 10.3 Some of the fish species occupying small drainage basins (300 km^2 or less) in (a) the Grand River system, southern Ontario, and (b) in the Nida River system, south-central Poland. (Reproduced from Mahon 1984.)

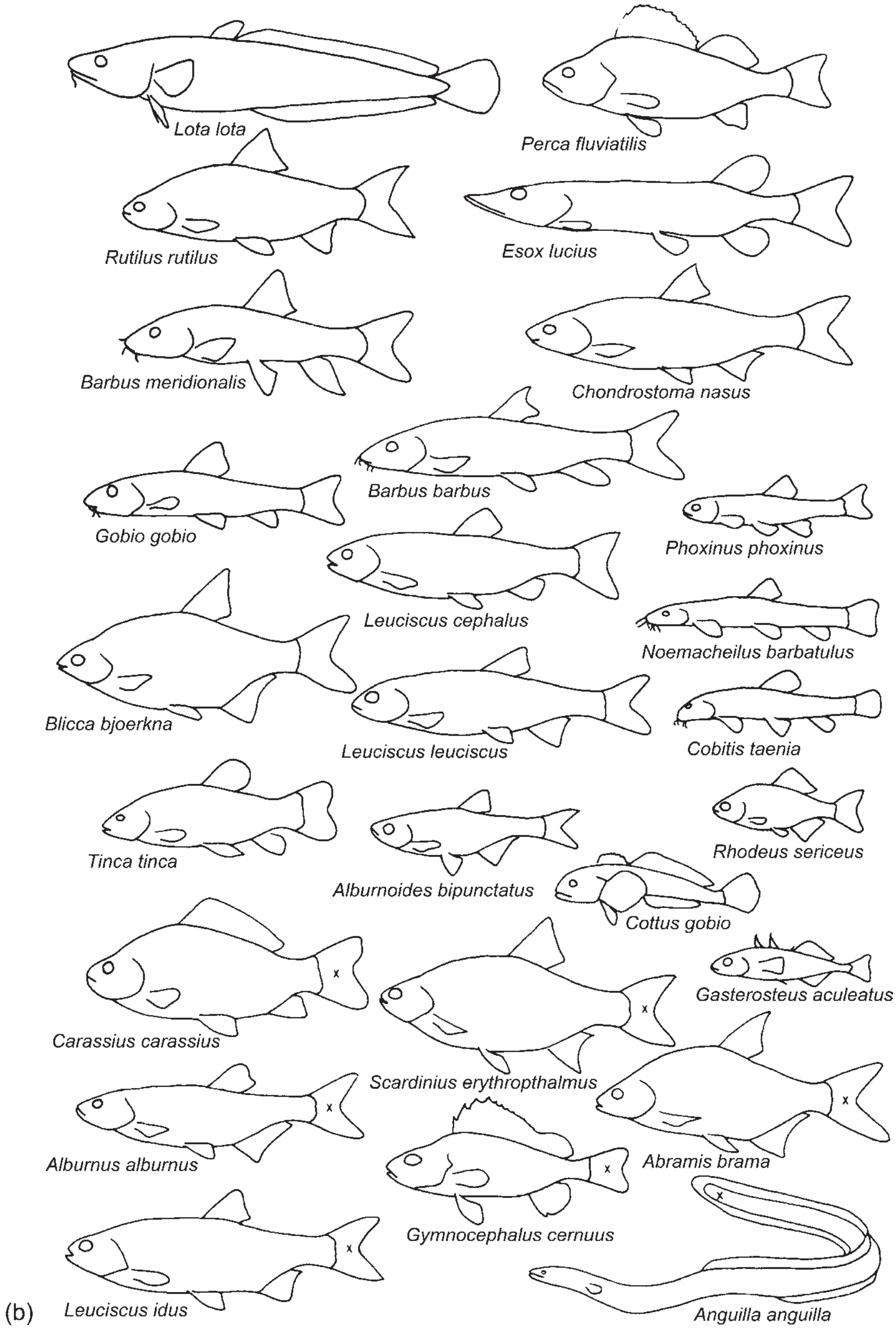

FIGURE 10.3 (*cont.*)

at a decelerating rate. The latter relationship has been reported from streams of widely different regions (Figure 10.4b), and clearly illustrates the dependence of local species richness on sampling effort. Statistical methods can be used to extrapolate the relationship between number of species and sample size to estimate the true number of taxa in the assemblage (Colwell and Coddington 1994). Using 25 individual stones as the sampling unit, Melo and Froehlich (2000) were able to characterize invertebrate richness for a series of streams in Brazil, and compare sites and seasonal patterns. However, new taxa accumulated even when as many as 150 individual stones were sampled locally at a site (Melo and Froehlich 2001).

Another very general finding from species collections is that a few species are common and most are quite rare. A collection of 52,000 insect specimens that emerged as adults from a stream flowing underneath an 11 m^2 greenhouse near Schlitz, Germany, yielded a total of 148 species, but the 15 most abundant species contributed 80% of the total number of individuals (Illies 1971). Woodward et al. (2002) report a similar finding for the Broadstone Stream, United Kingdom, which is relatively species-poor due to the stream's natural acidity. Demonstrating remarkable consistency over 24 years of study, a core community of eight taxa always was present and contributed 75% or more of total individuals (Figure 10.5). A practical consequence of the tendency for a few species to dominate an assemblage is that collection of a small number of samples will include most of the common species, whereas further sampling effort will continue to produce additional species almost (but not quite) indefinitely. This underlies the relationship between sample size and local species richness (Figure 10.4), which in turn influences the amount of sampling effort necessary to characterize a system.

Why a few species should be more abundant, widespread, and successful and many species quite rare remains one of the great enigmas of ecology. Species that have wide regional

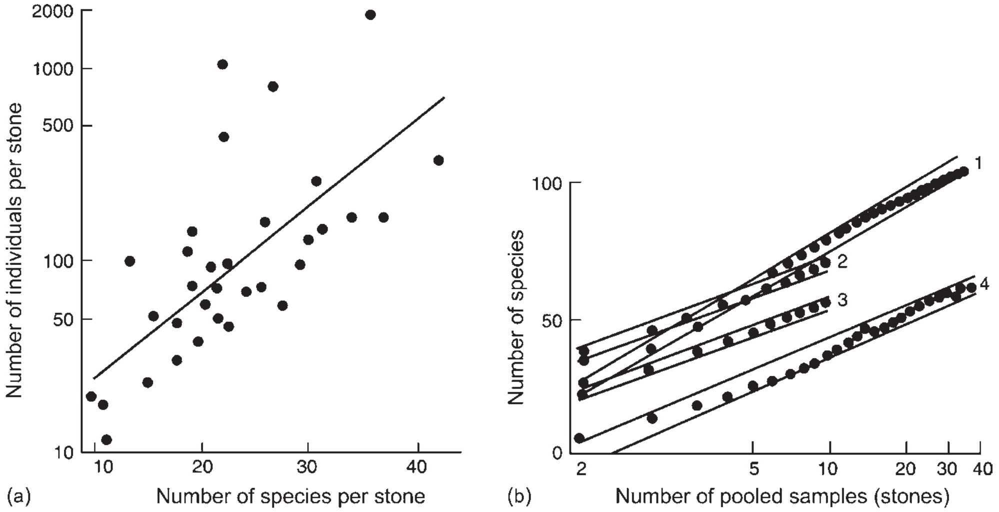

FIGURE 10.4 (a) The number of species collected increases with the size of the sample, illustrated by Kuusela's (1979) study of the fauna on individual stones in a large Finnish river. (b) The cumulative number of species collected increases with the logarithm of cumulative number of stones sampled: 1 = River Javavankoski, Finland (Kuusela 1979); 2 = Vaal River, South Africa (Chutter and Noble 1966); 3 = Lytle Creek, Utah (Gaufin et al. 1956); 4 = Rio Java, Costa Rica (Stout and Vandermeer 1975). Solid lines are 95% confidence limits.

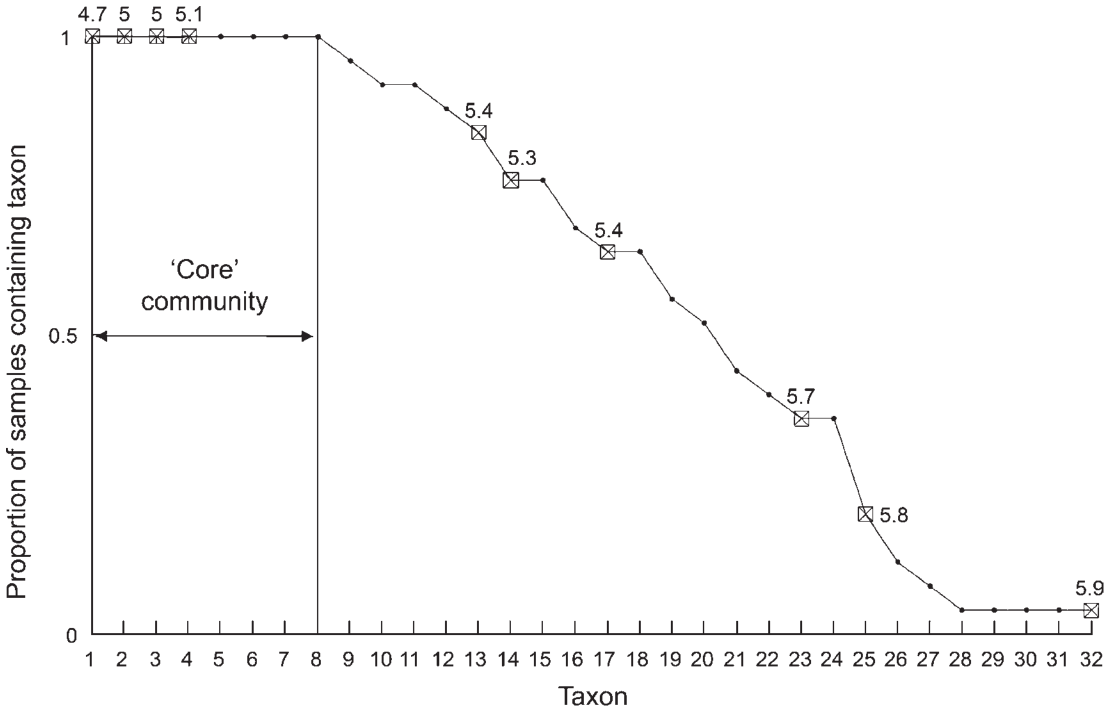

FIGURE 10.5 The proportion of sampling occasions that included each taxon over 24 years of study in the Broadstone Stream, United Kingdom. Numbers along the lower axis refer to individual species. The core community consisted of eight taxa that were always present. These included: 1, *Nemurella pictetii*; 2, *Leuctra nigra*; 3, *Plectrocnemia conspersa*; 4, *Sialis fuliginosa*; 5, Pentaneurini; 6, Ceratopogonidae; 7, *Heterotrissocladius marcidus/Brillia modesta*; 8, *Polypedilum abicorne*. The pH optima for individual taxa are indicated where known. (Reproduced from Woodward et al. 2002.)

distributions usually are locally abundant as well (Gaston and Blackburn 2000), as Heino (2005) demonstrated from a comparison of stream insects collected within one drainage with distributional data from a countrywide data set. Although such a relationship can be an artifact of sampling, it is likely that the explanation has an ecological basis in organism–niche relationships, dispersal abilities, and population growth rates.

When one takes into account the many factors that influence regional diversity, the myriad environmental conditions that make a locale more or less welcoming for particular species, and the variable extent of sampling effort, it is hardly surprising that reported diversity at the local scale varies enormously. Because most species are minor components of ecological webs, the completeness of the species list may not matter greatly. Nonetheless, the few exhaustive inventories are of interest because they give a sense of just how biologically diverse stream communities can be. Perhaps the most complete species lists come from long-term studies of a small German stream, the Breitenbach (Table 10.1), and of the Broadstone Stream in the United Kingdom (Schmid-Araya et al. 2002). More than 1,000 invertebrate species have been collected from the Breitenbach, and because this list was compiled using aerial as well as aquatic collections, it is uncertain what fraction derives from habitats other than the stream, including a small impoundment and other standing water habitats,

TABLE 10.1 A total of 1,085 species of metazoans reported as of 1989 from a 2 km stretch of the Breitenbach, a small stream near Schlitz in northern Germany. (From Zwick 1992.)

Insecta	*Number*	*Other Metazoa*	*Number*
Diptera	468	Nematoda	141
Coleoptera	71	Rotatoria	130
Trichoptera	57	Annelida	56
Ephemeroptera	18	Platyhelminthes	50
Plecoptera	18	Crustacea	24
Hymenoptera	3	Hydrachnellae	22
Megaloptera	2	Mollusca	12
Planipennia	2	Gastrotricha	6
Odonata	1	Vertebrata	3
		Nematomorpha	1
Total	640		445

but probably less than one third. This compilation indicates that the greatest invertebrate diversity is located in a few groups, including several minute, interstitial phyla (Nematoda, Rotatoria, Annelida, and Platyhelminthes) and the highly diverse Diptera, especially the midge family Chironomidae. In general, it is the smallest taxa that are most diverse (Palmer et al. 1997). The Broadstone Stream is relatively depauperate because of high natural acidity; however, its count of 131 invertebrate species likewise reflects high representation by small taxa that are often overlooked (Schmid-Araya et al. 2002).

Studies of the number of diatom species that colonize glass slides suspended in the current also suggest that local species richness is proportional to regional species richness (Patrick 1975). In two species-rich streams of the eastern United States, between 79 and 129 diatom species colonized glass slides; in two species-poor streams on Dominica, West Indies, the range was 46–61 species. Comparisons of species-rich and species-poor streams in the United States gave a like result: 160 species were collected on slides in a stream where the species pool was approximately 250; fewer than 30 were found in a stream with roughly 100 total species.

Fish inventories can be complete, particularly in temperate regions where local diversity frequently is of the order of 10–100 species and taxonomic uncertainty is minimal. As many as 50–100 species can be collected from a stream reach, although reports in the range of 20–50 species are more common (Horwitz 1978). Despite the scarcity of complete inventories of invertebrates and algae, there can be little doubt that, at least in temperate streams, the number of taxa in both groups exceeds the number of fish species by an order of magnitude.

In summary, there are numerous factors that contribute to some areas being relatively rich in species while other areas are less so. A first level of explanation must take into account regional diversity, which is influenced by climate history, topography, and geography; intensity of the sampling effort at both within and between-habitat levels; and the variability of the physical environment and the habitat. There is also good reason to believe that interactions between species, which in turn probably vary in their intensity depending upon environmental conditions, play a major role in determining local species richness. This provides the link between the topics of species diversity and community structure, and we turn now to the latter.

10.3 Community Structure

Community structure refers to the organization of a biological community based on numbers of individuals within different taxonomic groups and functional roles, and the underlying processes that maintain that organization. Explorations of this topic center around a few core concepts: that communities are nonrandom assemblages whose interactions result in predictable and repeatable patterns, that existing communities are stable and resist change when challenged by the normal range of environmental conditions and invasion by members of the existing species pool, and that structure emerges from a combination of habitat matching and species interactions. Variation in the composition of the regional species pool and local environmental conditions over space and time result in much variability in natural communities, but the composition of particular communities nonetheless is governed by a small number of underlying principles (Begon et al. 2005). The countering view states that assemblages are an unstructured sample of whichever species are able to survive and reproduce under local environmental conditions, changing as conditions change and by chance. A more formalized version, the neutral model of Hubbell (2001), considers all species to be essentially interchangeable, and so random replacement following stochastic colonization and extinction determines the momentary composition of short-lived assemblages.

The discussion of community structure and the rules that might govern community assembly has generated a rich literature in ecology. To enter into this topic, it is useful to distinguish some key ideas, keeping in mind that they are not fully independent. Niche-based models focus on the interplay between biotic interactions (usually predation, herbivory, and competition) and abiotic forces (primarily habitat and disturbance) that determine the suitability of a place for a particular species. The habitat template model (Southwood 1988) emphasizes the association of species with habitat features, such that individual species occur where they are best suited and more species are found where habitat conditions are most diverse. In this long-favored explanation of stream community structure, the physiological, morphological, behavioral, and life history attributes of individual species determine which will successfully colonize and maintain populations in a particular environment. Both abiotic and biotic factors can be visualized as a series of filters that determine the subset of the regional species pool that is most likely to successfully colonize and maintain populations.

Disturbance models emphasize the interplay between species interactions and variation in flow, temperature, and other environmental factors that periodically reduce the abundance of some or all species in an assemblage. Because predation, competition, and herbivory can potentially eliminate local populations, disturbance can limit the effectiveness of strongly interacting species, and facilitate or prevent recolonization by displaced species. A focus on disturbance seems appropriate to fluvial ecosystems because they appear to be highly variable and occasionally harsh environments. In addition, benthic invertebrates and algae are patchily distributed, and this suggests that disturbance, biotic interactions, and recolonization may combine to govern population dynamics at the local scale (Townsend 1989). Because dispersal ability varies among species, individual mobility, propensity to drift, and aerial flight ability all are important traits that may permit the persistence of weak competitors and vulnerable prey in environments where they might otherwise lose out.

10.3.1 Consistency in assemblage composition

Evidence that communities are structured by deterministic processes has often been sought through analysis of patterns in species composition. Consistency in assemblage composition over time, and similarity in assemblage structure among locations whose environments are comparable, argues against randomness and in favor of underlying processes. The core community of eight taxa described earlier for the Broadstone Stream (Figure 10.5) was present throughout the more than 20-year study period, and species turnover generally was low. This high persistence of assemblage composition and dominance by the same handful of species in the Broadstone Stream strongly suggests that the local assemblage dominants are not simply a random sampling of a larger species pool, but instead are those whose attributes allow them to be especially successful in the environmental conditions at that location.

The degree of community persistence appears to vary depending on environmental conditions, for reasons that are only partly understood. Two surveys of 27 streams in the same locale as the Broadstone Stream suggested greater persistence within cold- than warm-water streams (Townsend et al. 1987). Species persistence of fish assemblages was high and similar in two streams surveyed 9 years apart, but the difference between the two collections was greater in the stream that exhibited higher seasonal and year-to-year variation in flow regime, maximum summer temperatures, and frequency of dewatering (Ross et al. 1985). Other studies that have reported less overall persistence in assemblage structure (Grossman et al. 1982) have attributed this finding to environmental variability. Based on 10 years of sampling in Coweeta Creek, North Carolina, Grossman et al. (1998) concluded that environmental variability in flows rather than habitat or resource availability best explained variation in fish assemblages. Indeed, lack of assemblage persistence or of relationships between species composition and habitat variables may be a frequent finding wherever unpredictable floods and droughts introduce high temporal variation into stream assemblages (Angermeier and Schlosser 1989).

Spatial comparisons of biological assemblages also provide insight into the roles of structuring mechanisms versus chance in community assembly. Arguing that a neutral model based on dispersal would lead to greatest similarity amongst adjacent sites, whereas community structuring mechanisms are supported if assemblages from different streams resemble one another to the degree that their local ecological conditions also are similar, Thompson and Townsend (2006) compared macroinvertebrate assemblages from ten grassland streams in the Taeiri catchment, South Island, New Zealand. Assemblage similarity was best explained by spatial proximity for species with low dispersal ability, a mixed model worked best for species with moderate dispersal abilities, and neither model worked especially well for species of high dispersal ability. The ability of such a comparison of natural assemblages to test niche versus neutral explanations faces an important challenge in the tendency for ecological conditions also to show spatial correlation. Because they could document no influence of distance on similarity of physical and chemical conditions for the ten streams, Thompson and Townsend (2006) judged this not to be a concern, and attributed the observed negative relationship between spatial distance and community similarity to distance limitations of aerial dispersal and the possible influence of chance order of arrival on community assembly.

The fish assemblages of tropical floodplain rivers provide a natural experiment in community assembly because seasonal fluctuations in discharge result in repeated cycles of extirpation and colonization of floodplain habitat at the local scale. By experimentally manipulating habitat complexity, Arrington et al. (2005) showed that species differences in dispersal ability significantly affected assemblage response to habitat. Dispersal was most important to community dynamics in newly formed habitat patches, whereas abundances of individual species increasingly were influenced by habitat characteristics in older patches.

Investigation of patterns in assemblage composition over time and space does not by itself provide strong evidence for the processes that underlie community structure. Nonetheless, this approach is indicative that patterns are repeatable and persistent, and so encourages us to seek explanations. Dispersal and recolonization ability clearly play a role, interacting with the various environmental and biotic factors operating across multiple scales to determine which of the many potential colonizers will be successful in establishing local populations.

10.3.2 The habitat template and species traits

Habitat template theory places particular emphasis on the matching of habitat requirements of individual species to the abiotic and biotic conditions of a locale (Southwood 1988, Townsend and Hildrew 1994). Increasingly, such efforts examine the traits of species with the expectation that attributes such as size, body shape, life span, and mode of dispersal will help us understand why certain species succeed where others do not, and also may provide clues regarding the environmental factors that are responsible. A conceptual elaboration of this approach connects the regional to the local species pool through a hierarchical series of filters that determines the likelihood that a particular subset of colonists will be successful at a locale (Figure 1.5, Tonn et al. 1990, Poff 1997). The idea that biological assemblages and their responses to environmental variables should be viewed from the perspective of species traits rather than taxonomic identity is attracting wide use (Poff et al. 2006), with applications to community assembly (Poff 1997, Lamouroux et al. 2004), assessment of stream health (Barbour et al. 1999, Statzner et al. 2004), ecosystem function (Naeem and Wright 2003), and in predicting species invasions (Olden et al. 2006).

Efforts to demonstrate that species traits match with environmental variables have met with at least moderate success. To test the hypothesis that functional organization of fish communities is related to hydrological variability, Poff and Allan (1995) described habitat, trophic, morphological, and tolerance characteristics using six categories of species traits for each of the 106 species present at 34 sites in Wisconsin and Minnesota. Two ecologically-defined assemblages were identified, associated with either hydrologically variable streams (high variation in daily flows, moderate frequency of spates) or hydrologically stable streams (high predictability of daily flows, stable baseflow conditions). Fish assemblages from variable sites had generalized feeding strategies, were associated with silt and general substrate categories, were characterized by slow-velocity species with headwater affinities, and were tolerant of sedimentation. These findings indicate that hydrologic regime acts as an environmental filter, supporting theoretical predictions that variable habitats should harbor resource generalists whereas stable habitats should include a higher proportion of specialist species.

The hierarchical filter model implies that associations should exist between traits of the species assemblage and habitat variables at multiple spatial scales. Lamouroux et al. (2004) assessed correlations between traits and environmental variables across spatial scale within two river basins in France, after first summarizing the functional composition of invertebrate communities using 60 categories of 12 biological traits (Table 10.2). Roughly half of the tests were significant at the microhabitat scale and about one fourth at the reach scale; although a number of invertebrate traits differed between basins, this was not attributable to between-basin habitat differences. In this example, filters at the microhabitat scale clearly were most influential.

Any consideration of species traits must recognize that some traits tend to co-occur and others may rarely if ever be found in the same species. For example, large body size, long life span, and low reproductive potential form one common suite of attributes; small body size, short life span, and high reproductive potential another. These are frequently referred to as slow and fast, or K and r species, respectively (Begon et al. 2005). Mixtures between these two suites of attributes are rare, suggesting a trade-off exists between two alternate lifestyles, or at least that they represent two ends of a spectrum. Using 11 ecological traits and 11 biological traits, Usseglio-Polatera et al. (2000) identified such gradients in body size, reproductive rate, and feeding ecology within 472 European macroinvertebrate taxa. Because they were able to aggregate taxa into groups with similar traits, they speculate that improved resolution of habitat affinities or response to pollution might be attained using a subset of species sharing a similar suite of traits, rather than the entire assemblage.

TABLE 10.2 Trait categories and their modalities from an analysis of relationships between species traits and environmental variables for invertebrate assemblages of streams in France. (Adapted from Lamouroux et al. 2004.)

Trait	*Modalities*
Maximum size	Seven categories from <2 to >80 mm
Body flexibility	None (<10°), low (10°–45°), high (>45°)
Body form	Streamlined, flattened, cylindrical, spherical
Life span	<1 year, >1 year
Voltinism	<1, 1, >1 generation/year
Aquatic stages	Egg, larva, nymph, imago
Reproduction	Ovoviviparous, individual eggs[a], egg masses[b], asexual
Dispersal	Aquatic active, aquatic passive, aerial active, aerial passive
Resistance form	Eggs, cocoons, cells, resists desiccation, diapause/dormancy, none
Respiration	Tegument, gill, plastron, spiracle (aerial)
Locomotion/relation to substrate	Flyer, surface swimmer, swimmer, crawler, burrower, interstitial, temporarily attached, permanently attached
Feeding habits	Absorber, deposit feeder, shredder, scraper, filter feeder, piercer, predator, parasite, parasitoid

[a] Isolated eggs can be free or cemented to substrate
[b] Egg masses can be free, cemented, in vegetation, or deposited terrestrially

10.3.3 Disturbance

Hurricanes, fires, floods, and droughts are well-known examples of extreme disturbances that episodically cause high mortality to populations of many species in forest, grassland, coral reef, river, and other ecosystems. Because species vary in their resistance to disturbance, as well as rates of recolonization and recovery, disturbance can ameliorate strong biological interactions and help to maintain populations of species that might otherwise be eliminated by their consumers or competitors. Streamflow is both the most obvious and the most readily quantified disturbance variable in fluvial ecosystems, and as was discussed in Section 2.3.3, flow variability is evident at all scales from the turbulence around a stone to the occasional extremes of major floods and droughts. Thus small-scale disturbance might act almost continuously, whereas larger disturbances occur less frequently. Seasonal temperature extremes, pathogen outbreaks, sediment pulses from bank failure, and the arrival of a novel species each might constitute a disturbance to a particular system.

Two major axes of environmental variation that affect stream community structure are environmental harshness and disturbance frequency. These axes are independent, as one environment might be uniformly harsh, a second subject to frequent and extreme disturbances (Peckarsky 1983). Both act to restrict the abundance and diversity of species that are found at a location, but they differ in that perennially harsh environments such as those that are very cold or highly acid have an ongoing effect, whereas disturbance implies an alternation with periods of more benign conditions. Thus, harsh environments would be expected to contain relatively few species and experience less species replacement, whereas frequently disturbed environments would be expected to contain more species and exhibit higher species turnover. Because strong biotic interactions including competition and predation can reduce species diversity, it may be that an intermediate level of disturbance promotes diversity by ameliorating species effects on one another (Connell 1978, Ward and Stanford 1983).

Because individual species differ in their vulnerability to a particular disturbance event, reflecting many aspects of morphology, behavior, and lifestyle, it is important to recognize that the impact of the same disturbance may differ among species (Lytle and Poff 2004). In addition, between-habitat differences occur as a consequence of bed and substrate characteristics, influencing the availability of refuges within the substrate (Matthaei et al. 1999) and resulting in microhabitats where disturbance is less pronounced (Lancaster 2000, Matthaei et al. 2000).

An analysis of flow regimes for the United States (Poff and Ward 1989) offers a useful framing of disturbance in a hydrologic context (Figure 10.6). Using a number of measures expected to characterize flood frequency, seasonal flood predictability, flow intermittency, and overall flow variability, and hydrologic data from 78 stream gauges across the lower United States, these authors identified nine categories of flow regime. Although the exact number of such categories is somewhat arbitrary, the various metrics described in Section 2.4 provide effective means to quantify flow variation.

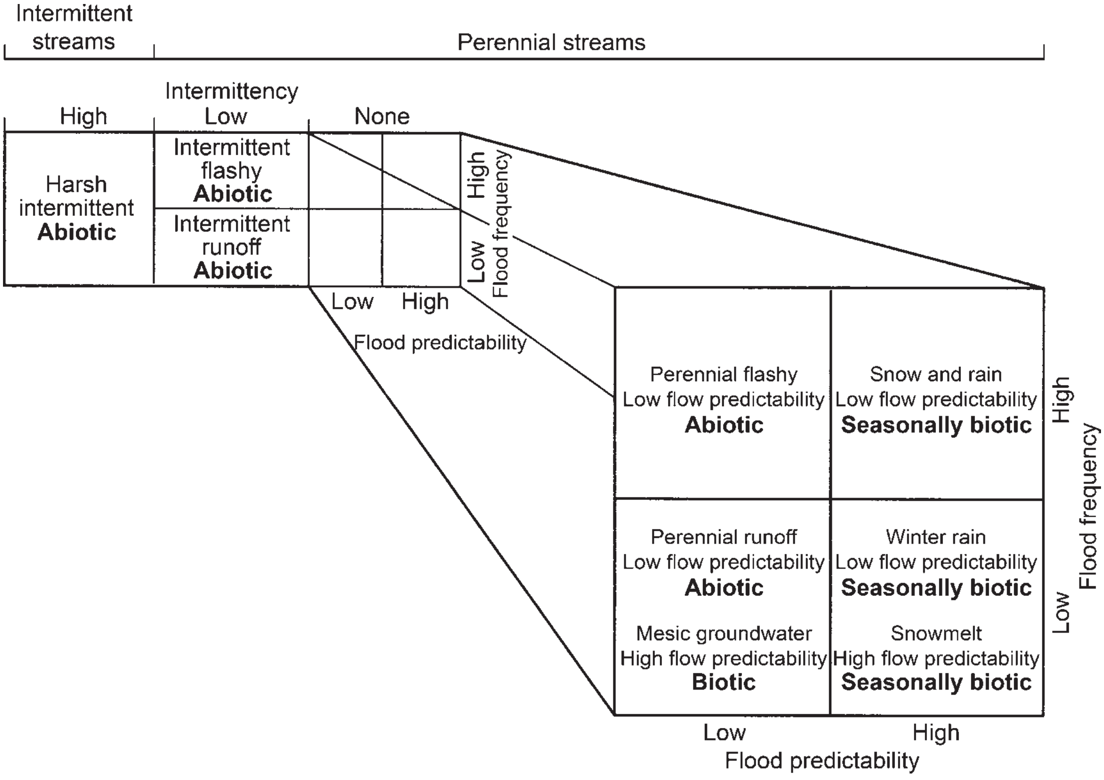

FIGURE 10.6 Conceptual model of nine stream types based on several temporal measures of discharge regime. The degree of intermittency is the first classification variable. For streams of low intermittency and for perennial streams, flood frequency provides additional separation. For perennial streams, flood predictability also must be considered. Names ("winter rain") are indicative of environmental conditions resulting in hydrographs of a particular class. Additional descriptions ("abiotic," "seasonally biotic") are Poff and Ward's (1989) predictions of the relative contributions to community structure of abiotic and biotic processes for each stream type. (Reproduced from Poff and Ward 1989.)

10.3.3.1 Species-level effects of disturbance

Changes in local and seasonal abundances of the stream biota in response to flow variation received frequent mention in previous chapters. Periphyton, benthic macroinvertebrates, and fishes all can be strongly influenced by fluctuations in flow. In piedmont rivers of the Venezuelan Andes, benthic invertebrates are subject to frequent flash floods during the rainy season and droughts during the dry season. Total macroinvertebrate abundance exhibited a strong negative relation with average monthly rainfall, used as a surrogate of flow because no stream gauges were available (Flecker 1992b). Numbers rebounded during flood-free periods due to colonization and recruitment, resulting in a strong positive relationship between insect abundances and time elapsed since the last storm (Figure 10.7).

Flow variation also can mediate species interactions. Throughout most of Arizona, the introduced mosquitofish *Gambusia affinis* has replaced a native poeciliid, the Sonoran topminnow *Poecilopsis occidentalis*, largely through predation on juveniles (Meffe 1984). In mountainous regions subject to extreme flash floods, however, long-term coexistence of the two species results from the native fish's superior ability to avoid downstream displacement. Hydropsychids and simuliids exhibit a similar interaction seasonally in coastal Californian streams (Hemphill and Cooper 1983). On hard substrates in fast-flowing sections, black fly larvae are more abundant in spring and early summer, while caddis larvae predominate thereafter. Winters of high discharge lead to greater numbers of simuliids, and winters of low flow lead to higher densities of hydropsychids. By scrubbing substrate surfaces with a brush, Hemphill and Cooper showed that disturbance benefited simuliids because they were the more rapid colonizers, whereas caddis larvae were superior at monopolizing space on rock surfaces. As time passed since the last disturbance, hydropsychid larvae gradually replaced simuliids due to their aggressive defense of net sites.

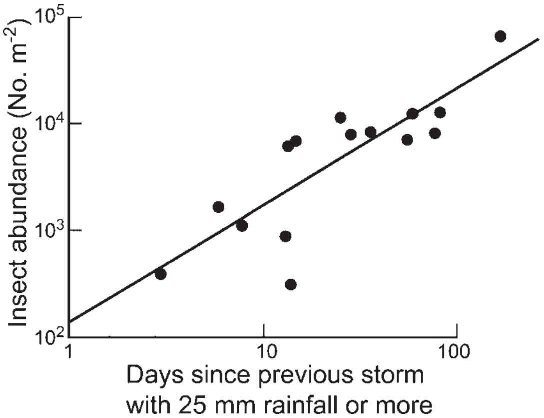

FIGURE 10.7 The number of aquatic insects in a river of the Andean foothills subject to a pronounced dry season and frequent floods during the rainy season. Time elapsed since the most recent rainfall event >25 mm is used in lieu of streamflow data. (Reproduced from Flecker and Feifarek 1994.)

Because the stream benthos is subject to ongoing turbulence and disturbance, it is possible that the displacement of species through biological interactions may be interrupted routinely, resulting in a continuously shifting mosaic of habitat conditions and species colonization and replacement. This is the model of patch dynamics (Townsend 1989), and it is consistent with the patchy distribution of algae and invertebrates on the streambed (Downes et al. 1998). A fluctuating environment combined with continual dispersal and colonization permits more species to co-occur than would be true if conditions exhibited greater constancy. It also confers some regularity to pattern, because environmental circumstances are predictable in the aggregate even though they are unpredictable for any given place and time.

Organisms that modify habitat, referred to as ecological engineers, have the potential to influence habitat structure and heterogeneity and thereby affect other species (Jones et al. 1994). The grazing fish *Parodon apolineri* apparently is such a species, creating observable grazing scars and a patchy distribution of algae and sediments on stone surfaces. By quantifying the spatial pattern of scars in a neotropical stream and by experimentally manipulating densities of *Parodon*, Flecker and Taylor (2004) demonstrated that grazing enhanced habitat heterogeneity, although with time or at higher densities grazing tended to reduce algae and sediments to a more uniform condition of low abundance. However, the hypothesized correspondence between habitat heterogeneity and richness of the algal and invertebrate assemblages was not observed, perhaps because the timescale at which those taxa respond was slower than the loss and renewal dynamics generated by grazing *Parodon*.

Because flow variation is such a pervasive feature of the fluvial environment, many organisms show adaptation to resist or minimize its effects (Lytle and Poff 2004). Timing of life cycle events such as egg-laying or emergence can be effective when flow extremes have a degree of predictability. The emergence of young rainbow trout from spawning gravel in spring appears to be an example of synchronizing a sensitive life cycle stage with the long-term average dynamics of the flow regime. The rainbow trout *Oncorhynchus mykiss*, one of the most widely introduced species worldwide, succeeds in new environments where the flow regime matches its native range and fails in other environments where it does not, apparently because floods harm trout fry (Fausch et al. 2001). Position shifts to protected areas are a common behavioral response to high flows, such as the relocation of fishes from the thalweg to the floodplain during a flood event in an Illinois river (Schwartz and Herricks 2005). In arid streams of the southwestern United States prone to flash flooding, giant water bugs (Belostomatidae) crawl out of streams in advance of the flood, using rainfall as the cue (Lytle 1999). Morphological adaptations including streamlining and other adaptations to minimize drag were described in Section 5.1.4.

10.3.3.2 System-wide effects

Disturbance has been shown to have dramatic, ecosystem-wide effects. Examples include those where floods and droughts are of sufficient magnitude that habitat is disrupted and many of the organisms present are displaced, when river basins of different disturbance regimes are compared, and when disturbance most severely affects a species that is a strong interactor within a community.

Sycamore Creek, Arizona, is a desert stream subject to extreme flash floods that might occur a few times annually. Fisher et al. (1982) describe the recovery of the system following a late summer flood until another flood some 60 days later restarted the sequence. Biomass of algae and invertebrates were reduced by nearly 100%, but recovery occurred quickly, particularly by the algae, which initially were dominated by diatoms and later by filamentous green and blue-green algae (Figure 10.8). Macroinvertebrate recovery also was rapid, but slower by several weeks than the algal recovery. Nutrient uptake and community metabolism changed over community succession, and this highly productive system began to export surplus primary production. The Sycamore Creek example nicely demonstrates the effects of a disturbance that occurs with unpredictable regularity, and so ecosystem dynamics can only be understood within the cycle of disturbance and recovery. Periodic drought obviously can severely disrupt stream ecosystems as well. Based on an evaluation of resilience and recovery of Sycamore Creek to a number of spates and droughts, Boulton et al. (1992) concluded that droughts had the greater impact.

Any pattern of disturbance that recurs with some long-term regularity is referred to as a disturbance regime. Riseng et al. (2004) characterized disturbance in 97 Midwestern streams that differed in their frequency of spates and droughts using several measures of low and high flow occurrence, substrate movement, and summer water temperature (which can reach stressful

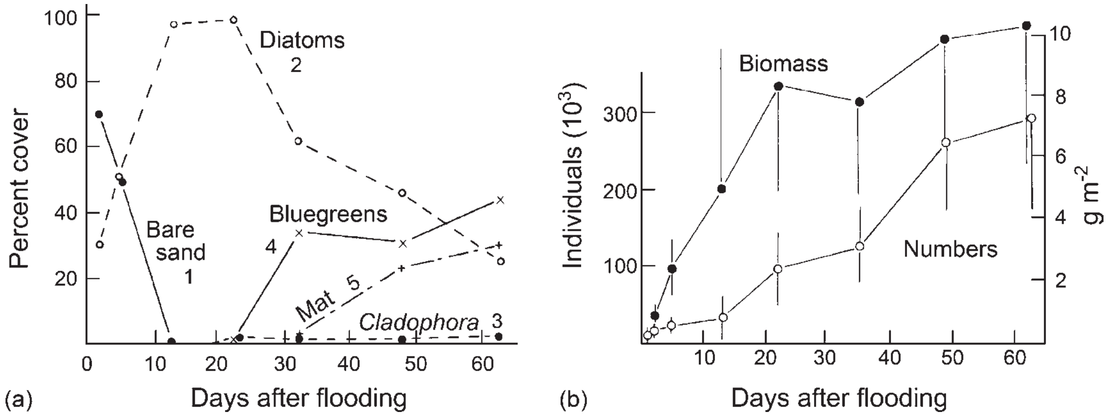

FIGURE 10.8 Temporal succession of the biota in Sycamore Creek, Arizona, following flooding. (a) Percent cover of algal patch types; (b) mean invertebrate numbers and biomass after flooding. Values are means and 95% confidence intervals. (Reproduced from Fisher et al. 1982.)

levels during low flow periods). In locations where scouring floods reduced consumer biomass, algal biomass was strongly influenced by nutrient supply, whereas in more stable streams grazers depressed algal biomass regardless of nutrient concentration. The different disturbance regimes identified in this study were clearly a product of regional patterns in geology and precipitation, and so exhibited a degree of spatial predictability.

When species that are strong interactors are eliminated or rendered ineffective by disturbance, shifts in disturbance regime can turn trophic cascades on or off. In some California rivers, a grazing caddis larva is abundant during flood-free periods and escapes most predation due to its large size and robust case, but it is highly vulnerable to high flows and rolling rocks during floods (Wootton et al. 1996). During flood-free periods and in dammed rivers, the main energy pathway is from algae to the caddis; however, after flooding occurs in unregulated river segments, more energy flows to smaller grazers and then to young steelhead. In essence, disturbance regime acts as a switch, causing one of two possible food web configurations to become dominant.

10.4 Food Webs

The network of interactions depicted in a food web provides the most complete yet succinct visual summary of a biological community. The study of food webs has a long history in ecology, incorporating at least two major lines of inquiry: one emphasizing how species are inextricably linked through their interactions with one another, hence focusing on population and community dynamics; the other concerned with the flux of organic matter and energy. Most examples can be categorized very roughly as connectance food webs, which attempt to identify all possible linkages; energy flux food webs, which quantify organic matter flow along a limited number of major pathways; and trophic-interaction food webs, which emphasize population processes and species interactions. As the field continues to mature we should expect to see increasing effort to merge the patterns depicted in food web structure with the processes of energy flow and species interactions.

An impressively detailed food web for the Broadstone Stream in southern England provides an excellent example of a connectivity food web (Figure 10.9). All species are of equal importance in a connectance web and all lines are of equal weight, because the web is constructed from diet presence–absence data. This food web is amongst the most detailed on record and includes all of the benthic community including macrofauna, meiofauna, protozoa, and algae (Schmid-Araya et al. 2002, Woodward et al. 2005). It includes 131 consumer species supported by eight basal resources and three additional food sources such as eggs, for a total of 842 links. The meiofauna comprised 70% of the species present, demonstrating the need to include small-bodied organisms in the analysis. Food web structure varied seasonally due to

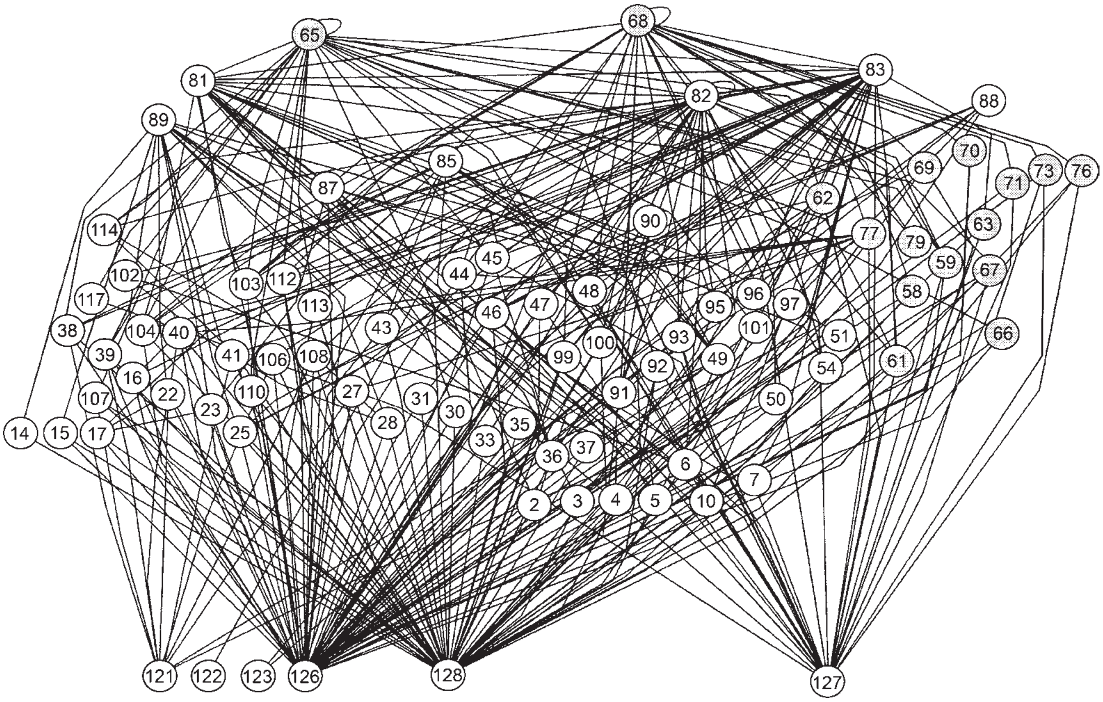

FIGURE 10.9 Connectivity food web for the invertebrate community in Broadstone Stream (Autumn 1996). Numbers represent species and food items: Protozoa: 1–10. Turbellaria: 11. Rotifera: 12–37. Nematoda: 38–41. Oligochaeta: 42–48. Tardigrada: 49 and 50. Acari: 51–56. Insecta: Odonata: 57 *Cordulegaster boltonii*; Plecoptera: 58 *Leuctra nigra*, 59 *Leuctra hippopus*, 60 *Leuctra fusca*, 61 *Nemurella pictetii*, 62 *Siphonoperla torrentium*, 63 Plecoptera larvulae, 64 *Leuctra nigra* adult; Trichoptera: 65 *Plectrocnemia conspersa*, 66 *Potamophylax cingulatus*, 67 *Adicella reducta*; Megaloptera: 68 *Sialis fuliginosa*; Coleoptera: 69 *Platambus maculatus*, 70 Helodidae Gen. sp., 71 Elmidae sp.; Diptera: Ceratopogonidae 72 *Bezzia* sp.; Tipulidae: 73 *Limonia* sp., 74 *Limonia modesta*, 75 *Dicranota* sp., 76 *Pedicia* sp., 77 *Limnophila* sp., 78 *Hexatoma* sp., 79 Limoniinae Gen. sp.; 80 *Rhypholophus* sp.; Chironomidae: 81 *Macropelopia nebulosa*, 82 *Trissopelopia longimana*, 83 *Zavrelymyia barbatipes*, 84 *Conchapelopia viator*, 85 *Apsectrotanypus trifascipennis*, 86 *Zavrelymyia* sp. 2, 87 *Paramerina* sp., 88 *Krenopelopia* sp., 89 *Pentaneura* sp., 90 *Natarsia* sp., 91 *Prodiamesa olivacea*, 92 *Brillia modesta*, 93 *Heterotrissocladius marcidus*, 94 *Heterotanytarsus* sp., 95 *Eukieferiella* sp., 96 *Georthocladius luteicornis*, 97 *Corynoneura lobata*, 98 *Chirononomus/Einfeldia* sp., 99 *Polypedilum albicorne*, 100 *Micropsectra bidentata*, 101 *Mectriocnemus* sp. Adult; Simuliidae: 102 *Simulium* sp. Crustacea: Ostracoda:103; Cladocera:104–105; Copepoda: Cyclopoida: 106–111; Harpacticoida: 112–116; algae and plant material: 118–122. Various: 123 Plecoptera eggs, 124 Turbellaria eggs, 125 Rotifera eggs, 126 fine organic matter (FPOM), 127 coarse organic matter (CPOM), 128 *Leptothrix ochracea*. (Reproduced from Schmid-Araya et al. 2002.)

changes in species richness, resulting in temporal changes in the proportion of species at the top and the base of the food web. Despite its complexity, relatively simple patterns in food web structure could be found in relation to body size. Meiofaunal and macrofaunal subwebs were effectively two compartments because large prey were invulnerable to small predators and large predators were not effective in consuming very small prey (Woodward et al. 2005).

Measurement of energy flux provides a quantitative assessment of the strength of linkages along each pathway. In Figure 10.10 we see a less-detailed food web, but one that quantifies organic matter pathways by converting information from gut analyses into annual ingestion rates for caddisfly larvae dwelling on snag habitat in the Ogeechee River, Georgia (Benke and Wallace 1997). The pathways from amorphous detritus and diatoms to several filter-feeding caddis larvae were particularly strong, but *Hydropsyche rossi* derived substantially more energy from consuming animal prey than did the other filter feeders. Hall et al. (2000) constructed food webs based on the analysis of organic matter flow for a reference stream in the southern Appalachians and a stream where leaf litter was excluded. Their analysis included nearly 90% of invertebrate production, but <30% of total links, suggesting that not all feeding links need be identified for this approach to be successful. The main basal sources in the reference stream were leaf detritus, bacterial carbon (C), and animal prey, with each contributing 25–30% of the energy supply. A few pathways accounted for most organic matter flow,

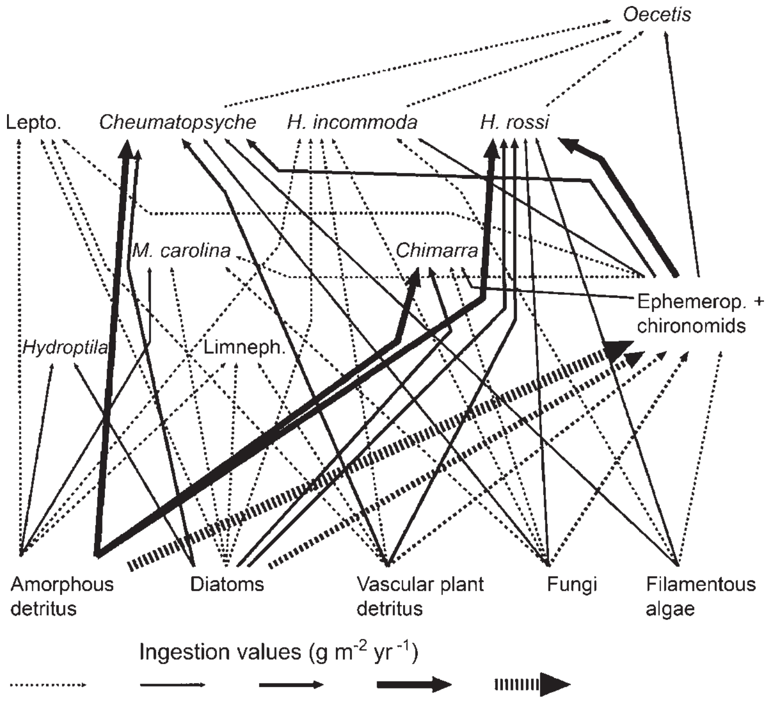

FIGURE 10.10 Energy flow food web for caddisfly larvae in the Ogeechee River, Georgia. The thickness of the arrow represents the ingestion fluxes. Abbreviations: Ephemerop = Ephemeroptera, Lepto = Leptoceridae, Limneph = Limnephilidae, *M. carolina* = *Macrostemum carolina*. (Reproduced from Benke and Wallace 1997.)

and largest flows were associated with detritivores due to their low assimilation efficiency. In the litter exclusion stream, flows to predators were reduced, a few pathways dominated, and consumption rates per biomass were higher, indicating strong interactions with the remaining common taxa.

Although gut content analysis remains a widely used approach to the estimation of energy fluxes, despite the difficulty of identifying bits of soft-bodied prey and amorphous detritus, analysis of the natural abundance of stable isotopes in basal resources and in consumers is providing important new insights into energy flows and trophic position (Peterson and Fry 1987). The ratio of the naturally occurring ^{13}C isotope of C relative to the more abundant ^{12}C, expressed as $\delta^{13}C$, is a useful diet tracer because C is the main elemental component of organic matter, it passes through food chains with little alteration of its isotopic composition, and $\delta^{13}C$ values often differ between major groups of primary producers such as benthic algae, macrophytes, and terrestrial plants. In addition, the $\delta^{13}C$ of consumer tissues directly reflects the mixture of prey resources consumed and assimilated over previous weeks, months, or even years depending on the tissue studied (Finlay 2001). The application of stable isotope methods has led to key insights that would have been difficult to achieve using prior methods. For example, despite the abundance of detritus from macrophytes and floodplain forests in large tropical rivers such as the Amazon and Orinoco, $\delta^{13}C$ analyses of consumers indicate a minor contribution of this material to animal food webs. Instead, phytoplankton and periphyton are the critical energy sources for most fish species (Araujo-Lima et al. 1986, Hamilton et al. 1992).

10.4.1 Resource subsidies

Food web studies have added significantly to our understanding of the magnitude of various energy pathways and how these pathways differ in importance with environmental context, particularly landscape setting. Energy subsidies to fluvial ecosystems that can be extremely important to ecosystem metabolism include leaf litter, the infall of terrestrial invertebrates, and the carcasses and reproductive products of migrating fishes. Salmonids in small streams can obtain half or more of their energy from the consumption of terrestrial insects, suggesting that streamside forest management may be an important consideration in salmon management (Wipfli 1997). These exchanges can be bidirectional, as exemplified by the dependence of spiders and lizards in riparian zones on the emergence of aquatic insects (Sabo and Power 2002).

Evidence from a variety of ecosystems reveals that energy subsidies are an important and widespread facet of food web ecology (Polis et al. 1997). Exclusion of leaf litter inputs to an Appalachian stream altered basal resources and organic matter flow to predators in the study by Hall et al. (2000), described above. The input of terrestrial insects to fishes can be an important energy subsidy to top consumers, as Nakano et al. (1999) demonstrated by placing a fine-mesh net over a forest stream in Japan. The exclusion of terrestrial invertebrates resulted in greater fish predation on benthic aquatic invertebrates, triggering a trophic cascade and an increase in periphyton biomass. Further, the biomass of herbivorous invertebrates and periphyton did not differ between treatments with or without fish when terrestrial invertebrate inputs were allowed, suggesting that the supply of arthropods from land normally prevented strong top-down control (Baxter et al. 2005). The complicated consequences for food web interactions due to external subsidies is also evident in a competitive shift in feeding by native Dolly Varden charr (*Salvelinus malma*) in northern Japan in response to nonnative rainbow trout (Baxter et al. 2004). Trout were better able to consume the terrestrial invertebrates that fell into the stream, forcing charr to feed on herbivorous invertebrates and causing an increase in periphyton biomass. However, the biomass of adult aquatic insects emerging from the stream decreased, and this in turn reduced the density of spiders in the riparian forest.

For migratory and mobile species, stable isotope analysis has been useful in determining the location where C was assimilated, thus providing insight into the magnitude of cross-system subsidies. Differences in the $\delta^{13}C$ of muscle tissue in the migratory *Semaprochilodus insignis* established that C produced in blackwater systems contributed to fish stocks harvested from white-water systems of the Amazon (Benedito-Cecilio and Araujo-Lima 2002). Because epilithic algae, detritus, and algal filaments varied in abundance among benthic habitats and streams in the headwaters of the Eel River of northern California, Finlay et al. (2002) were able to use C isotope ratios to assess habitat use by different consumers. The $\delta^{13}C$ values of collector–gatherers and scrapers indicated a reliance on algae from local sources within their riffle or shallow pool habitats, whereas filter feeders derived more C from upstream shallow pools. Algal production from shallow pools was the dominant resource base for vertebrate predators in late summer regardless of the habitat where they were collected. The drift of pool insects into riffles, rather than movement of trout among habitats, was the presumed mechanism, illuminating between-habitat subsidies parallel to cross-ecosystem subsidies.

10.4.2 Landscape position

Due to all of the differences in basal resources, productivity, and habitat conditions that are associated with stream location and position along the river continuum, it is apparent that food web structure will change with landscape position (Woodward and Hildrew 2002a). Landscape features determine the stream ecosystem's physical setting including flow regime and habitat features, influence the relative importance of basal resources, affect the magnitude of external subsidies of nutrients, detritus, and prey, and vary from place to place, conveying a high degree of individuality to the species assemblage and food web structure at each locale (Woodward and Hildrew 2002a). Models of stream ecology, particularly the river continuum concept (Figure 1.7), attempt to explain changes in the structure and function of stream communities within the context of the landscape, including longitudinal patterns and shifts in energy inputs between forested and open sites (Vannote et al. 1980). The influence of the riparian corridor on basal resources is well known, especially in small streams where the extent of summer shade and autumn leaf fall acts as a switch between allochthony and autochthony. Linkages between aquatic and terrestrial food webs associated with consumer trophic levels can be surprisingly strong, as illustrated by the reciprocal subsidies of insects between streams and riparian zones. The strength of trout-induced trophic cascades can depend on the supply of terrestrial invertebrates (Nakano et al. 1999). Even the frequency of pollinator visits to riparian plants can be affected by fish predation on larval odonates, which determines the abundance of adult dragonflies and hence predation pressure on pollinating insects (Knight et al. 2005).

In addition to the location-specific influence of landscape setting on the supply of energy and nutrients, and the interactions among species within stream communities, physical and biological processes serve as links between adjacent and distant locations. Downstream transport of nutrients and organic matter by river flow and lateral exchanges with the floodplain during seasonal inundation are the dominant physical processes. Long-distance fish migrations by Pacific salmon import quantities of marine-derived C and nutrients from the oceans into headwater streams, providing nourishment to aquatic and terrestrial consumers and fertilizing the growth of riparian vegetation (Willson and Halupka 1995). Prochilodontid fishes of South America make seasonal spawning migrations of hundreds of kilometers from floodplains to upland rivers where they are consumed by apex predators (Winemiller and Jepsen 1998). Migratory fishes may be simply the most apparent example of the way that movements of organisms connect distant ecosystems. Through dispersal, movements among habitats, and occasional displacement, many fishes both as individuals and populations are functionally connected across scales from reach to river basin (Fausch et al. 2002).

10.5 Community Composition and Ecosystem Function

Intact biological assemblages with a diverse mix of species are expected to carry out various ecosystem functions including primary production, organic matter decomposition, nutrient cycling, and secondary production of harvestable species at their natural and presumably optimal levels. As species are lost from ecosystems due to the relentless pace of human activities (Chapter 13), the extent to which system function and resilience depend on the number and characteristics of species present becomes an issue of considerable concern (Covich et al. 2004).

The expectations that biodiversity matters to ecosystem function and also that high biodiversity serves as a buffer against the consequences of species loss have theoretical and empirical support (Loreau et al. 2001), primarily from terrestrial ecosystems and at relatively low levels of diversity. Several mechanisms potentially are responsible (Giller et al. 2004). When species have complementary (overlapping but not identical) roles, the rate and efficiency of a process should increase when multiple species are present, and especially whenever the activities of one species facilitate those of a second. Thus, a species loss is expected to lower the efficiency of the process in question. When species have redundant roles, the loss of one species may not immediately result in a decline in the rate or efficiency of some process, but the presence of multiple species provides insurance against a breakdown in ecosystem function should one or more species be adversely affected by environmental change. Complementarity, facilitation, and redundancy are mechanisms linking biodiversity to ecosystem function. On the other hand, the particular suite of traits and functional role of individual species also must be carefully considered. Individual species can have unique roles in ecosystems, be disproportionately abundant, dominate energy fluxes (Figure 10.10), and strongly influence other members of the assemblage (Figure 9.11). In some instances, individual species have been shown to play such a strong and unique role that species identity rather than overall diversity is of primary importance. This raises the possibility that a positive relationship between biodiversity and ecosystem function may be an artifact of sampling, because these species with unique traits and roles are more likely to be encountered when more of the species pool is included in an experimental study.

Facilitation of feeding efficiency was demonstrated by the enhanced particle capture of a mixed assemblage of three species of filter-feeding caddis larvae versus capture rates by single species in a laboratory stream (Cardinale et al. 2002a). “Current shading” was reduced at higher species diversity, with the consequence that diverse assemblages were able to capture a higher fraction of suspended particles than could any monoculture (Figure 10.11). This hydrodynamic facilitation was due to the alteration of near-bed flows by capture nets, which resulted in increased bed roughness, higher near-bed velocities, and thus higher capture rates.

Leaf litter breakdown is a key ecosystem process in detritus-based stream ecosystems (Figure 7.3), serving as a basal energy resource to numerous detritivores and ultimately converting organic matter inputs to CO_2. The breakdown of organic matter by physical abrasion, microbes, and shredders is a key ecosystem process that is well studied and relatively easy to manipulate. Using laboratory microcosms, Jonsson

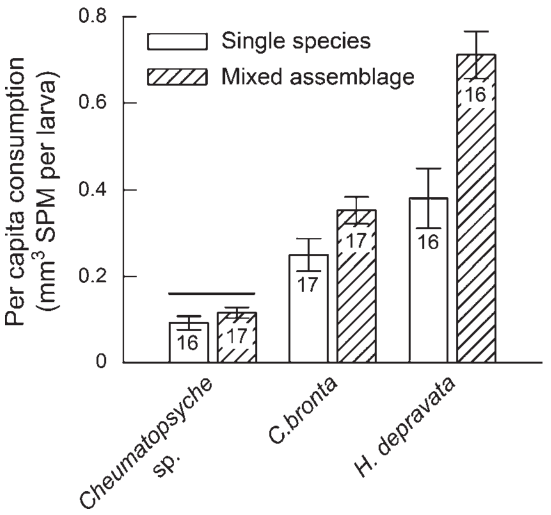

FIGURE 10.11 Per capita consumption of suspended particulate matter (cubic millimeters per larva) in single-species and mixed-species assemblages of filter-feeding caddisfly larvae in laboratory streams. Interspecific facilitation is indicated by the higher per capita capture rates in mixed assemblages. (Reproduced from Cardinale et al. 2002.)

and Malmqvist (2000) demonstrated that leaf mass loss increased with number of shredder species present, due either to differences in mode of feeding, facilitation of feeding efficiency, or both. By assembling a data set of litter breakdown studies from 36 streams of northern Sweden and northeastern France, Dangles and Malmqvist (2004) were able to evaluate the influence of species richness versus relative abundance components of diversity (Figure 10.12). The litter decomposition rate increased with the number of species present, but at a lower rate at sites with low dominance. In other words, detrital processing was more rapid in streams that were strongly dominated by one or a few species. Other studies have shown that the presence or absence of a single species, *Gammarus fossorum*, has a disproportionately strong influence on litter breakdown, and it is noteworthy that the highest breakdown rate in Figure 10.12 occurred in a stream where this amphipod was the sole shredder present.

In contrast to the demonstrated influence of shredder diversity on leaf breakdown, fungal diversity apparently had no effect of leaf mass loss or fungal spore production (a measure of microbial production) in stream microcosms (Dang et al. 2005). This was true with oak and alder leaves, at high and low nutrient levels, and across a range of 1–8 fungal species. There was some suggestion of greater variability in fungal activity at low fungal diversity, consistent with a portfolio effect (the averaging and dampening out of the influence of extreme species as richness increases, just as a diverse stock portfolio is expected to guard against swings in a single stock's value). Although Barlöcher and Corkum (2003) reported a positive effect of fungal diversity on leaf decomposition rates, their result is less convincing because those authors relied on initial inoculates rather than realized communities, which typically have greater unevenness.

If species loss is expected to result in reductions in ecosystem function, then highly diverse communities may be better buffered by their presumed greater levels of complementarity and redundancy, and therefore less affected by the loss of a single species. Thus, it is intriguing that a particularly strong example of species identity has been reported from a hyperdiverse tropical stream. During the dry season, the flannel-mouth characin *Prochilodus mariae* migrates from floodplain locations into headwater streams in the foothills of the Venezuelan Andes, where it feeds on organic-rich sediments on the streambed, creating visible feeding scars and enhancing sediment transport. As Taylor et al. (2006) document with comparisons between open and *Prochilodus*-restricted stream sections, this one species of detritus-feeding fish uniquely influences C flow and ecosystem metabolism. In its absence, the amount of particulate organic carbon (POC) on the streambed was higher, the downstream flux of POC declined due to reduced bioturbation

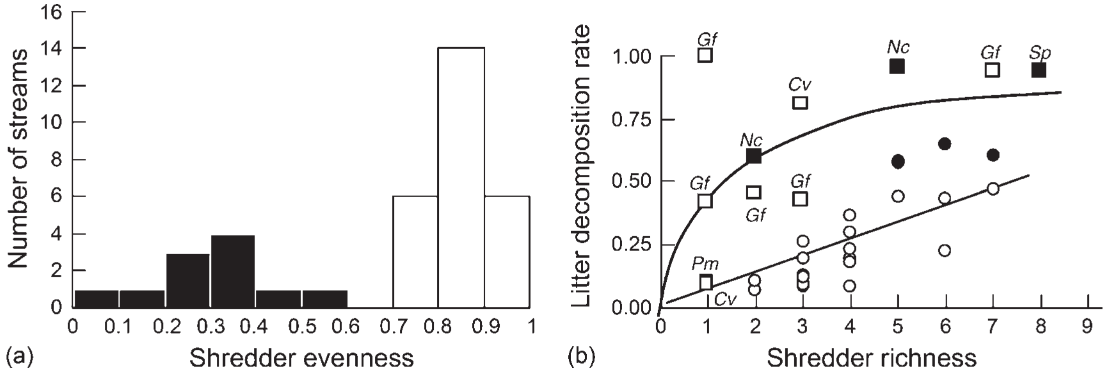

FIGURE 10.12 (a) Frequency of stream sites where the shredder community showed high dominance – low evenness (*shaded bars*) versus high evenness (*open bars*) for 36 streams in France and Sweden. (b) Litter decomposition rate as a function of number of shredder species at high (*squares*) and low (*circles*) dominance sites in northern Swedish (*closed symbols*) and French (*open symbols*) streams. Gf, *Gammarus fossarum*, Cv, *Chaetopteryx villosa*, Sp, *Sericostoma personatum*, Nc, *Nemoura cinerea*, Pm, *Protonemura meyeri*. (Reproduced from Dangles and Malmqvist 2004.)

and consumption, heterotrophic respiration increased due to greater biofilm growth, primary production doubled, and because respiration increased more than primary production, net ecosystem metabolism showed a greater deficit. This example is of more than academic interest: fishes of the Prochilodontidae are the most important commercial species of South America and are declining due to the combined influence of dams and overfishing. Changes to ecosystem function seem all too likely to occur over large areas of the Neotropics due to the loss of species in this family.

10.6 Summary

Community structure refers to the organization of a biological assemblage based on numbers of individuals within different taxonomic groups and functional roles, and the underlying processes that maintain that organization. Numbers of species, their functional roles and relative abundances, and energy pathways through food webs are useful descriptors of community structure. The assembly and maintenance of a local community from a regional species pool results from the matching of individual species to available resources and habitats, influenced by disturbance and dispersal, and further modified by the internal dynamics of species interactions.

Local biological diversity is a subset of regional species richness, which in turn is a function of area, climate, and history. The number of species is greater in large river basins than smaller basins, and increases downstream partly due to the effect of increasing river size, and also because some species such as large river fishes are not adapted to smaller streams. Thus, species addition as well as replacement occurs along a river's length. Different geographic regions typically have their own distinctive biota, attesting to chance differences in the establishment and diversification of particular taxa and the local interplay of environmental and biological forces that direct evolutionary change. North America has nearly three times as many species of fishes as does Europe, and this is largely because the North American fauna had a much larger area free from glaciation and easier routes for recolonization, whereas mountain ranges running from east to west in Europe limited faunal dispersal routes. Although the historical biogeography of aquatic insects is less well known, diversity in major insect groups likewise shows continental-scale patterns such that certain groups are largely missing from some regional species pools. One of most general patterns in biogeography is for species richness to increase from high latitudes toward the tropics. Well documented for freshwater fishes, the existence of a latitudinal diversity gradient for aquatic insects is subject to debate.

The processes that influence the assembly and maintenance of local communities from their regional species pool include niche-based models that focus on the interplay between biotic interactions and abiotic forces, the habitat template model based on the association of species with habitat features, and disturbance models that emphasize the interplay between species interactions and variation in environmental factors that periodically reduce the abundance of some or all species in an assemblage. These are not mutually exclusive, and all can be incorporated into a framework that connects the regional to the local species pool through a hierarchical series of filters including landscape setting, resource and habitat conditions, environmental variability, and interactions with other species.

Disturbance, usually associated with hydrologic variability as well as temperature extremes, pathogen outbreaks, sediment pulses, and species invasions, is an important force structuring stream communities. Streams experiencing environmental conditions that are persistently or very frequently harsh are likely to support fewer species than would be found in more benign environments. But because species vary in their resistance to disturbance and in their rates of recolonization and recovery, disturbance can ameliorate strong biological interactions and help to maintain populations of species that might otherwise be eliminated by their consumers or competitors. When floods or droughts occur with unpredictable regularity, characteristic flow regimes can be shown to determine community composition, the dominant interaction pathways, and organic matter dynamics.

The network of interactions portrayed in a food web provides the most complete yet succinct visual summary of a biological community. Identification of all links, although rarely achieved, serves as a useful reminder of the potential complexity within biological communities. Most energy flows through a subset of species, and typically it is the common species that dominate energy pathways. Food web studies reveal that exchanges of energy among ecosystems can have profound effects on both energy pathways and species interactions. These subsidies include allochthonous litter inputs, the exchange of invertebrates between the stream ecosystem and the terrestrial riparian zone, and upstream–downstream transfers due to water flows and the migrations of fishes. Because the magnitude and nature of subsidies varies with longitudinal position and the surrounding terrestrial ecosystem, the network of interacting species within stream ecosystems is strongly influenced by landscape setting. The loss of species due to human activities is an increasingly serious concern, and raises the possibility that simplified communities may become less productive and less resilient.

Chapter eleven

Nutrient dynamics

Energy enters the biosphere principally as sunlight and is transformed into energy-rich organic substrates by photosynthesis and chemosynthesis. This organic matter, consumed either living or dead, fuels the metabolism of heterotrophs and in the process is returned to its inorganic state as respired carbon dioxide (CO_2). Various chemical compounds of life must be acquired by plants in order for synthesis of new organic matter to take place, and by animals and microbes to sustain their growth and metabolism. Although energy exhibits a one-way flow from synthesis to dissipation via ecosystem metabolism, the chemical constituents of living organisms are continuously reutilized as they cycle between the biota and the environment. These chemical constituents are referred to as nutrients because they are necessary to sustain life, and the supply of nutrients often determines the biological productivity of an ecosystem.

Heterotrophs obtain most of their nutrients from their food and by ingesting or absorbing water. Usually they are limited by energy in the form of organic carbon (C), rather than nutrients, although heterotrophic bacteria and fungi can be nutrient limited. Autotrophs are often limited by the availability of nutrients. Elements that are most heavily utilized are referred to as macronutrients, and include nitrogen (N), phosphorus (P), potassium, calcium, sulfur, and magnesium. Other elements including iron, manganese, copper, silica, molybdenum, chloride, and zinc are required in smaller quantities and are referred to as trace elements or micronutrients. The demand for certain nutrients, especially N and P, is much greater than their availability in aquatic systems; as a consequence the supply of N and P often limits biological activity. Human activities have profoundly altered N and P dynamics by increasing the available supply in surface waters, resulting in eutrophication of lakes, rivers, and coastal zones worldwide (Carpenter et al. 1997).

Nutrients in dissolved inorganic form enter a stream reach from upstream, groundwater and surface runoff, and atmospheric inputs. Nutrients are incorporated into organic form by biological uptake and assimilation, move through the food web by consumption, and subsequently are mineralized to inorganic form by excretion and the decomposition of organic matter (Figure 11.1). Although the cycling of nutrients between abiotic and biotic compartments often is thought of as taking place within fixed boundaries, unidirectional flow adds a pronounced spatial dimension to nutrient cycling in running waters. Nutrients generated at one location typically will be transported some distance before subsequent reutilization. The term nutrient spiraling describes the interdependent processes of nutrient cycling and downstream transport (Webster and Patten 1979). Nutrients that are in demand relative to their supply should be taken up rapidly, resulting in short

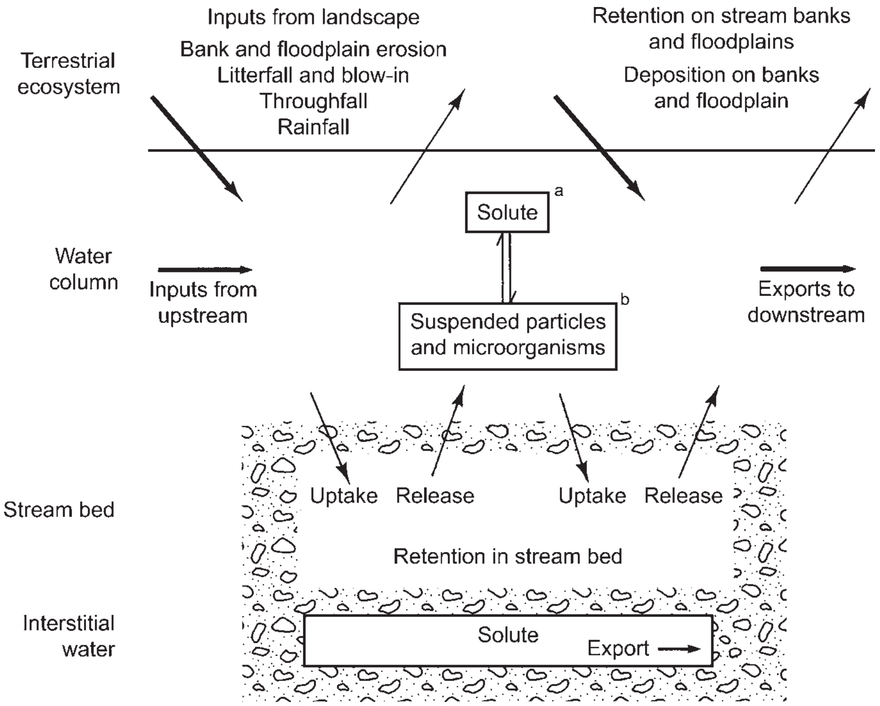

FIGURE 11.1 Conceptual diagram of solute processes in streams. Arrow widths indicate approximate magnitude of process. Most materials are transported in dissolved form (a), but phosphorus, trace metals, and hydrophobic organics are transported mainly as particulates (b). (Modified from Stream Solute Workshop 1990.)

transport distances and rapid cycling relative to elements whose supply is less critical. Nutrient dynamics in streams are further complicated by various abiotic uptake and release mechanisms that partially regulate nutrient concentrations and, particularly in the case of N, by several transformations among inorganic states that yield energy to specialized bacteria.

In this chapter we examine the often complex relationships between availability of inorganic nutrients and their utilization by the biological community. There are, broadly speaking, two perspectives: how nutrient supply affects biological productivity, and how processes within the stream ecosystem influence the quantity of nutrients that are transported downstream. As previously discussed in Chapters 6 and 7, nutrient supply can limit rates of photosynthesis and organic matter breakdown and thus the rate at which basal resources for stream food webs are produced. Rivers transport substantial quantities of dissolved materials to receiving lakes and oceans (Chapter 3), and so instream transformation, storage, and removal processes may be significant in large-scale element budgets. Especially in the case of N and P, which can cause algal blooms in coastal and lentic waters, nutrient dynamics within river systems may influence the extent of eutrophication of receiving water bodies.

11.1 Sources and Cycling of Nitrogen and Phosphorus

Nitrogen and P are the major nutrients that have been found to influence rates of primary production and the activity of heterotrophic microbes. Research has shown that benthic algal productivity can be limited by either N or P singly, be co-limited by both, or not be nutrient limited. Sources and supplies of N and P vary considerably with geology, soils, climate, and vegetation, and their concentrations often are substantially elevated owing to anthropogenic inputs.

11.1.1 Nitrogen sources and quantities

Nitrogen is abundant in the environment as N_2, but it is N bonded to oxygen, hydrogen, or C such as nitrate, ammonium, and organic N that comprises reactive N, and until recently this originated mainly by biological N fixation (Wetzel 2001). As a consequence of the synthesis of nitrogenous fertilizers, burning of fossil fuels, and wide cultivation of crops such as soybeans that have N-fixing microbial symbionts, annual N fixation from anthropogenic sources now exceeds natural fixation (Vitousek et al. 1997).

Nitrogen occurs in freshwater ecosystems in many chemical states (Table 11.1). Dissolved inorganic nitrogen (DIN) includes ammonium (NH_4^+), nitrate (NO_3^-), and nitrite (NO_2^-). Dissolved organic nitrogen (DON) consists of amino nitrogen compounds (polypeptides, free amino compounds) and other organic molecules, and most particulate organic nitrogen (PON) occurs as bacteria and detritus. Total N includes all dissolved and particulate forms including both organic and inorganic. Nitrogen also occurs in gaseous forms as dinitrogen N_2 and in association with oxygen as NO_x. Inorganic N forms (ammonium, nitrate, and nitrite) are generally determined through colorimetric methods, although nitrate must be reduced to nitrite by passing the sample through a column filled with cadmium granules. Because standard methods of analysis do not distinguish nitrite from nitrate and the former is usually a minor fraction, they typically are combined and reported as nitrate. The determination of particulate and dissolved organic forms is more complex because it involves digestion of the sample after separation of dissolved forms from particulate forms by filtration.

Based on a review of nutrient concentrations in world rivers, the average for total N, including rivers that are enriched by human activity, is 0.94 mg L^{-1} (Meybeck 1982). In natural systems with little human influence, concentrations of DIN are low, around 0.12 mg L^{-1} and include about 0.1 mg L^{-1} NO_3-N, 0.001 mg L^{-1} NO_2-N, and 0.015 mg L^{-1} NH_4-N. DON is nearly always a major fraction of TDN in natural rivers (40%

TABLE 11.1 Major forms of nitrogen and phosphorus found in natural waters (after Meybeck 1982). Nitrogen also is present as dissolved N_2 gas (not shown).

Nitrogen		
Dissolved Inorganic Nitrogen	Total Dissolved Nitrogen	Total Nitrogen
NO_3^- nitrate		
NO_2^- nitrite		
NH_4^+ ammonium		
Dissolved Organic Nitrogen		
Particulate Organic Nitrogen		
Phosphorus		
Dissolved Inorganic Phosphorus (PO_4^{-3} orthophosphate or soluble reactive phosphorus)	Total Dissolved Phosphorus	Total Phosphorus
Dissolved Organic Phosphorus	Total Organic Phosphorus	
Particulate Organic Phosphorus		
Particulate Inorganic Phosphorus		

world average), and can be up to 90% in arctic and humic tropical rivers with high organic N content of soils and minimal anthropogenic DIN. Particulate N, including PON and ammonia, and organic N adsorbed to particles, may be important in some circumstances.

Based on more than 1,000 stream sites in North America and New Zealand that included a wide range of human influence, the lowest one third of sites had $< 0.7\,\mathrm{mg\ L^{-1}}$ TN whereas the highest third exceeded $1.5\,\mathrm{mg\ L^{-1}}$ (Dodds et al. 1998). Nitrogen concentrations are strongly influenced by land use in settled areas, and especially by agriculture (Figure 11.2). In undisturbed tropical rivers, present-day concentrations likely represent natural values, which for total N were reported to range between 0.27 and $1.05\,\mathrm{mg\ L^{-1}}$ (Lewis et al. 1999). Because nitrate concentrations were relatively low, varying from 0.09 to $0.19\,\mathrm{mg\ L^{-1}}$, TN must include a high fraction of DON in these pristine rivers. Lowest values occur in areas of high runoff, which also support the greatest amount of vegetation.

The sources of these various forms of N in streams include atmospheric deposition, N fixation, and terrestrial inputs carried in runoff and groundwater. Atmospheric deposition as precipitation and dry fallout occurs primarily in the form of ammonium and nitrate, although organic forms also can be important (Holland et al. 1999, Neff et al. 2002). Nitrogen gas is abundant in the atmosphere and soluble in water, where it can be transformed by N-fixing bacteria, principally cyanobacteria, into N forms that can then be used by other organisms. Nitrogen from the land enters streams as runoff from soil and vegetation and in groundwater, depending on precipitation and hydrologic flowpaths (Hagedorn et al. 2000). During baseflow, most inputs are from subsoil leaching. Inputs from throughfall (rain that drips from vegetation) can be significant at the beginning of a rain event; subsequently, inputs via shallow flowpaths from topsoils rich in DON are more important. Because the atmosphere is the main reservoir of N, rock weathering is usually discounted

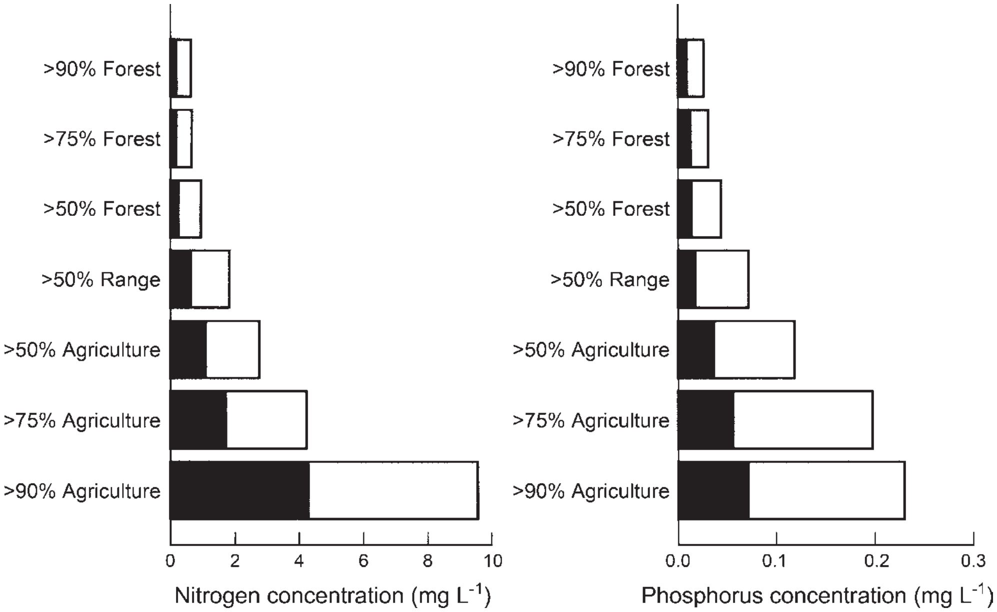

FIGURE 11.2 Concentrations of nitrogen and phosphorus from 928 streams of the United States that were considered to be relatively uncontaminated but affected to varying degrees by fertilizer runoff. The inorganic fraction of the total is shaded for each nutrient. (Based on data in Omernik 1977.)

as a source. However, recent evidence indicates that some sedimentary rocks contain large amounts of fixed N, and so weathering may provide significant amounts of nitrate to running waters in some circumstances (Holloway et al. 1998, Thompson et al. 2001, Williard et al. 2005).

Nitrogen inputs often vary seasonally due to the effects of the growing season and hydrology. Due to uptake of N by terrestrial vegetation, streamwater concentrations tend to be lower during the growing season and higher during the dormant season (Vitousek and Reiners 1975). Spatial variation in streamwater nitrate concentrations is influenced by nitrification in upland soils, which affects the extent to which catchments retain or export nitrate via streamflow (Likens and Bormann 1995, Bernhardt et al. 2005a). In Sycamore Creek, a desert stream in Arizona where N is limiting to biological production, N fixation by the cyanobacteria *Anabaena* and *Calothrix* contributed up to 85% of the total N inputs to benthic communities. Fixation rates were highest during summer and autumn, and low during winter and spring due to seasonal differences in the abundance of cyanobacteria (Grimm and Petrone 1997). In a stream in the Pacific Northwest draining a N-rich riparian forest, a spring nitrate pulse was attributed to snowmelt flushing of nitrate that had accumulated in soils due to organic matter decomposition, and additional peaks were observed during rain storms (Bechtold et al. 2003). The relative contributions of groundwater versus surface and subsurface runoff can also contribute to temporal or spatial variation in nutrient supplies. In a Mojave desert stream, nitrate concentrations in groundwater inputs varied among three sources by more than tenfold (Jones 2002). In a Kansas stream, groundwater from agricultural fields increased nitrate concentrations during periods of low flow whereas concentrations decreased during periods of high flow, probably due to dilution from undisturbed upland reaches (Kemp and Dodds 2001).

Principal anthropogenic inputs of N to streams include agricultural fertilizers, atmospheric deposition, N-fixing crops, and human and animal waste (Boyer et al. 2002). As a consequence of this enrichment, >10% of the rivers in the UK have nitrate-N concentrations as high as $9–25\,\mathrm{mg\,L^{-1}}$, more than three orders of magnitude above background concentrations (Heathwaite et al. 1996). So important is human influence that Caraco and Cole (1999) could explain over 80% of the 1,000-fold variation in nitrate export from 35 global rivers using a simple model based on fertilizer use, atmospheric deposition, and human sewage. Point sources from sewage were important in highly populated watersheds but nonetheless were smaller than inputs from fertilizer application and atmospheric deposition. The production of commercial fertilizers has increased greatly since 1950 (Schlesinger 1997), which undoubtedly accounts for significant increases in nitrate concentrations in rivers. Although some fertilizer is assimilated by crops, when applied at high levels, substantial amounts of N leach into surface and groundwater, resulting in increases in river nitrate concentrations (Heathwaite et al. 1996, Gächter et al. 2004). The cultivation of crops that harbor N-fixing bacteria also increases the amount of reactive N in soils, representing as much as half of the inputs due to fertilizer application (Vitousek et al. 1997). Increased atmospheric deposition of N is primarily the consequence of the burning of fossil fuels to generate electricity and in automobiles. Preindustrial N deposition likely was higher in the tropics than in the temperate zone because natural volatilization processes that release N oxides into the atmosphere, including biomass burning and soil emissions, are greater in tropical regions.

11.1.2 Nitrogen cycling

The N cycle is complex (Figure 11.3), due to the many chemical states in which N is found and

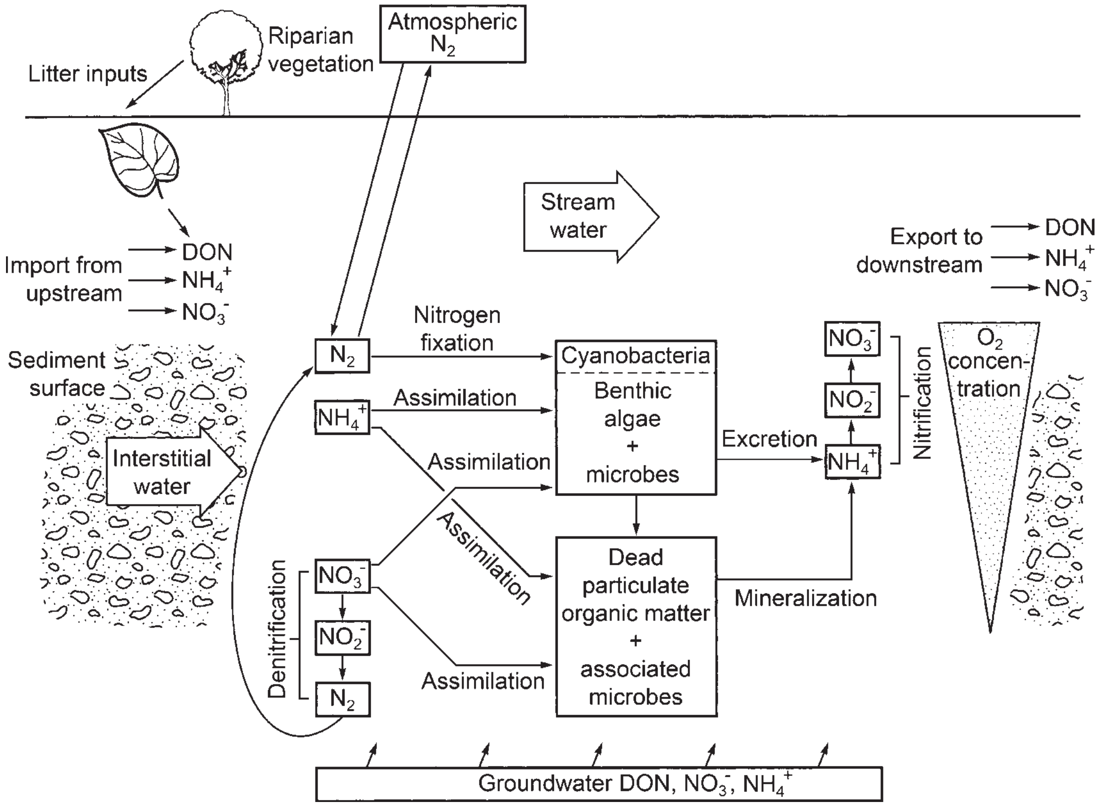

FIGURE 11.3 Nitrogen dynamics in a stream ecosystem. Bioavailable inorganic nitrogen consists mainly of nitrate and ammonia, which is immobilized by autotrophs and microbial heterotrophs in biofilms or in suspension, and by higher plants. Assimilatory uptake refers to nutrients that are incorporated into cellular constituents and are potentially available to higher trophic levels. Excretion, decomposition, and production of exudates are the principal pathways by which elements are recycled to an inorganic state. Various dissimilatory transformations of inorganic forms of nitrogen by bacteria add to the complexity of the nitrogen cycle. Cyanobacteria and other microorganisms capable of nitrogen fixation transform N_2 gas into ammonia. Nitrification, which takes place under aerobic conditions, and denitrification, which takes place under anaerobic conditions, further influence the quantities and availability of dissolved inorganic nitrogen (DIN).

the central role of bacteria in its transformation from one form to another. To understand the complexities of the N cycle, it helps to recognize that some transformations are to obtain N for structural synthesis (assimilatory uptake), while others are energy-yielding reactions (dissimilatory uptake). Nitrogen fixation and assimilation of DIN by autotrophs and heterotrophs are in the former category, whereas nitrification and denitrification are reactions where bacteria obtain energy by using ammonia as a fuel or nitrate as an oxidizing agent.

Primary producers rely primarily on the surrounding water to supply the nutrients needed for protein synthesis. Bacteria and fungi can meet much of their nutrient requirements from their C substrate, but when that substrate is poor in nutrients, these microorganisms also rely on nutrients in the water. Biological uptake and incorporation of nutrients into new tissue is referred to as immobilization, and may be by autotrophs or heterotrophs. Ammonium is taken up more readily than nitrate, which requires energy to convert into ammonium prior to assimilation. Since ammonium usually is a small fraction of DIN compared to nitrate, N fixation, in which bacteria and cyanobacteria convert N gas to NH_4^+ and incorporate this ammonium into bacterial biomass, may be favored under N limitation. However, N-fixation by cyanobacteria also is energetically costly, requires molybdenum, and is restricted primarily to taxa with specialized cells called heterocysts that protect enzymes from oxygen.

Nitrification and denitrification are energy-yielding reactions carried out by specialized bacteria that do not assimilate the N but transform it between various inorganic oxidation states. Nitrification, the oxidation of ammonium to nitrate, can be an important source of nitrate to streamwater (Bernhardt et al. 2002). Its rate depends on the availability of ammonium and dissolved oxygen, and on the abundance of nitrifying bacteria (Kemp and Dodds 2002a, Bernot et al. 2006). Significant nitrate generation can occur within the hyporheic zone provided oxygen does not become limiting due to inadequate water exchange or very high bacterial respiration (Holmes et al. 1994, Edwardson et al. 2003). In denitrification, certain bacteria use nitrate as an electron acceptor to oxidize organic matter anaerobically in energy-yielding reactions analogous to aerobic respiration, and in the process reduce nitrate to nitrous oxide and nonreactive N_2. Because the end product is N_2 gas, which is unavailable to most of the biota and can outgas back to the atmosphere, denitrification represents an important pathway by which excess N can be permanently removed from aquatic ecosystems.

11.1.3 Phosphorus sources and quantities

Phosphorus occurs in streamwater as orthophosphate (PO_4^{3-}) dissolved in water and attached to inorganic particles in suspension, as dissolved organic molecules and in particulate organic form mainly in bacteria and detrital particles (Table 11.1). Total phosphorus (TP) is determined by analyzing unfiltered samples and includes all forms of P, including those present in organisms, detritus, and adsorbed to inorganic complexes such as clays and carbonate (Wetzel 2001). The various P fractions are analyzed using filtration and digestion to separate its forms, followed by measurement using colorimetry and additional reactions. Total dissolved P is determined from water passing through a 0.45 μm filter and includes organic (colloids, esters) and inorganic (orthophosphate and polyphosphates) forms. An operational category known as soluble reactive phosphorus (SRP) based on the reaction of soluble P with molybdate is commonly used as a measure of orthophosphate (PO_4^{3-}). However, there is evidence that the SRP fraction can also include polyphosphates and therefore may overestimate orthophosphate concentrations (Dodds 2003). In common usage, orthophosphate, phosphate, SRP, and dissolved inorganic P are interchangeable terms that refer to the form of P available for organisms to take up.

Both SRP and TP are widely used as indicators of trophic status, and there is some controversy over which is the preferred measure. SRP usually is considered the best indicator of what is immediately available for uptake, but because P cycles rapidly among its various states, TP may be a better measure of overall availability of P. The usefulness of SRP versus TP in predicting algal productivity likely varies with the residence time of P in the ecosystem, because a longer residence time allows for more efficient use of P by the biota (Edwards et al. 2000). Thus SRP may be most effective in predicting algal production when water residence time is short, as in small streams. However, for broad comparisons of trophic status and nutrient limitation across stream ecosystems, TP may prove to be more useful as a measure of overall P availability (Dodds 2003).

According to Meybeck (1982), average natural levels of dissolved P worldwide are very low, around 0.01 mg P L^{-1} for PO_4^{3-}, and 0.025 mg P L^{-1} for total dissolved P (Table 11.2). In a compilation of over 1,000 temperate zone sites including both minimally altered and disturbed streams, the lowest one third had TP concentrations below 0.025 mg L^{-1} and the highest one third of sites had TP concentrations above 0.075 mg L^{-1}. The median TP concentration for these sites (0.045 mg L^{-1}) exceeded the estimated median TP concentration corrected for human influence (0.023 mg L^{-1}) by less than a factor of 2, indicating that anthropogenic influence on P concentrations is less severe than for N (Smith et al. 2003). A compilation of over 600 streams of high altitude catchments in the UK found that SRP concentrations were below 0.01 mg P L^{-1} at half of the sites and below 0.03 mg P L^{-1} in most (Mainstone and Parr 2002). Large rivers of the Neotropics, with areas of extensive undisturbed forest underlain by crystalline rock, can have very low P concentrations. In undisturbed clear and blackwater tributaries of the Orinoco Basin, Venezuela, SRP concentrations were below 0.004 mg P L^{-1}, and the upper range of TP was below 0.01 mg L^{-1} (Castillo et al. 2004). In contrast, whitewater rivers, where suspended sediment concentrations are greater, can exhibit higher P concentrations. In the Apure, a moderately disturbed white water tributary of the Orinoco, TP concentration averaged 0.19 mg L^{-1} (Lewis and Saunders 1990).

In contrast to N, which is abundant in the atmosphere, the principal reservoir for P is rocks and sediments. It is released slowly by weathering, and in unpolluted waters often is in short supply relative to metabolic demand. Phosphorus levels are generally higher in regions

TABLE 11.2 Phosphorus and nitrogen concentrations in various rivers. Values indicate average or range ($\mu g\ L^{-1}$). "nd" indicates that phosphorus was nondetectable, which corresponds approximately to values at or below 1 $\mu g\ L^{-1}$.

River	*Nitrate*	*Total N*	*SRP*	*Total P*	*Reference*
World average	100	940	8	555	Meybeck, 1982
Amazon System					
Solimões above Içа	200	638	28	422	Lewis et al., 1995; 1999
Negro	42	199	0.6	–	Lewis et al., 1995; 1999
Jurua	202	494	2.0	21	Lewis et al., 1995; 1999
Trombetas	52	407	19	347	Lewis et al., 1995; 1999
Amazon at Obidos	140	505	22	239	Lewis et al., 1995; 1999
Orinoco System					
Blackwater tributaries	2–80	230–355	Nd-3.5	Nd-7.6	Weibezahn, 1990, Castillo et al. 2004
Clearwater tributaries	68–157	235–380	Nd-3.8	Nd-9.1	Weibezahn, 1990, Castillo et al. 2004
White water tributaries	111–135	957	44–75.3	188	Weibezahn, 1990
Lower Orinoco	80	460	10	65	Lewis et al., 1995; 1999
Other rivers					
Yukon	34		1.6		Guo et al. 2004
Mississippi	1400	2260	64	200	Goolsey et al. 1999
Ohio	1240	1980	37	176	Goolsey et al. 1999
Loire	2560		79		Meybeck et al. 1988
Nile	35–823	840–6810	3.1–80	–	Abdelhamid et al. 1992.
Changjian	984		25		Liu et al. 2003
Huanghe	1694		11		Zhang 1996

draining sedimentary rock deposits, and low in regions of crystalline bedrock. Dillon and Kirchner (1975) reported greater P export from Ontario streams draining watersheds of sedimentary origin compared to those of igneous origin. Sedimentary watersheds with phosphate-bearing limestone contained substantially more phosphate in streamwater in comparison to watersheds where sandstone and shales were the main geologic types present (Thomas and Crutchfield 1974). High SRP concentrations in a Costa Rican stream influenced by geothermal activity indicate that geothermal groundwater can be a significant source of P (Pringle et al. 1993).

Atmospheric inputs, although small, can be significant in areas where P is scarce, like the Caura River, a tributary of the Orinoco (Lewis et al. 1987). The forest canopy also is a source of P because of leaching when rain and cloud water deposition drip from vegetation surfaces. In relatively undisturbed parts of the Upper River Severn in Wales, UK, P concentrations in throughfall and stemflow were markedly higher than observed in rain water, illustrating the strong influence of the vegetation canopy (Neal et al. 2003). Overall, however, P inputs from the atmosphere are minor.

Phosphorus generated from plant breakdown and stored in the soil organic layer is an important input, entering streams by surface runoff and subsurface pathways (McDowell et al. 2001). Because orthophosphate readily adsorbs to charged particles, clays in particular, it is transported with sediment that is eroded during storms, especially where slopes are steep and vegetation cover is minimal. Phosphorus concentrations in surface runoff vary with the amount of P in surface soils (Sharpley et al. 1995, Weld et al. 2001) and the proximity of P-rich soils to the stream channel (Sharpley et al. 1999). However, uptake of P by plant roots and immobilization by soil microbes can reduce concentrations in mineral soil water (Kaiser et al. 2000, Goller et al. 2006). In a montane forest in Ecuador, the soil organic layer was the main source of organic P while forest canopy drip was the main source of inorganic P. Because P concentrations in streamwater were as low as observed in rainfall, it appears that mineral soil in this system was a major P sink (Goller et al. 2006).

Anthropogenic sources include municipal and industrial wastewater, termed point source pollution because it enters surface waters at a point, usually through a pipe; and fertilizers and manure from farm fields, referred to as nonpoint sources because of their diffuse entry into streams via surface and subsurface runoff (Edwards et al. 2000, Goller et al. 2006). Dissolved inorganic P often is in the range of 0.05-0.10 mg P L^{-1} in streams receiving agricultural runoff, and can reach 1 mg P L^{-1} below sewage outlets. The majority of large lowland rivers in the UK have concentrations above 0.3 mg P L^{-1}, and some are above 1 mg P L^{-1} (Mainstone and Parr 2002). Point sources such as sewage treatment plants discharge P in dissolved forms. Because dissolved P is highly bioavailable and the supply is essentially constant throughout the year, including during the growing season when low flows result in less dilution, sewage waste effluent can have a disproportionately large influence on receiving waters. Nonpoint P inputs commonly are transported in particulate form in association with sediments, particularly where erosion is high, although P originating in fertilizer and manure also can be transported in dissolved forms (Hatch et al. 1999, Vanni et al. 2001). This can change temporally because of human activities and hydrology. For example, P loss from fertilized grasslands is likely to be primarily in dissolved forms during baseflow, whereas particulate forms are more likely to be transported during stormflow (Heathwaite and Dils 2000). Because much of the diffuse P supply is associated with sediments and storms, often during the nongrowing season, there is a high likelihood that these inputs will be exported downstream (Mainstone and Parr 2002).

11.1.4 Phosphorus cycling

Phosphorus dynamics in streams is influenced by physical, chemical, and biological processes (Figure 11.4). The principal biological processes are autotrophic and heterotrophic uptake of dissolved inorganic P and its assimilation into cellular constituents, transfer of organic P through the food chain, and its eventual release and mineralization by excretion and the decomposition of egested material. Algae and microbes in biofilms likely obtain the majority of their P from the water column, but rooted macrophytes and benthic algae can remove P from the sediments as well. Phosphorus may be excreted or released following cell lysis directly as dissolved inorganic P, or released as dissolved organic P, which subsequently is mineralized to orthophosphate by bacterial activity. The decomposition of organic matter including feces, dead organisms, and leaf litter also releases P into the water column and sediment pore water (Mainstone and Parr 2002). In addition to these biological processes, P availability is influenced by physical–chemical transformations. Sorption of orthophosphate onto charged clays and charged organic particles occurs at relatively high P concentrations, while desorption is favored by low concentrations. Sorption–desorption reactions thus act as a buffer on dissolved P concentrations. In addition, under aerobic conditions, dissolved inorganic and organic P both may complex with metal oxides and hydroxides (such as $Fe(OH)_3$) to form insoluble precipitates. This phosphate is released under anaerobic conditions, and since the extent of the anaerobic zone tends to vary seasonally with organic matter loading, the availability of dissolved phosphate varies accordingly.

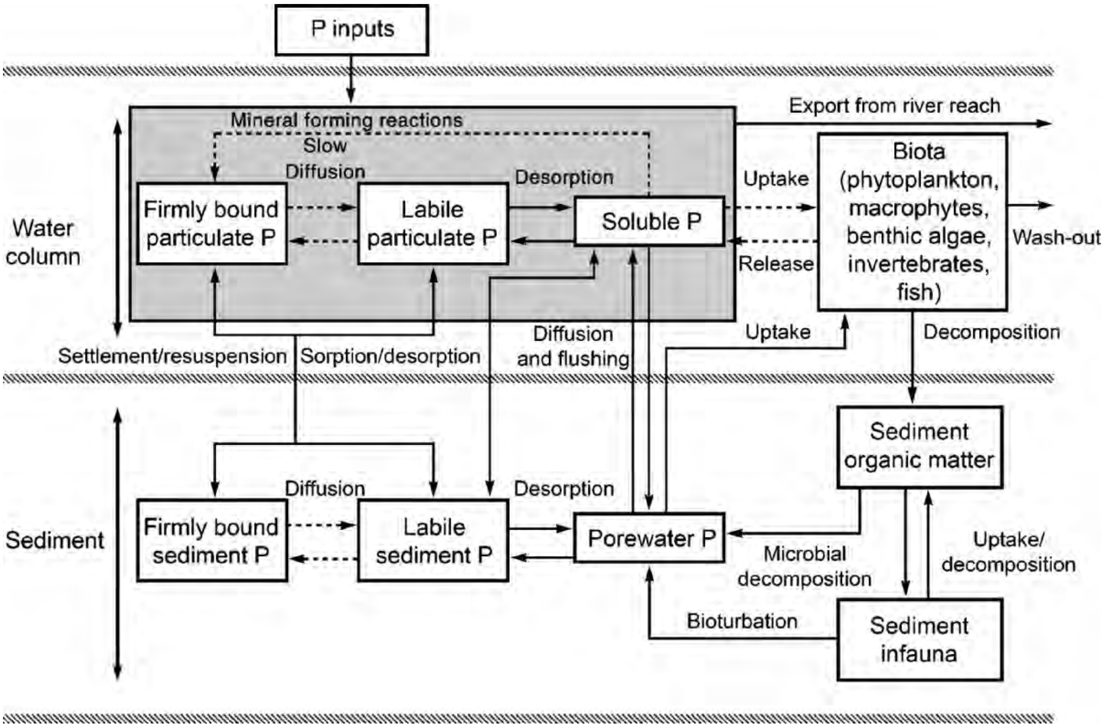

FIGURE 11.4 The cycling of phosphorus in river sediments and water column. (Reproduced from Mainstone and Parr 2002.)

11.2 Transport and Spiraling

Nutrients in stream ecosystems are most available to autotrophs and microbial heterotrophs when present as inorganic solutes in streamwater. Biotic and abiotic uptake processes, almost exclusively associated with the streambed in smaller rivers and streams, transform and temporarily retain dissolved nutrients as they are transported downstream by flow, but eventually these bound nutrients will return to the water column in mineral form. Thus, uptake and retention slows the downstream passage of dissolved materials, and nutrient cycles are stretched into downstream spirals. To accommodate this unique feature of nutrient cycling in lotic ecosystems, stream ecologists have developed models that quantify transport distance and uptake rates, using the transport dynamics of a dye or other nonreactive solute for reference (Newbold et al. 1982a, Webster and Valett 2006). Since biotic and abiotic uptake occurs primarily at sediment surfaces, exchange of water between the channel and interstitial areas can greatly influence nutrient dynamics. Further, because uptake is not solely the result of biological assimilation but also includes physical–chemical processes and dissimilatory transformations, the terms solute dynamics and solute spiraling are more inclusive of all processes (Stream Solute Workshop 1990).

Solutes that are not readily utilized by the biota or otherwise transformed from state to state by physical and chemical processes are referred to as conservative, and pass unaltered through the stream ecosystem. Reactive solutes, especially those that regulate metabolic processes, have their downstream passage retarded by uptake and temporary storage. Sodium and chloride are examples of conservative solutes whereas N and P are reactive (Wetzel and Likens 1991, Webster and Valett 2006). This distinction between conservative and reactive solutes, while useful, is not absolute, and may depend upon the relationship between supply and demand for a particular element at a particular time and place.

11.2.1 Physical transport

Solute dynamics are closely coupled with the physical movement of water, and the net flux is downstream. The modeling of a conservative solute in transport involves only physical processes and so is less complex than models for reactive solutes. If a conservative solute is released at some point, and measurements are made at another location downstream, the concentration will be observed to rise, reach a plateau, and then decline as the pulse passes the point of monitoring (Figure 11.5). A first approximation to this curve can be achieved with a basic equation describing advection and dispersion, taking into account stream dimensions and water velocity. The solute is transported from its point of release due to the unidirectional force of current (advection), and disperses due to molecular diffusion and primarily by turbulent mixing. Under certain simple conditions, which include a uniform channel,

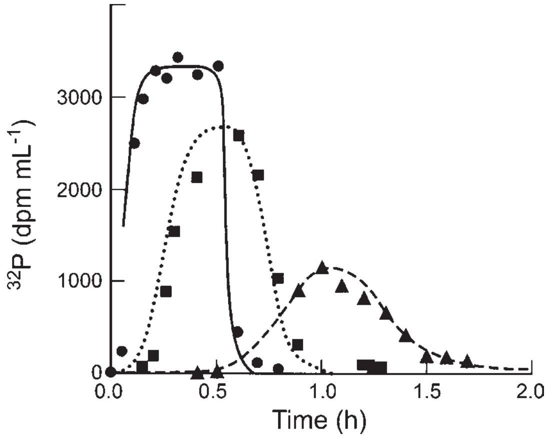

FIGURE 11.5 Concentrations of ^{32}P in streamwater at 15 (●), 47 (■), and 120 m (▲) locations downstream of a 30 min release of radioactive phosphorus in a small woodland stream. (Reproduced from Newbold et al. 1983.)

constant discharge, and no subsurface flow, the change in solute concentration (C) over time is described as follows:

$$\frac{\partial C}{\partial t} = -v\frac{\partial C}{\partial x} + D\frac{\partial^2 C}{\partial x^2} \qquad (11.1)$$

The first term describes downstream advection and is proportional to water velocity, v. The second term describes mixing of the solute randomly throughout the water mass according to a dispersion coefficient, D.

More complicated models are needed to account for additional variables such as groundwater and tributary inputs, channel storage, and subsurface flow (Stream Solute Workshop 1990). Solute dynamics are less complex in large rivers compared to small streams because large rivers generally have low slopes, are deeper than the roughest bed feature, and have relatively uniform and perhaps regulated flows. Small streams tend toward the opposite characteristics and often have substantial exchange of surface water with interstitial water, back eddies behind obstructions, and areas of slow-moving water (Bencala and Walters 1983). The net effect is that water and solutes move downstream more slowly than would be expected based on the main flow of current. This can be demonstrated by releasing a conservative solute such as a dye and recording its passage at successive distances downstream. Tracer quantities decline due to mixing and dilution. In addition, the time between tracer release and its downstream arrival is longer than would be predicted from water velocity in the main channel, and the peak broadens as one proceeds downstream.

One can model the complex effects of surface–subsurface exchange and back eddies by assuming that solutes are temporarily retained in a "transient storage zone" of slowly moving or even stationary water. Solute diffuses into the storage zone during the initial passage of the pulse, and is released back into the stream as the pulse passes and stream concentrations decline. The equations to describe the temporal and spatial changes in the concentration of a conservative solute, including transient storage are:

$$\frac{\partial C}{\partial t} = -v\frac{\partial C}{\partial x} + D\frac{\partial^2 C}{\partial x^2} + \alpha(C_S - C) \qquad (11.2)$$

$$\frac{\partial C_S}{\partial t} = -\alpha\frac{A}{A_S}(C_S - C) \qquad (11.3)$$

where A (m^2) is the main channel cross-sectional area and A_S is the cross-sectional area of the modeled storage zone. The rate of dispersion of solute in or out of this zone is proportional to the difference between solute concentration in the storage zone (C_S) and in the water column (C), and the transient storage exchange coefficient (α). These equations can become more complex when other terms like groundwater inputs are included (Webster and Valett 2006). Adding a term for transient storage permits the model to account for significant features of the observed passage of a solute pulse that Equation 11.1 is unable to mimic. Specifically, measured passage of a tracer pulse usually shows the rising shoulder of the actual pulse to be more gradual and the descending tail to be prolonged relative to the symmetrical curve generated by the first equation.

It should be recognized that these models are empirically useful descriptions of observed dynamics in which transient storage clearly takes place. However, the storage zone component of the model is an abstraction. In contrast to the cross-sectional area of the stream channel, which can be measured directly, A_S is determined by fitting the model to observed solute dynamics. Nonetheless, storage zones exist and are numerous. Bencala and Walters (1983) recognized five in their study of solute transport in a small mountain stream, including turbulent eddies generated by large-scale bottom irregularities, large but slowly moving recirculating zones along the sides of pools, small but rapidly recirculating zones behind flow obstructions, side pockets, and flow in and out of beds of coarse substrate.

11.2.2 Nutrient spiraling

The processes of advection, dispersion, and transient storage included in the above models describe only the influences of hydrology and the channel upon the downstream transport of a solute. However, reactive solutes experience additional processes that retard their downstream passage. By comparing the passage of reactive and conservative solutes, the magnitude of these additional processes can be quantified. Some reactive solutes may have their dynamics governed solely by physical–chemical processes such as sorption–desorption, whereas nutrients are strongly influenced by biological processes, although physical–chemical processes also can be important. To accommodate these processes of uptake and mineralization or release of a reactive solute, the hydrologic models of the previous section must be modified to include an uptake rate and a release or mineralization rate. By adding these additional terms to Equation 11.1, changes in the concentration of a solute as it passes a point over time is modeled as:

$$\frac{\partial C}{\partial t} = -v\frac{\partial C}{\partial x} + D\frac{\partial^2 C}{\partial x^2} - \lambda_c C + \frac{1}{z}\lambda_b C_b \quad (11.4)$$

Additional terms include depth (z), the dynamic uptake rate (λ_c), the mineralization rate (λ_b), and the mass per unit of area of immobilized nutrient in the streambed (C_b) (Webster and Valett 2006).

The complete cycle of a nutrient atom as it is transported downstream includes its transformation from inorganic to organic form by biological uptake and its subsequent release and mineralization (Newbold et al. 1981). Therefore, spiraling length (S, in meters) is the sum of the distance traveled in dissolved inorganic form in the water column, called the uptake length (S_W), and the distance traveled within the biota before being mineralized and returned to the water column, called the turnover length (S_B) (Figure 1.6).

$$S = S_W + S_B \quad (11.5)$$

Uptake length is a measure of nutrient limitation and efficiency of nutrient use in streams, with short travel distances indicating high demand relative to supply and greater retentiveness by the stream ecosystem, whereas long travel distances indicate the opposite. Turnover length is a measure of distance traveled by the atom within the biota until its eventual release back into the water column, thus completing one spiral passage downstream. The biological compartment generally is associated with the streambed, as attached microorganisms, periphyton, and benthic invertebrates. Typically an atom will travel the greatest distance in the water column, and so one expects S_W to be much greater than S_B. In fact, field studies have shown that S_W represents the greatest fraction of total spiraling distance, so most studies focus on uptake length and related metrics including uptake velocity and areal uptake rate. In addition, the uptake of dissolved available nutrient from the water column is easier to quantify than its subsequent release.

Uptake length is estimated using plateau values of the concentration of a reactive solute at successive points downstream from its release (Figure 11.5). Certain conditions must be met and are evidenced by the simultaneous arrival of a definite plateau of both conservative and reactive solute. Plateau concentrations of the reactive solute, corrected for dilution by dividing through by the conservative tracer, will form a straight line plot against distance on a logarithmic scale. The slope (k_w) is $1/S_W$. The term k_w, also known as the longitudinal uptake rate, is the dynamic uptake rate (λ_c) of Equation 11.4 divided by velocity (v):

$$k_w = \frac{\lambda_c}{v} \quad (11.6)$$

Uptake length depends strongly on discharge and velocity and thus varies with stream size, and so it is desirable to standardize S_W by converting it to a measure of the uptake velocity (v_f) of the solute. Also referred to as the mass transfer coefficient, v_f quantifies the velocity at which a molecule moves from the water column to the stream bottom as a result of biotic or abiotic processes. It is calculated as:

$$v_\text{f} = \frac{v\ z}{S_W} \tag{11.7}$$

Because it includes depth and velocity in its calculation, v_f standardizes S_W for discharge and so is best suited to comparisons across stream ecosystems (Davis and Minshall 1999, Webster and Valett 2006). By combining v_f and nutrient concentrations in streamwater, the amount of inorganic nutrient immobilized by the streambed per unit of time can be expressed as an areal uptake, *U*, in the units mass per area per time, as:

$$U = v_\text{f}\ C \tag{11.8}$$

Uptake velocity quantifies the benthic demand for a nutrient in relation to its supply.

11.2.3 Methodological issues

Estimation of nutrient uptake rates in streams requires the release of a measurable pulse of a nutrient. This can be accomplished by adding a large quantity of nutrients so that the pulse is detectable above ambient concentrations or through the release of trace amounts of stable or radioactive isotopes (Mulholland et al. 2002). Short-term nutrient additions, typically with orthophosphate-P, ammonium-N, or nitrate-N, are relatively simple and inexpensive. The passage of the nutrient pulse, corrected for dilution from the simultaneous release of a conservative solute, is the basis for estimating S_W and v_f. However, nutrient addition is likely to saturate biological uptake, and so this method may overestimate S_W and underestimate v_f. The release of isotopes avoids this problem because only small quantities are needed. In a comparison of methods in a small woodland stream, using an isotope-labeled nitrate release with and without simultaneous nitrate enrichment, transport distance was estimated to be 36 m using the tracer alone and 100 m when the stream was enriched (Mulholland et al. 2004).

Experimental releases of ammonium and nitrate labeled with the stable isotope ^{15}N are becoming widely used, but because only the radioactive isotope of P (^{32}P) is readily available and its release into the environment is heavily restricted, nutrient tracer studies are presently conducted almost exclusively with N. Although tracers have obvious advantages, they are expensive, especially for larger streams that would require greater quantities of stable isotope. Short-term nutrient releases are a less costly alternative, especially when multiple comparisons are needed across sites or over time (Tank et al. 2006), and can be improved upon by adding the smallest amount that can be detected and by conducting a series of additions using different concentrations (Mulholland et al. 2002, Payn et al. 2005).

In addition to providing more reliable estimates of uptake lengths and rates, tracers provide the opportunity to quantify transformations among nutrient forms and the role of different biotic compartments in nutrient uptake and retention (Mulholland et al. 2000, Webster et al. 2003). For example, by following the movement of ^{15}N-labelled ammonium in a Kansas prairie stream, Dodds et al. (2000) were able to measure not only uptake of ammonium but also its rate of transformation to nitrate, and trace the amount of N assimilated by primary producers and microbes and subsequently into primary consumers and predators. Although nutrient addition studies provide some insight into transformations by comparing the relative amounts of different forms of a nutrient entering and exiting an enriched stream reach, tracer studies are ideal for quantifying nutrient turnover within compartments.

11.3 Factors Influencing Nutrient Dynamics

The capacity of lotic ecosystems to influence the dynamics of nutrients during their downstream passage depends upon abiotic and biotic processes that determine uptake rates and transformations, and these in turn are governed by a number of environmental factors, especially discharge and its variability. Meyer and Likens (1979) suggest that streams can occupy very different states in terms of nutrient processing: a throughput mode at high discharge, and a processing-retention mode at low flows. Streams with high rates of nutrient inputs relative to processing capacity and flashy flows will be in throughput mode most of the time, whereas streams with low nutrient inputs relative to demand and more stable flows will be in processing-retention mode more of the time, especially during the growing season. Channelized agricultural streams are a good example of the former (such as Illinois farm streams, Royer et al. 2004), and undisturbed small woodland streams of the latter (such as Walker Branch, Tennessee, Mulholland 2004).

Even under the conditions of base flow when nutrient studies typically are conducted, rates of nutrient uptake and transformation vary considerably. A ^{15}N tracer study in headwater streams from biomes throughout North America reported wide variation in rates of ammonium uptake and its nitrification to nitrate (Peterson et al. 2001), and equally wide variation was observed among multiple streams within the Hubbard Brook Experimental Forest, New Hampshire (Bernhardt et al. 2002). Stream size explains some of this variation, because smaller streams have a greater area of streambed relative to water volume. In addition, abiotic exchange mechanisms are influenced by sediment characteristics, pH, and nutrient concentrations in streamwater, and biotic uptake and release varies with overall biological productivity. Current evidence documents that in small streams that are not overly enriched, instream processes exert considerable control over nutrient cycling and transport under low-flow conditions. Evidence also suggests that transport dominates instream processing to a greater degree in larger rivers, and transport has primacy during episodic high flows when the majority of annual nutrient export occurs.

11.3.1 Abiotic controls of nutrient dynamics

Precipitation and sorption onto sediments are physical–chemical processes that can have a strong influence upon phosphate and a lesser influence upon ammonium-N, whereas nitrate-N apparently is little affected by physical–chemical removal. Sorption of phosphate ion onto charged clays and charged organic particles occurs when SRP concentrations in stream or sediment pore water are high relative to an equilibrium SRP value of no net exchange, and desorption occurs when SRP concentrations are lower (House 2003). Phosphorus sorption to suspended sediments is rapid, and is fastest with smaller particles such as silts compared with coarser particles. Because of the association of P with sediments, amounts of particulate and total P in streamwater often vary temporally in parallel with concentrations of suspended sediments (Jordan et al. 1997, Ekholm et al. 2000). The affinity of orthophosphate for sediments is also responsible for the link between sediment and P concentrations in surface runoff. Once this particulate inorganic P enters the river, lower concentrations of dissolved inorganic P in streamwater result in desorption and thus an increase in bioavailable P.

Sorption–desorption processes can act as a buffer on streamwater nutrient concentrations by removing them from solution when concentrations are high and releasing them when concentrations are low. In a study of N dynamics in Bear Brook, Richey et al. (1985) concluded that sorption of ammonium to sediments was a significant storage during summer and autumn.

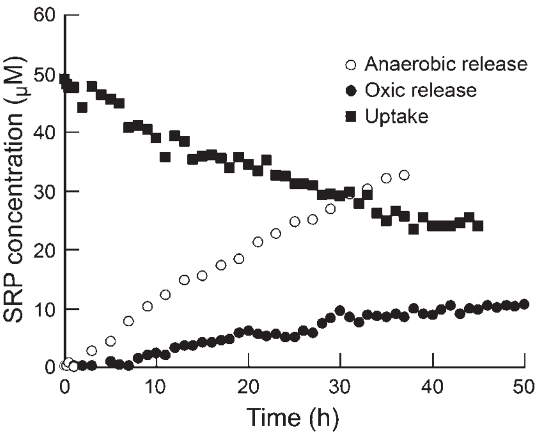

FIGURE 11.6 Net uptake and release of soluble reactive phosphorus (SRP) by river sediments. Uptake (■) was measured after spiking the overlying water with orthophosphate. The greater release of SRP under anaerobic (○) compared with aerobic (●) conditions is attributed to the dissolution of phosphate that had precipitated with Fe hydroxide minerals. (Reproduced from House 2003.)

Nutrients sorbed onto sediments can be released back into the water column after weeks or months (Peterson et al. 2001). In streams that receive high nutrient inputs such as from waste water treatment plants, storage of sorbed ions in the sediments can be substantial. In a highly enriched Arkansas stream below a wastewater treatment plant, P dynamics were dominated by short-term, abiotic storage and release processes, which acted to stabilize high P concentrations over time (Haggard et al. 2005). Stream sediments may be a temporary storage site for ammonium, as Triska et al. (1994) showed by periodically retrieving sediment-filled bags from a third-order gravel and cobble bed stream in California. Comparison of the amount of ammonium extracted from the sediments to that present in interstitital water showed that sorbed ammonium was highest during summer base flows and lowest during winter stormflow.

In addition to sorption–desorption processes, under aerobic conditions both SRP and dissolved organic P may complex with metal oxides and hydroxides to form insoluble precipitates, and under anaerobic conditions this phosphate is released back into the water (Figure 11.6). Because the extent of the anaerobic zone varies seasonally and spatially with the amount of organic matter in the sediments and thus the extent of microbial respiration, the availability of dissolved phosphate varies accordingly. Phosphorus can also coprecipitate with calcite under high pH conditions that result from decreases in CO_2 or HCO_3^- levels due to the photosynthetic activity of macrophytes and benthic algae (Mainstone and Parr 2002, House 2003).

11.3.2 Hydrologic processes

Variation in discharge on seasonal and annual timescales has a strong influence over whether nutrients are stored or exported. Based on estimates of inputs, outputs, and storage of P in Bear Brook, New Hampshire, Meyer and Likens (1979) estimated that 48% of annual inputs and 67% of exports occurred during 10 days of the water year. In contrast, phosphorous accumulated for 319 days of the year of study, and this storage presumably increased the opportunity for instream processing. Nutrients accumulate during low flows because they occur mainly in association with fine particulates, whose transport is dependent upon discharge, and in biofilms, whose biomass accumulates during periods of low flow.

Uptake length, the distance traveled by a nutrient atom before immobilization, increases with discharge and water velocity, as was documented in a cross-biome comparison of ammonium S_W in 11 North American rivers (Figure 11.7) (Peterson et al. 2001, Webster et al. 2003). The uptake length for ammonium and particulate N also increased with stream size within the Kuparuk River watershed of Alaska in response to increases in water velocity and depth (Wollheim et al. 2001). Similar results were obtained in two New Zealand streams, where temporal variation in uptake lengths of ammonium, nitrate, and phosphate was largely explained by changes in water velocity and depth (Simon et al. 2005). An increase in uptake length at higher discharge likely is the consequence of the reduced opportunity for solutes in streamwater to interact with sediment surfaces and biofilms (Peterson et al. 2001). Because of the strong dependence of S_W on stream velocity and depth, uptake velocity v_f is increasingly preferred in order to standardize for these variables.

Storage zone mechanisms constitute an important hydrologic influence over nutrient dynamics. Transient storage typically takes place over short distances and timescales, and includes both hyporheic and surface areas (Harvey et al. 1996, Brunke and Gonser 1997). Transient storage has the potential to increase nutrient processing by slowing the rate of downstream transport and increasing the exposure of dissolved nutrients to locations of high nutrient uptake. This effect is likely to be greatest when storage is the result of surface–subsurface exchange (Figure 11.8) because water entering sediments will come in close contact with biofilms, whereas storage in pools and back eddies is less likely to have this effect (Hall et al. 2002).

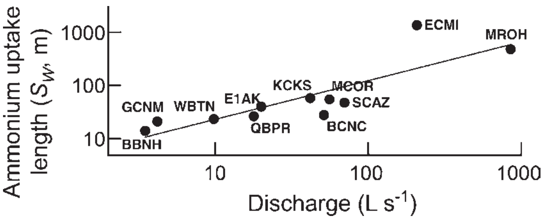

FIGURE 11.7 Relationship between uptake length and stream discharge from ^{15}N-ammonium tracer additions at 11 stream sites in the United States: Ball Creek, North Carolina (BCNC); West Fork Walker Branch, Tennessee (WBTN); Sycamore Creek, Arizona (SCAZ); Bear Brook, New Hampshire (BBNH); Gallina Creek, New Mexico (GCNM); Quebrada Bisley, Puerto Rico (QBPR); Kings Creek, Kansas (KCKS); Eagle Creek, Michigan (ECMI); Mack Creek, Oregon (MCOR); E1 Outlet, Alaska (E1AK); East Fork Little Miami River, Ohio (MROH). (Reproduced from Webster et al. 2003.)

Transient storage varies with numerous stream features including channel geomorphology, stream size, discharge, and flow obstructions (D'Angelo et al. 1993, Harvey et al. 1996, Morrice et al. 1997). It is greatest in headwater streams and declines with increasing stream size and discharge, most likely because of reductions in channel complexity and the increased cross-sectional area of the wetted channel. From studies of streams in the Appalachian and Cascade Mountains, estimates of A_S/A were greatest in first-order streams, where they averaged 1.2, and lowest in fifth-order sites, where A_S/A was 0.6 in an unconstrained reach and 0.1 in a constrained reach (D'Angelo et al. 1993). In the eighth-order upper Willamette River, Oregon, which has extensive gravel beds promoting hyporheic flow, A_S/A averaged 0.28 and was highest in two unconstrained reaches where the river was able to rework its gravel bed (Fernald et al. 2003). The size of the transient storage zone varied from 0.16 to 0.71 among 13 forested headwater streams in New Hampshire (Hall et al. 2002), somewhat lower than at Appalachian sites and consistent with the shallow hyporheic zone of New

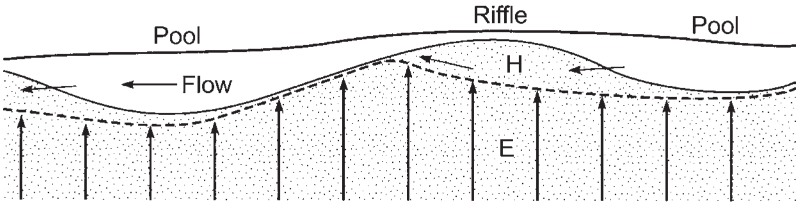

FIGURE 11.8 Postulated distribution of hyporheic zones (H) and groundwater zones (E) beneath a pool–riffle–pool sequence in a Michigan river, as inferred from temperature profiles. (From White et al. 1987.)

Hampshire sites. Values of A_S/A greater than 1 have been recorded in streams with highly permeable bed material (Valett et al. 1996, Martí et al. 1997, Butturini and Sabater 1999). In an Antarctic stream fed by glacial meltwater, A_S/A exceeded 1 in all stream reaches due to high gradient and porous alluvial materials (Runkel et al. 1998).

Transient storage within the stream channel is highly influenced by obstructions such as boulders and wood. When vegetation and wood were removed from a vegetated agricultural stream and a forested blackwater stream, transient storage area decreased by 61% and 43%, respectively (Ensign and Doyle 2005). When flow baffles were then added to create in-channel transient storage, A_S increased more than threefold in the agricultural stream and more than doubled in the blackwater stream.

Although transient storage is expected to increase uptake rates due to longer exposure of dissolved nutrients to sediments and biofilms, results are equivocal. Phosphorus uptake measured with the stable isotope of P (^{33}P) in two forested streams was greater in the stream that had deeper sediments and so presumably also had a larger transient storage zone (Mulholland et al. 1997). Uptake velocities for ammonium and phosphate increased markedly following the addition of flow baffles to the blackwater stream studied by Ensign and Doyle (2005). Valett et al. (1996) found a positive relationship between transient storage and uptake in a stream in New Mexico with a large storage zone, but both were also correlated with discharge, and so the causal relationship is unclear. In Sycamore Creek, Martí et al. (1997) saw no relationship between nutrient uptake length and size of the transient storage zone, even though the latter varied greatly following a flood disturbance. In a comparison of 13 forested headwater streams in New Hampshire, transient storage explained only 35% of between-stream variation in ammonium v_f during summer months and 14% on an annual basis, possibly because storage occurred primarily in pools owing to the shallow hyporheic zone of these bedrock streams (Hall et al. 2002). Similarly, an interbiome study comparing ten undisturbed streams reported a low correlation between ammonium uptake and transient storage (Webster et al. 2003). In three New Zealand streams, SRP and nitrate uptake were uncorrelated with transient storage, and here again surface pools accounted for a large proportion of transient storage (Niyogi et al. 2004).

In some circumstances, including when the hyporheic zone is minimal and surface algae and biofilms are productive, transient storage associated with the bed surface may be of primary importance. By adding NaCl as a conservative tracer, Mulholland et al. (1994) showed that transient storage was greater in experimental streams with high biomass of filamentous diatoms and blue-green algae compared with streams that contained low algae biomass. In a meltwater stream in the McMurdo Dry Valleys, Antarctica, nitrate removal in the hyporheic zone accounted for 7–16% of the total loss, and the majority was believed to be taken up by algal mats on the stream surface. Hyporheic transient storage was a small fraction of stream channel area in a Mediterranean stream and so did not play an important role in nutrient uptake, which likely occurred in surface sediments (Butturini and Sabater 1999). In a study conducted in 12 tropical streams in Brazil, reaches with greater A_S/A and longer water residence times such as pools and marshes showed higher ammonium uptake rates than did runs and meanders (Gucker and Boechat 2004). Because transient storage occurred mostly in surface waters and accounted for 52–85% of ammonium uptake, surface transient storage zones were important locations of ammonium retention.

11.3.3 Biotic controls of nutrient cycling

Nutrient uptake and cycling is expected to vary directly in response to biotic demand by primary producers and heterotrophic microorganisms in biofilms and other sites of high biological activity, and thus ultimately be influenced by the environmental factors that control rates of primary and microbial production. More productive systems should cycle nutrients at higher rates, owing to higher uptake rates as well as higher rates of regeneration due to consumption, excretion, and egestion and subsequent mineralization. Animal consumers such as herbivores can stimulate rates of production by increasing the turnover of producers and regenerating nutrients that help to meet producer demand. The dissimilatory activities of nitrifying and denitrifying bacteria change the concentrations of various forms of inorganic N, enhancing or limiting its bioavailability. The efficiency with which stream ecosystems are able to utilize, retain, and recycle nutrients is largely determined by environmental factors that influence uptake and assimilation by the biota and, in the case of N, the various biologically mediated transformations that determine its chemical form.

11.3.3.1 Assimilatory uptake

The influence of the benthic algal community upon nutrient uptake is nicely illustrated by Grimm's (1987) study of successional events in Sycamore Creek, Arizona. Following a flood that eliminated virtually all of the biota, biomass accumulated rapidly and then more slowly as the system acquired a thick periphyton mat and high densities of invertebrates. Measurements of hydrologic inputs and outputs of N and N storage in the biota documented substantial retention of inorganic N within the 90 m reach due to N uptake and accumulation in living tissue. In a subsequent study of the same system using nitrate and chloride additions to measure uptake length, Martí et al. (1997) showed that nitrate S_W was short relative to other published studies, consistent with evidence that N was limiting in this desert stream. Nitrate uptake length in Sycamore Creek doubled after a modest midsummer flood, but the system returned to low flow conditions within hours and algal recovery occurred within weeks. Using streamwater N concentrations sampled during a much larger flood studied by Fisher et al. (1982), Martí et al. determined that N retention is minimal immediately after a flood, but recovers quickly as the biota become reestablished (Figure 11.9). These studies clearly show that nutrient retention depends on the development of the algal mat, which in turn is strongly influenced by disturbance frequency in this desert stream. The composition of the mat was also found to be important, as N retention was significantly lower when N-fixing cyanobacteria made up greater than 10% of periphyton.

Rates of uptake of ammonium and nitrate and the relative importance of assimilatory and dissimilatory processes vary widely among studies that have used ^{15}N tracer releases in small streams. In a comparative study of 11 headwater streams from biomes throughout North America, removal of ammonium was attributed primarily to assimilation by autotrophs, bacteria, and fungi, and sorption to sediments (70–80% for

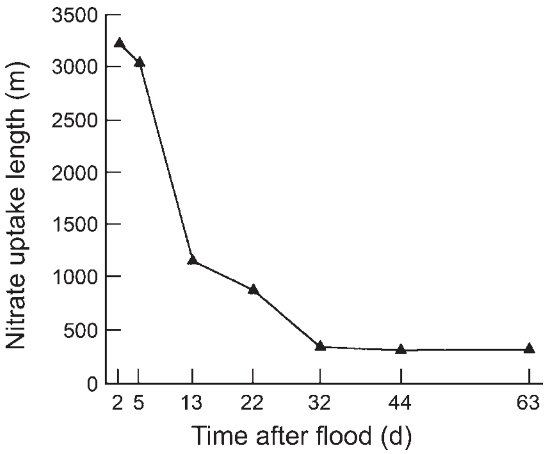

FIGURE 11.9 Decline of nitrate uptake length as the periphyton mat and associated organisms recovered following a large flood in Sycamore Creek, Arizona, estimated from natural declines in nitrate concentrations in streamwater. (Reproduced from Martí et al. 1997.)

all combined ammonium uptake on the stream bottom), and secondarily to nitrification (20–30%) (Peterson et al. 2001, Webster et al. 2003). Rates of uptake and nitrification varied as widely among forested New Hampshire streams as was observed in the cross-biome study of Peterson et al. (Bernhardt et al. 2002). Variation in stream hydraulic features and availability of organic C likely are responsible for much of this variation, and there is some evidence that rates of nitrification may be reduced when inputs of nitrate are high.

Biotic demand has been shown to influence removal of phosphate, particularly during periods when streams receive fresh inputs of leaf litter. Phosphorus uptake lengths were negatively correlated with amount of leaf litter in a woodland stream, reflecting microbial demand associated with decaying leaves (Mulholland et al. 1985a). When sediment microbes were killed using chlorine in streamside artificial channels, uptake lengths more than doubled, confirming that biotic uptake influenced spiraling distance (D'Angelo et al. 1991). When leaf litter and then wood was removed from an Appalachian headwater stream, nutrient uptake lengths increased substantially in comparison to a reference stream (Webster et al. 2000). A comparison of two streams that differed in community respiration (CR) found a higher demand for P in the stream with the higher CR (Mulholland et al. 1997).

Hydrology is a key environmental variable affecting nutrient dynamics in streams, influencing inputs, the magnitude of transient storage, and, acting through velocity and discharge, the abundance of primary producers and the retention of particulate organic matter. Collectively these effects of streamflow determine whether the stream is shifted toward throughput or processing mode as the Sycamore Creek example illustrates. In Antarctic streams, where algal mats dominated by filamentous cyanobacteria decrease during periods of extreme low flows as well as in response to scouring high flows, nutrient retention varies accordingly (McKnight et al. 2004). Other environmental variables can limit primary producers (Section 6.1.1), of course, and thus also reduce nutrient uptake. In a comparison of forested versus logged reaches of a Mediterranean stream, Sabater et al. (2000) found greater algal biomass in open relative to shaded reaches, and uptake lengths for ammonium and P also were shorter in the open reaches. Retention efficiency was greater overall for ammonium than for phosphate, but the latter was more affected by shading (Figure 11.10). The uptake velocity for P was correlated to primary production in both reaches, suggesting that its retention was due to algae. However, v_f for ammonium was poorly correlated with algal measures, indicating that microbial heterotrophic

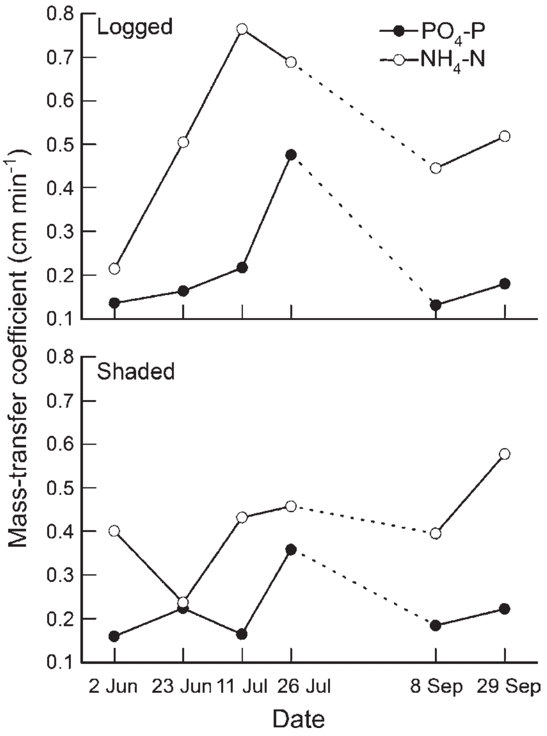

FIGURE 11.10 Temporal variation in ammonium and phosphate mass transfer coefficients (v_f) in logged and shaded stream reaches. (Reproduced from Sabater et al. 2000.)

processes or abiotic mechanisms were responsible. Environmental factors that influence algal and microbial production often vary seasonally, leading to changes in nutrient uptake and retention. In two tussock grassland streams in New Zealand, uptake velocity was highest during the spring and lowest during fall and early winter, which corresponded to changes in algal abundance (Simon et al. 2005).

Aquatic macrophytes and bryophytes are capable of removing substantial amounts of nutrients from flowing water. Meyer (1979) recorded significant removal of P as a pulse passed over a bryophyte bed in a forested stream in New Hampshire. In Walker Branch, Tennessee, ammonium uptake by the bryophyte *Porella* represented 41% of total N retention at the end of a 6-week ^{15}N addition experiment (Mulholland et al. 2000). Although laboratory studies show that rooted aquatic plants reduce porewater nutrient pools by their metabolic uptake, field studies in the middle Hudson River showed either no such reduction due to submerged aquatic vegetation, or enrichment of nutrient porewater pools (Wigand et al. 2001). The explanation for this apparent contradiction is thought to be the accumulation of allochthonous particulate organic matter in vegetation beds and its mineralization by microbes, which replenishes pore water concentrations. In effect, the uptake and sequestration of nutrients by macrophyte beds is masked by processes that promote replenishment of porewater nutrients, thereby enhancing nutrient retention in the river system (Wigand et al. 2001). A similar effect has been observed in the Spree River, Germany, where macrophyte beds slowed currents and increased water residence time, enhancing organic matter deposition and contributing significantly to monthly P retention (Schulz et al. 2003).

Seasonality in biological activity has been shown to impose seasonal trends on nutrients. In a forested headwater stream in Tennessee, streamwater nitrate and phosphate concentrations were lowest in autumn and early spring, corresponding to periods of highest heterotrophic and autotrophic activity, respectively (Mulholland 2004). High uptake rates are seasonally driven by microbes colonizing fresh leaf litter and the photosynthetic demands of algae and bryophytes, and are reduced by winter discharges that flush organic matter and by shading due to summer leaf-out, respectively. In this system, instream processes can remove up to 20% of the nitrate and 30% of the phosphate that enters the stream annually (Mulholland 2004).

Nutrient uptake rates generally increase with increases in nutrient concentrations until supply exceeds biotic demand, at which point saturation of nutrient uptake occurs (Dodds et al. 2002, Simon et al. 2005). In agricultural streams of the Midwestern US where nutrient concentrations were 10–100 times greater than in pristine systems, nitrate uptake appeared to be saturated because uptake was not higher at the more enriched sites and v_f declined at sites with greater concentrations. Uptake of P and ammonium were not saturated because both increased with higher water column concentrations, but declining v_f at high concentrations suggests that both may have been approaching saturation (Bernot et al. 2006). At the highly enriched site below a sewage treatment plant in Arkansas, described previously, biological uptake had no discernible effect on P concentrations; instead, buffering by abiotic uptake and release mechanisms stabilized streamwater concentrations (Haggard et al. 2005).

11.3.3.2 Dissimilatory transformations

By transforming ammonium into nitrate, nitrifying bacteria can influence the concentrations of each form of N in streamwater as well as the possibility of its eventual permanent removal through denitrification to nonreactive N_2. Nitrification accounted for over half of total ammonium removal in Eagle Creek, Michigan (Hamilton et al. 2001), and in Quebrada Bisley, Puerto Rico

(Merriam et al. 2002), but for <20% in Walker Branch, Tennessee (Mulholland et al. 2000). The resultant nitrate can be immobilized by the biota, exported downstream, or transformed into N_2 gas by denitrifying bacteria. Nitrification was implicated as a source of nitrate in a Mojave desert stream, where streamwater nitrate concentrations were two times greater than expected from groundwater inputs (Jones 2002). Mineralization of organic N to ammonium followed by nitrification to produce nitrate was thought to be responsible for the additional nitrate in streamwater. Because nitrifying bacteria require aerobic conditions, nitrification rates should be greater where subsurface flows provide oxygenated water, such as in shallow, disturbed sediments. Nitrification rates within the hyporheos of Sycamore Creek were highest in regions of downwelling, which presumably supplied organic C and oxygenated water (Jones et al. 1995). In this system, most of the N demand of surface algae was met by hyporheic mineralization of ammonium and subsequent nitrification, demonstrating the importance of the coupling of surface and subsurface systems.

The reduction of nitrate to nonreactive N_2 gas by denitrifying bacteria is an important pathway in the N cycle because it represents the only process that permanently removes reactive N from the stream network. Denitrification rates are enhanced under conditions of high nitrate and organic matter availability and low oxygen concentrations. Denitrifying bacteria can be found in association with FBOM and senescing mats of *Cladophora* and cyanobacteria, where anoxic zones develop that bacteria can utilize (Triska and Oremland 1981, Kemp and Dodds 2002a, b). Sediment-rich streams in agricultural watersheds exhibit high denitrification rates (David and Gentry 2000, Royer et al. 2004), but nitrate levels nonetheless remain high owing to very high inputs of nitrate from fertilizer.

Denitrification rates tend to be higher under conditions of low flows and shallow depths, owing to greater interaction of water with sediments, and so the smaller and shallower lower-order tributaries likely play a disproportionate role in nitrate removal (Alexander et al. 2000). In a headwater stream in Tennessee, denitrification accounted for 16% of total N uptake (Mulholland et al. 2004), and estimates from individual stream reaches generally find N removal attributed to denitrification to be <20% (Seitzinger et al. 2002). Based on a review of published studies of N loss determined by direct measurements and mass balance estimates, Seitzinger et al. conclude that the amount of N lost from all streams of a catchment is much greater than the fraction removed from a single reach, because of the cumulative effect of N removal along the entire flow path. For their model constructed for rivers of the Northeastern US, from 37% to 76% of N inputs were lost by denitrification along the river network, about half in first through fourth-order streams, and the remainder in higher-order rivers. This differs from the findings of Royer et al. (2004) reported above, who suggest that flood plains and wetlands may be more important than headwater streams as locations of denitrification in the agricultural Midwest.

The measurement of denitrification rates is an area of continuing methodological improvement, but still faces measurement challenges. Direct measurement requires field chambers to enclose sediment cores or transport of sediment slurries to the laboratory, both of which may introduce artifacts (Martin et al. 2001). Recently developed ^{15}N tracer techniques (Rysgaard et al. 1993) applied to whole stream reaches (Mulholland et al. 2004) allow direct measurement of nitrate uptake and denitrification rates by quantifying both the removal of $^{15}NO_3$-N from the water column and the direct labeling of $^{15}N_2$ and $^{15}N_2O$ gases. Although the loss of nitrate from streamwater commonly is attributed to denitrification, dissimilatory reduction of nitrate to ammonium (DNRA) has recently been proposed as an alternative pathway. Because the end product is ammonium rather than N_2

gas, this process does not result in permanent removal of N from the stream system (Whitmire and Hamilton 2005).

11.3.3.3 Role of consumers

The animal community directly influences nutrient cycling by consumption and assimilation of algal and bacterial production, and by the subsequent release of nutrients by egestion of feces and excretion of urine. By consuming lower trophic levels, especially primary producers and heterotrophic microorganisms, animal consumers enhance the rate of regeneration of nutrients by excretion and egestion, thus replenishing the pool of available inorganic nutrients. Most excreted nutrients are inorganic forms such as ammonium and phosphate, and thus are available to primary producers, but some nutrients such as urea are excreted as organic forms. Egested materials also are in organic forms and so must undergo decomposition and mineralization by microbes to be available for uptake and assimilation. Because nutrient availability can strongly limit overall productivity of a stream ecosystem, high rates of consumption and secondary production can stimulate nutrient cycling and thus help to maintain a system in a highly productive state.

Sycamore Creek, Arizona, is an example of a stream that sustains very high rates of secondary production despite being strongly N limited (Grimm and Fisher 1986), evidence of a high rate of nutrient regeneration and probably of reingestion of feces (Fisher and Gray 1983). Based on laboratory estimates of mass-specific excretion and egestion rates, Grimm (1988) estimated that up to one third of ingested N was converted to ammonium and so was readily available to autotrophs. About half of ingested N was egested as fecal material and presumably was recycled via reingestion by consumers, or became available for uptake following leaching or microbial breakdown. Although Grimm was unable to determine the exact amount of recycled N, which she estimated to fall between 15% and 70% of whole stream N retention, even the lower value implies a significant role for animals in nutrient regeneration in this highly productive, N-limited system. Consumer excretion was also shown to make a major contribution to the nutrient demand in a highly productive geothermal spring stream in Yellowstone National Park, with warm temperatures throughout the year and high primary productivity due to abundant filamentous algae and vascular plants (Hall et al. 2003). The exotic snail *Potamopyrgus antipodarum* consumed 75% of algal production and its excretion supplied two thirds of the algal mat's ammonium demand. High snail biomass rather than high per-biomass rates of consumption and excretion explained the snail's dominant role in nutrient flux in this atypical system.

Retention versus release of nutrients by consumers is influenced by body size, temperature, and the consumer's metabolic demand. The amount of nutrients excreted per unit body mass and time usually decreases with increasing body mass as a consequence of the scaling of metabolism with body size (Vanni 2002). Excretion rates increase with temperature due to the influence of temperature on metabolic rate. For animals to maintain relatively constant nutrient content of their body mass, they will incorporate nutrients at a rate necessary to meet their metabolic needs and excrete nutrients not needed for growth (Sterner and Elser 2002, Cross et al. 2005). Ecological stoichiometry theory further asserts that animals feeding on a nutrient-poor diet will retain more nutrients relative to those feeding on a nutrient-rich diet, and the ratio of nutrients retained versus excreted should reflect any imbalance between the nutrient requirements of the consumer and the nutrient ratio in the food supply. In general, the N/P ratio released by an animal should be negatively correlated with that of its body mass and positively correlated with that of its food (Vanni 2002). A comparison of excretion rates and ratios for N and P for 28 species of fishes and amphibians in Río las Marías, an Andean piedmont stream in Venezuela, supports expectations from stoichiometry theory (Vanni et al. 2002). Phosphorus excretion rates and N/P excretion ratios were negatively correlated with body P content and body N/P ratios, respectively (Figure 11.11). Total excretion by the assemblage of consumers in this stream was estimated to meet 49% of algal demand for N and 126% of algal demand for P. Interestingly, armored catfish have a very high body content of P, consume a stoichiometrically imbalanced diet that is low in P, and produce excretions of low P content and high N/P ratios (Hood et al. 2005). As a result, these herbivorous fishes appear to act as P sinks, decreasing the availability of P for algae, which in turn may result in lowering the quality of food available to consumers.

Animals also transport nutrients among habitats and across ecosystems by their movements and migrations. Emergence of the adult stages of aquatic insects is one such process but various authors agree that it is a small fraction of overall nutrient transport (<1%, Meyer et al. 1981, Grimm 1987, Naiman and Melillo 1984, Triska et al. 1984), although potentially important to animal consumers of the riparian zone as a supply of organic C (Section 10.4.1). In contrast, spawning runs of anadromous fish may import substantial amounts of marine-derived nutrients to streams and lakes by their excretion, release of gametes, and their own mortality, especially if many or all die after reproducing. Spawning salmon provide an important nutrient subsidy to freshwater ecosystems of the Pacific Northwest that are generally nutrient-poor (Naiman et al. 2002). Where salmon are abundant, a large proportion of the N in the stream biota likely is derived from spawning fish (Bilby et al. 2001), and significant quantities appear in riparian vegetation and a host of animal consumers. In Sashin Creek, Alaska, isotope analysis showed that N and C derived from a spawning run of Pacific salmon were incorporated into periphyton, macroinvertebrates, and fish (Kline et al. 1990). In a wine-growing region of California, cultivated grapes adjacent to Chinook salmon spawning sites obtained as much as 25% of their N from marine sources (Merz and Moyle 2006). A comparison of an Alaskan stream in which downstream reaches contained salmon but upstream reaches did not, found that salmon-supporting reaches had higher SRP concentrations, epilithon abundance, and chironomid biomass but mayfly biomass was lower (Chaloner et al. 2004). Because of declines in salmon populations, it is estimated that only 6–7% of the marine-derived N and P that historically was transported into the rivers of the Pacific Northwest by salmon is currently reaching those rivers (Gresh et al. 2000).

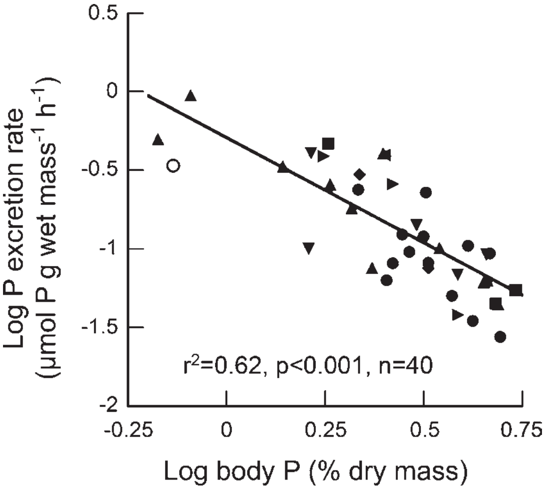

FIGURE 11.11 Relationship between phosphorus body content and excretion rate in fishes and amphibians in Río las Marías, Venezuela. (Reproduced from Vanni et al. 2002.)

Animal consumers also affect nutrient cycling indirectly, through their influence on benthic algal biomass, organic matter dynamics, and prey assemblages (Vanni 2002). Whenever grazing sharply reduces algal and biofilm biomass, uptake rates are expected to decrease and spiraling distance to lengthen, whereas moderate grazing that stimulates primary and microbial production should have the opposite effect. Consumption of algae and leaf litter by the snail *Elimia clavaeformes* in artificial channels stimulated mass-specific metabolic rates of microbial populations, but periphyton and microbial biomass were so reduced that overall biotic uptake of P declined (Mulholland et al. 1983, 1985a). As a result, spiraling distance was shortest in the absence of snails. Low grazing pressure by snails allowed the accumulation of an algal mat that created transient storage effects, which in turn enhanced nutrient recycling within the mat (Mulholland et al. 1994). The conversion of CPOM into FPOM by detritivores is likely to enhance transport of particulate N and P because fine particulates are more easily exported during storms, but may also favor retention whenever fine particles are consumed (Vanni 2002). Predators may affect nutrient regeneration through their influence on the prey size spectrum because mass-specific nutrient excretion declines with body size. If larger prey are preferentially ingested, the excretion rate of the remaining, smaller prey assemblage will increase (Vanni 2002).

11.4 Nutrient Budgets

Nutrient budgets provide an accounting of all inputs, exports, and internal stores for some delineated spatial unit, and in so doing, increase our understanding of how nutrients are utilized. Budgets have been constructed at the scale of the stream reach (Grimm 1987), catchment (Boyer et al. 2002), and large river basin or region (Howarth et al. 1996). Estimates of the quantity of riverine nutrients discharged to lakes and oceans provide critical information for the management of eutrophication, and also are strong indicators of anthropogenic enrichment due to nutrients applied to the land or added directly to the water. By quantifying changes in inputs over time and comparing catchments that experience different intensities of human activity, such analyses have contributed substantially to our understanding of changing anthropogenic influence.

A nutrient budget is constructed from estimates of all known inputs and outputs from a defined area. However, depending on the ease with which data can be obtained and the objectives of the study, budget calculations may be restricted to anthropogenic inputs and some terms may be omitted. For a catchment, the output is simply the total mass of nutrient exported by the river per unit time, divided by catchment area so that it is a yield (often reported as kg ha^{-1} year^{-1}). Catchment inputs include fertilizers, atmospheric deposition, N fixation, and nutrients contained in imported food and animal feed (Boyer et al. 2002). The latter is a net term, as a catchment may import more food and feed than it produces, or the converse. In the case of N, these terms are readily estimated and natural inputs are sufficiently small that their omission is of little importance. In the case of P, the principal anthropogenic inputs are fertilizer and imported food and feed. Natural inputs include precipitation and runoff from rock weathering and soils, and often are small compared with anthropogenic sources (Baker and Richards 2002).

Outputs are typically much less than inputs in budget calculations because storage in soils and river sediments is not accounted for and, in the case of N, denitrification can be a significant loss term. Nutrient budgets have proven to be especially useful in revealing differences in the magnitude of various inputs in cross-catchment comparisons, and as evidence that the increasing quantities of nutrients delivered to lakes and coastal waters over past decades has its origin in human activities that have increased nutrient loading to the land and directly to surface waters. For example, by summing all anthropogenic N inputs, Howarth et al. (1996) demonstrated that the quantities of N exported by major rivers of Europe and the United States into the North Atlantic Ocean are strongly determined by human activities (Figure 11.12).

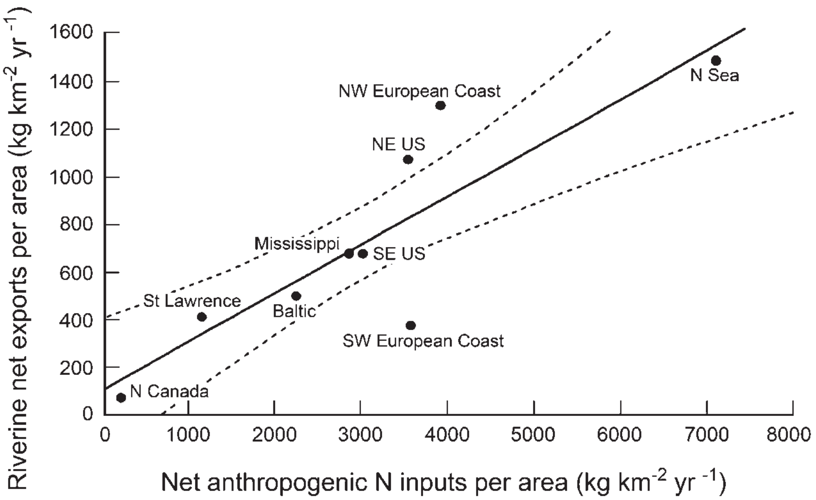

FIGURE 11.12 The relationship between river nitrogen export and net inputs of anthropogenic nitrogen to regions draining into the North Atlantic Ocean. Net inputs are the sum of fertilizer inputs, anthropogenic deposition, nitrogen fixation by crops, and imports of food and feed. (Reproduced from Howarth et al. 1996.)

11.4.1 Nitrogen

Nitrogen yields from undisturbed catchments are not well understood because recent human activities have more than doubled the global supply of reactive N, influencing most landscapes around the globe. Exports from undisturbed tropical rivers likely are minimally affected, however. Rivers of the Americas and the Gambia River in Africa had an average TN yield of 5.1 kg ha^{-1} year^{-1}. Because the nitrate yield was about half of the total and other forms of DIN typically are minor, export of N in organic form was substantial (Lewis et al. 1999). This contrasts with human-impacted rivers where most N is exported as nitrate. Total N yields from pristine temperate rivers are estimated to have ranged between 0.76 and 2.3 kg ha^{-1} year^{-1} (Howarth et al. 1996), which is consistent with an average value of 0.86 kg ha^{-1} year^{-1} for 85 relatively undisturbed sites in the United States (Clark et al. 2000). The higher N yields of pristine tropical rivers, in comparison with temperate systems in their undisturbed state, is attributed to greater N-fixation and atmospheric deposition, and to the absence of N limitation in tropical terrestrial systems, which favors the export of N (Downing et al. 1999, Holland et al. 1999).

Where anthropogenic inputs are important, N values are elevated, sometimes greatly. In the Ohio River, for example, the total N yield is 9.4 kg ha^{-1} year^{-1}, of which two thirds is nitrate (Howarth et al. 1996). An impressive 80% of the variation in the export of nitrate from 35 major world rivers was explained by fertilizer application, atmospheric deposition, and human sewage (Caraco and Cole 1999). Nitrogen yields of rivers draining northwestern Europe and the eastern United States are up to 19 times higher than under pristine conditions (Howarth et al. 1996). Indeed, most of the increase in total N is attributable to increases in nitrate, due mainly to increased fertilizer application. In a river draining an agricultural watershed in Illinois, nitrate concentrations were usually between 8 and 10 mg L^{-1} (David et al. 1997), far higher than recorded at undisturbed sites (Table 11.1). Long-term data from the Mississippi River establish that nitrate concentrations changed little from the turn of the century until the 1950s and then roughly doubled in the following 35 years, coincident with a steady rise in fertilizer application over the same time period (Turner and Rabalais 1991). In addition, atmospheric deposition of N in the northern hemisphere has increased by a factor of four, and some regions have experienced a 16-fold increase in comparison to preindustrial times (Holland et al. 1999).

The relative importance of various anthropogenic N inputs varies with the extent of human presence in catchments and especially with the intensity of agriculture. In a survey of 928 streams throughout the United States that were considered to be relatively uncontaminated but nonetheless affected to varying degrees by fertilizer runoff (Omernik 1977), concentrations of nitrate and TDN were proportional to percent of land in agriculture and inversely proportional to percent of land in forest (Figure 11.2). DIN increased from about 18% of total N in streams draining forested watersheds to nearly 80% in streams draining agricultural watersheds, presumably due to the use of N fertilizers. In rivers of the Chesapeake Bay drainage, percent of cropland correlated strongly with concentrations of nitrate and total N (Jordan et al. 1997). In tributaries of an agricultural catchment in southeastern Michigan, the ratio of agricultural to forested land explained 94% of the variation in annual average concentrations of nitrate (Castillo et al. 2000). In the mid-Atlantic region of the United States, half of the variation in total N concentrations was explained by the amount of agriculture in the catchment, and atmospheric deposition explained an additional 27% (Jones et al. 2001).

The Mississippi River Basin is an informative case study, important because N loading to the Gulf of Mexico appears to be responsible for a large anoxic region created by the decomposition of algal blooms resulting from the delivery of riverine nutrients (Section 13.2.3). Nitrate concentrations in the Mississippi River have increased markedly over the last 100 years, showing a particularly strong increase from 1970 to 1983, while fertilizer applications have increased sevenfold since 1960 (Goolsby et al. 1999). Nitrogen budgets reveal that almost 90% of the total N transported by tributaries of the Mississippi River derives from diffuse sources. Fertilizer and soil organic matter contribute 50%, atmospheric deposition, groundwater, and soil inputs supply 24%, and the application of animal manure provides 15% of total inputs. The remaining 11% is provided by discharges from waste water of urban and industrial origin. By region, the Ohio River is the source of one third of the nitrate discharged by the Mississippi into the Gulf of Mexico, but another third originates in the intensively agricultural lands of Illinois and Iowa despite the much smaller water discharge from that portion of the Mississippi Basin (David and Gentry 2000). The availability of such a detailed accounting is extremely useful because it helps to identify sources and thereby suggest what management practices should try to achieve.

Although agricultural activities are frequently the most important N input and atmospheric deposition also can be significant, the absolute and relative magnitude of anthropogenic sources varies greatly with human presence and activities. A comparison of 16 catchments in the northeastern United States, all with extensive forest cover (48–87%), found substantial differences in N inputs and exports related to variation in human population density and extent of agriculture (Boyer et al. 2002). Total inputs of N across the catchments was negatively correlated with the fraction of land area in forest, and positively correlated with the fraction of land area in agriculture and with the fraction of disturbed land (agriculture plus urban land) (Figure 11.13). On average, atmospheric deposition was the dominant N source (31%), followed by imports of N in food and feed (25%), fixation in agricultural lands (24%), fertilizer use (15%), and fixation in forests (5%). The lesser importance of fertilizer, relative to studies described above, is

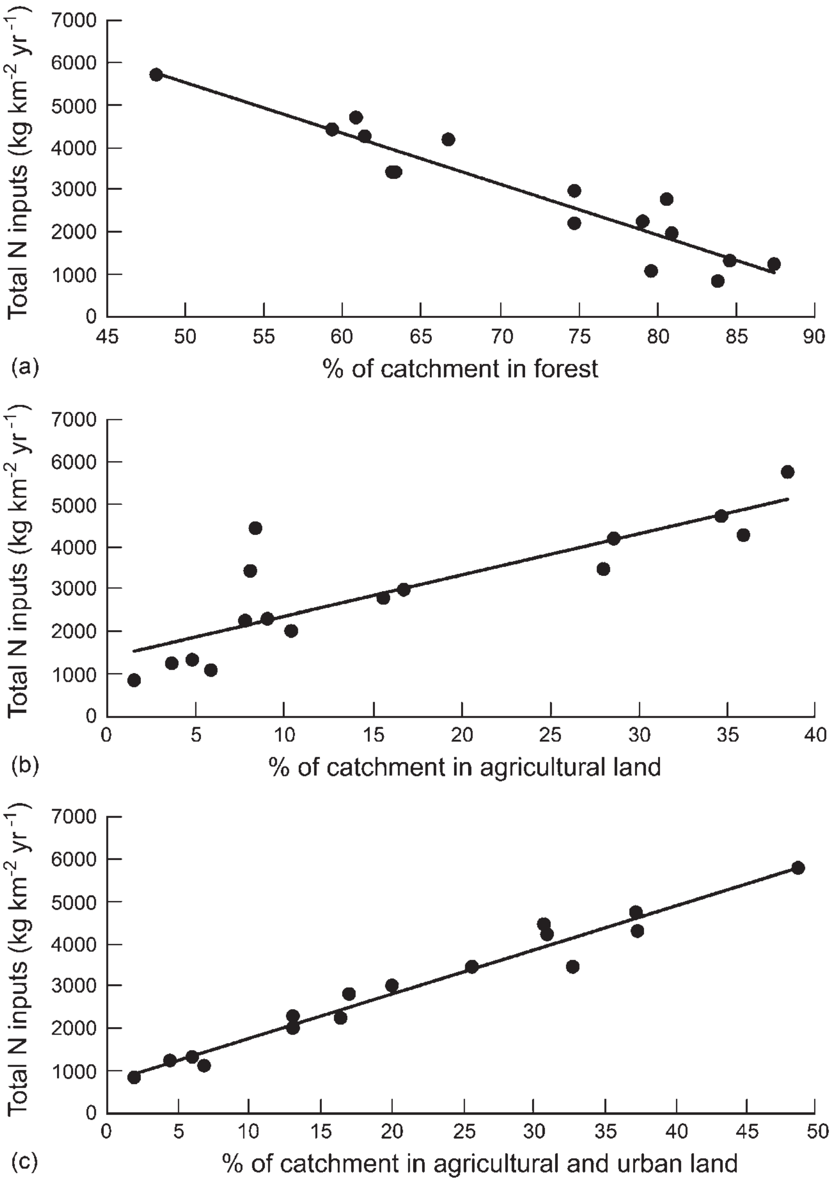

FIGURE 11.13 Nitrogen inputs estimated from budgets constructed for 16 catchments of the northeastern United States and draining to the North Atlantic Ocean are strongly correlated with land use in the catchments: (a) a negative relationship with forested land, (b) a positive relationship with agricultural land, and (c) an even stronger positive relationship with the sum of urban and agricultural land. (Reproduced from Boyer et al. 2002.)

unsurprising for catchments that are half or more forested. When all 16 catchments are compared, it is apparent that N inputs reflect various anthropogenic sources, which differ in both absolute and relative magnitude across forested, urban, and agricultural catchments.

Comparison of the export of N by rivers to all catchment inputs reveals that river export and human-derived inputs are highly correlated (Figure 11.12). On average rivers export only about 25% (Howarth et al. 1996, Boyer et al. 2002) to 40% (Goolsby et al. 1999) of these loadings. Denitrification in wetlands and aquatic ecosystems likely is a major sink for the remainder (van Breemen et al. 2002), but export of food and wood products also can be significant loss terms. There can be little doubt that high N yields, which in the rivers studied by Howarth et al. (1996) all exceed 10 kg ha^{-1} $year^{-1}$, are the result of increased nonpoint inputs due to fertilizers and atmospheric deposition, with the former responsible for roughly two thirds of the total.

11.4.2 Phosphorus

Estimates of natural background yields of TP from relatively undisturbed streams in the United States range up to 0.82 kg ha^{-1} $year^{-1}$ (Clark et al. 2000). For the Caura, a blackwater tributary of the Orinoco River, the annual P yield was 0.46 kg ha^{-1} $year^{-1}$. In the Apure, a moderately disturbed white water tributary of the Orinoco, the annual TP yield was 0.68 kg ha^{-1} $year^{-1}$ (Lewis and Saunders 1990). Phosphorus export from agricultural catchments can be much higher. Beaulac and Reckhow (1982) estimated TP yields at 2 kg ha^{-1} $year^{-1}$ for row crops, 1 kg ha^{-1} $year^{-1}$ for pastures, and 0.2 kg ha^{-1} $year^{-1}$ for forest. These values are consistent with estimates up to 1.9 kg ha^{-1} $year^{-1}$ for rivers of the Mississippi–Atchafalaya River Basin and between 0.7 and 1.1 kg ha^{-1} $year^{-1}$ in highly agricultural catchments in Illinois (Goolsby et al. 1999). In the Sandusky and Maumee rivers, two watersheds in Ohio that are greater than 75% agricultural area, P yields are near 1.4 kg ha^{-1} $year^{-1}$ (Baker and Richards 2002). Effluent from wastewater treatment plants can be an important source of P in heavily populated area. In the Illinois River, 70% of P inputs are contributed by sewage discharge, resulting in total P yields of 1.1 kg ha^{-1} $year^{-1}$ (David and Gentry 2000).

The mass balance relationship for P in river catchments is based upon inputs of fertilizers, manure, and sewage sludge applied to crop land, atmospheric deposition, and may include net import of food and feed (Baker and Richards 2002). Outputs are due to river export, and long-term storage can occur in soils. In comparison with N budgets, there is no biological fixation, atmospheric deposition is minor and often ignored, and there is no loss term analogous to denitrification. Natural weathering is difficult to determine, but may be small relative to other terms. From the perspective of river water concentrations and export, direct inputs from sewage treatment plants and surface runoff of animal waste can be a much larger contribution than is typical for N. For example, during periods of low flow, most P inputs to the Thame, a tributary of the Thames River in the United Kingdom, are from wastewater treatment plants and are delivered mostly as dissolved inorganic P. During high flows, diffuse sources represent 90% of the inputs and P is present mainly as particulate P in sediment runoff. On an annual basis, the outflow of wastewater treatment plants is important, contributing half of the TP load of the river (Cooper et al. 2002).

Urban watersheds of course will receive more of their P inputs from waste water whereas agricultural watersheds are more affected by nonpoint inputs carried in runoff. In the Swale River in Northern England, 85% of river export of P originated in its lowlands due to both sewage and agricultural inputs (Bowes et al. 2003). In the subtropical Richmond River in Australia, fertilizer accounted for 65% of total inputs of P. Phosphorus yields from streams of the Mid-Atlantic Region of the United States declined with increasing forest cover in their catchments, which was attributed to the role of riparian forest in reducing sediment and nutrient inputs (Jones et al. 2001). The percentage of agricultural land and mean slope explained much of the variation in P concentrations among Finnish streams (Ekholm et al. 2000). In addition to the direct effect of nutrient addition via fertilizers, agricultural activity disturbs soils and this leads to increased erosion, especially on steep slopes, enhancing transport of P in particulate form. Erodibility may in fact be a better predictor of P delivery from terrestrial to aquatic ecosystems than agricultural land area. In streams of the Chesapeake Bay drainage, P concentrations correlated with streamwater sediment concentrations but not with land area in agriculture, suggesting that factors influencing sediment loss were of primary importance (Jordan et al. 1997).

When budget calculations are made over an extended time period, it may be possible to detect not only long-term trends in inputs and outputs, but also infer changes in residence time as nutrients work their way through the catchment and into riverine export. Phosphorus inputs exceeded outputs for a number of catchments in Illinois for the years between 1965 and 1990, but were in balance thereafter, due to a reduction in fertilizer applications (David and Gentry 2000). However, P that accumulated in the soil during surplus years constitutes an important storage that must be gradually diminished before river exports can significantly decline, and as a consequence riverine exports may remain elevated for some time despite a reduction in inputs. In the Sandusky and Maumee Rivers, P concentrations and export have decreased over the period 1975–1995 even though inputs of P due to fertilizer continue to exceed its removal via crop harvest (Baker and Richards 2002). The likely explanation is that erosion control measures and changes in the timing of fertilizer application have been successful in reducing losses to the rivers, but P is accumulating in the soil compartment, and so remains a concern.

11.5 Summary

Nutrients are inorganic materials necessary for life, whose supply is potentially limiting to biological activity within lotic ecosystems. Although many macro- and micronutrients are required for enzymatic activity and protein synthesis, P and N are the primary nutrients that limit biological activity. In addition, the supply of silica can be important to diatoms because of the high silica content of their cell walls. Phosphorus and N occur in numerous forms including dissolved and particulate, and inorganic and organic. They are most bioavailable in their dissolved inorganic forms, as phosphate, nitrate, and ammonium. Their concentrations are very low in unpolluted waters, but are greatly elevated in many areas including most large temperate rivers due to human inputs of agricultural fertilizers, human and animal sewage, atmospheric deposition, and industrial pollution. Nitrogen and P concentrations in rivers often exceed the levels that cause eutrophication in standing water, and consequently the load of nutrients delivered to lakes and coastal waters by river export is a serious management concern.

There are, broadly speaking, two perspectives on nutrient cycling in lotic ecosystems: how nutrient supply affects biological productivity, and how processes within the ecosystem influence the quantity of nutrients that are transported downstream. Metabolic processes likely to affect and be affected by the supply of nutrients include primary production and the decomposition of organic matter by bacteria and fungi, and thus the rate at which basal resources for stream food webs are produced. Because rivers export substantial quantities of nutrients to receiving lakes and oceans, instream storage and removal processes have the potential to influence large-scale element budgets and reduce the quantity of nutrients delivered to receiving water bodies.

Nutrient cycling describes the passage of an atom or element from dissolved inorganic nutrient through its incorporation into living tissue to its eventual remineralization by excretion or egestion and decomposition. In many ecosystems nutrients largely cycle in place, but in lotic ecosystems, downstream flow stretches cycles into spirals. The distance traveled by an atom as inorganic solute before its immobilization in the streambed is called the uptake length, S_w. Because uptake length depends strongly on discharge and velocity it is desirable to standardize nutrient uptake by estimating an uptake velocity, v_f, which quantifies the velocity at which a molecule moves from the water column to retention sites on and within the streambed.

A number of biotic and abiotic processes influence nutrient spiraling. The immobilization of nutrients by autotrophs involves assimilatory uptake for the incorporation of nutrients into new tissue. Heterotrophs in biofilms and on organic substrates likewise require nutrients for synthesis of new structural compounds, but nitrification and denitrification are dissimilatory reactions where bacteria obtain energy by using ammonia as a fuel or nitrate as an oxidizing agent. In addition, both N and P can be removed from streamwater by abiotic processes. Sorption–desorption reactions, in which both inorganic and organic molecules are bound to the surfaces of sediments, can help to regulate nutrient availability by serving as temporary storage sites when a nutrient is present in streamwater at high concentrations, releasing it back into solution when concentrations decline. Under aerobic conditions, dissolved inorganic and organic P both may complex with metal oxides and hydroxides to form insoluble precipitates, which are released under anaerobic conditions.

The capacity of lotic ecosystems to influence the dynamics of nutrients during their downstream passage depends on the factors that influence biotic and abiotic uptake. Biological demand varies seasonally with environmental conditions that favor high rates of primary production and with the supply of organic substrate for heterotrophs, particularly leaf fall. During periods of high discharge, streams are in a throughput mode, exporting most of their annual load of nutrients in weeks to a few months of the year. During low flows, processing and retention are more important. Because the streambed and its interstices are locations of biofilm development and organic matter accumulation, subsurface flowpaths can retard the downstream passage of nutrients and increase their exposure to sites of uptake, thereby contributing to nutrient retention and utilization. Transient storage capacity, which accounts for the slow passage of a conservative tracer relative to water column flow, is a useful descriptor of the extent to which channel complexity affects downstream passage. Once nutrients are assimilated by primary producers and heterotrophic microbes, they can pass through multiple steps of food webs before their eventual mineralization to a bioavailable state. In some highly productive systems, recycling by consumers makes a significant contribution to nutrient availability, and in some circumstances selective retention of nutrients in consumer biomass may contribute to nutrient imbalances.

Nutrient budgets provide an accounting of all inputs, exports, and internal stores for some delineated spatial unit, such as a stream reach, catchment, or large river basin or region. Outputs are typically much less than inputs in budget calculations because storage in soils and river sediments is not accounted for and, in the case of N, denitrification can be a significant loss term. Nutrient budgets have proven to be especially useful in revealing the magnitude of anthropogenic inputs, which can vary substantially among forested, agricultural, and urban catchments. Nitrogen inputs have increased so greatly that river export is now nearly 20 times above estimated pristine conditions in some regions. Phosphorus yields have increased by a smaller amount but anthropogenic influences are nonetheless important, especially during summer low flows when inputs of bioavailable phosphate from sewage water can be a significant fraction of total flows.

Chapter twelve

Stream ecosystem metabolism

Sources of organic carbon (C) and thus energy to lotic ecosystems fall into two broad categories: autochthonous inputs by aquatic primary producers and allochthonous inputs of dead organic matter from terrestrial ecosystems. Heterotrophs – microorganisms, meiofauna, and macrofauna – decompose and consume these supplies of organic C, ultimately remineralizing some fraction of the total as carbon dioxide (CO_2), but also exporting substantial quantities to downstream ecosystems (Figure 12.1). Indeed, utilization and export are the two principal fates of organic C in stream ecosystems; although some storage occurs on the timescale of months to years, storage is thought to be negligible on longer timescales.

This whole-ecosystem view brings into focus a series of topics that comprise the study of stream metabolism. Allochthonous inputs of coarse, fine, and dissolved organic matter (DOM) are important in many stream settings, especially in small streams with a forested riparian, where algal primary production tends to be light-limited. Thus, it is suggested that allochthonous inputs will dominate in forested headwaters, a view with much supporting evidence. Autochthonous production by algae and other primary producers is expected to be of greater importance at roughly fourth- through sixth-order streams, and then less so in larger, deeper, and more turbid lowland rivers (Figure 1.7). This shift between autochthony and allochthony is also a shift between reliance on internal versus external energy sources, and it is expected to vary along the river continuum and with landscape setting (Vannote et al. 1980, Minshall et al. 1983). A stream reach with a low level of primary production (P) and a high level of respiration (R) clearly is dependent upon external energy inputs, either from the adjacent terrestrial ecosystem or from upstream sources. Thus, the P/R ratio, or P minus R (referred to as net ecosystem production, NEP), serves as an index of the relative importance of internal versus external organic C inputs, and may be used as a measure of any metabolic transitions that occur along a river's length. Stream ecosystems where NEP is positive are likely to export organic matter to downstream locations. When NEP is negative the stream ecosystem is dependent upon external energy sources, usually allochthonous detritus from the land.

Lotic ecosystems are open, which means that they import organic matter from upstream and export it downstream, and lateral exchanges can be substantial wherever the river is connected to a floodplain. Thus, transport is an important process in stream energy flux, and this may be especially true of particulate organic matter

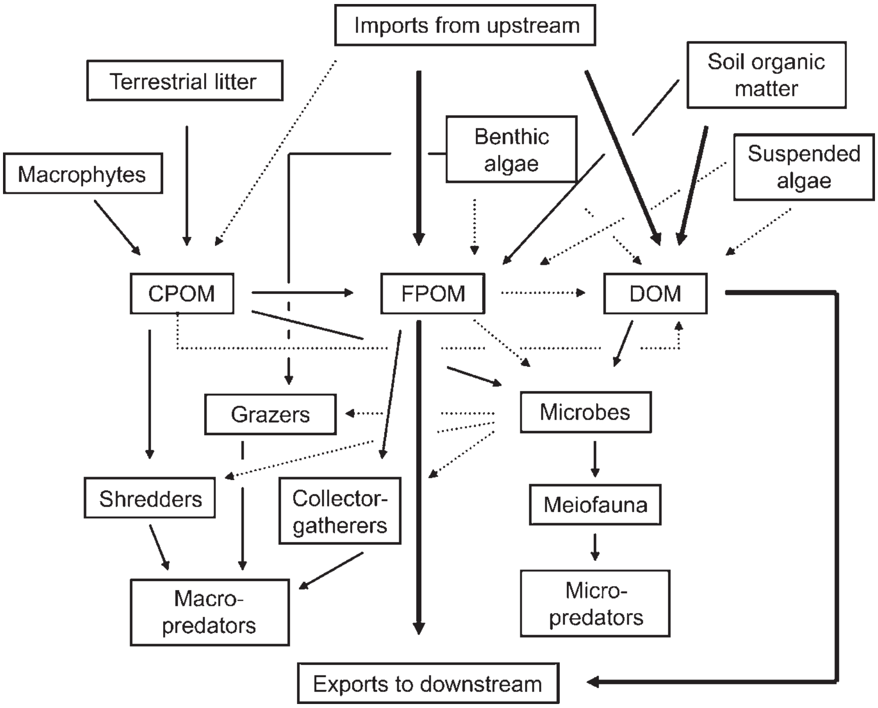

FIGURE 12.1 Simplified model of principal carbon fluxes in a stream ecosystem. Heavier lines indicate dominant pathways of transport or metabolism of organic matter in a woodland stream. Note that storage is omitted. (Modified from Wetzel 2001.)

(POM), where hydrologic variation and the presence of retention devices such as wood and boulders together determine whether POM resides in the stream system long enough for decomposition to occur. Stream ecosystem efficiency quantifies the extent to which all energy inputs are converted to CO_2 versus exported downstream. By integrating information concerning energy inputs, the processes of decay and consumption, and the transport of organic C into and out of stream reaches, one can investigate the overall efficiency of stream ecosystems, and whether efficiency varies as a function of types of inputs or landscape and longitudinal position. At least for streams dominated by allochthonous inputs of terrestrial POM, current evidence suggests ecosystem efficiency is low, especially in headwater reaches.

Quantification of inputs (primary production, POM and DOM), rates of utilization and transport, and standing stocks (typically coarse and fine benthic OM) are the main components in the analysis of C flux. These topics were discussed in detail in Chapters 6 and 7 and are revisited here, with the primary emphasis on estimates of amounts and rates. To address the relative importance of autochthony versus allochthony, utilization versus transport, and stream ecosystem efficiency, investigators have used P/R and NEP, attempted to calculate all inputs and outputs of organic matter using a budgeting approach, and developed measures of C retention and processing expressed as distance or time in transport as an indication of ecosystem efficiency. Although some quantities are difficult to measure and the open nature of lotic ecosystems creates special challenges, recent findings from the study of stream ecosystem metabolism provide clear evidence that stream size and characteristics of the surrounding catchment are important determinants of organic C inputs and utilization.

12.1 Autochthonous Production

The photosynthetic activities of benthic algae, macrophytes, and phytoplankton contribute the principal autochthonous inputs to lotic ecosystems. Gross primary production (GPP) is the total amount of new C fixed, and net primary production (NPP) is the difference between C fixed by autotrophs and their own metabolic demands. The symbol P introduced earlier and used in the P/R ratio (where R is respiration) is GPP. However, it is important to note that R is a measure of respiration of the total community or ecosystem, including both autotrophs and heterotrophs. Conceptually it is very useful to consider these separately as R_A and R_H, but in practice this is not feasible. For these reasons, P – R in lotic ecosystems is referred to as NEP, the excess of GPP over ecosystem respiration.

Benthic primary production has been estimated for many different stream types from changes in oxygen concentrations, either in enclosed benthic chambers designed to measure benthic primary production, or using open water methods that measure whole-ecosystem production and respiration (Section 6.1.3). Oxygen change in the dark provides an estimate of ecosystem respiration ($R_A + R_H$), which can be extrapolated over 24 h (Bott 2006). GPP is estimated by adding respiration during the light to net oxygen change in the light, and NEP is calculated as the difference between GPP and 24 h ecosystem respiration. Values are converted to C using the formula $\mathrm{g}\,C = 0.286 \times \mathrm{g\,O_2}$ and reported in g C $\mathrm{m^{-2}\,day^{-1}}$. Benthic chambers are especially useful for measuring local-scale heterogeneity and testing of environmental variables, but are difficult to scale up to the entire ecosystem unless well replicated. In addition, whole-ecosystem estimates are generally higher than chamber estimates (Webster et al. 1995, Mulholland et al. 2001), and current evidence suggests that the whole-ecosystem measures are more reliable. Initially the whole-ecosystem method was used primarily in unshaded, relatively productive systems; but due to improvements in technique (Marzolf et al. 1994, Young and Huryn 1998) it is now being used in smaller, shaded streams where high rates of reaeration and low rates of primary production make measurement more challenging. Owing to the diversity of methods used and the preference of individual investigators to express results as either GPP or NPP, the following discussion will use the term primary production regardless of which is reported; however the symbol P, widely used in discussions of stream ecosystem metabolism, invariably refers to GPP.

12.1.1 Algae

Benthic primary production is expected to be lower in forested than in open-canopy streams and to increase with stream order as streams widen and are less shaded by riparian vegetation. Using the whole-ecosystem method, Mulholland et al. (2001) determined primary production in eight first- through third-order streams in different biomes of North America. Light levels had the strongest influence over daily P, and for most sites light saturation was observed at levels consistent with chamber studies (Hill et al. 1995), although light saturation at high irradiance was not observed at a desert stream site. In their review of over 60 estimates from stream sites in eastern North America, Webster et al. (1995) found that primary production in forested streams was about half that of open streams, although results were highly variable. As expected, production was low in first- and second-order streams and highest in third- and fourth-order streams, and then declined at higher orders. McTammany et al. (2003) reported a pronounced longitudinal increase in primary production along the Little Tennessee River in North Carolina, including two fourth-order, one fifth-order, and one sixth-order reaches downstream from the intensively studied headwaters in the Coweeta Hydrologic Laboratory.

Most studies of GPP and R are of short duration, but measurement of daily rates continuously for 2 years in Walker Branch, Tennessee, provides an unusually detailed view of seasonal patterns and factors controlling stream metabolism (Roberts et al. 2007). This first-order, deciduous forest stream was net heterotrophic throughout the year except during the open-canopy spring, when GPP and ecosystem R were coequal (Figure 12.2). Leaf phenology was the main control of seasonal variation, day-to-day weather variation influenced light availability and GPP, and storms suppressed GPP in spring by scouring algae, but stimulated GPP in the autumn by removing leaf litter and increasing light availability. Daily R was controlled by autotrophic activity in the spring and allochthonous organic matter inputs from leaf litter in autumn. After an initial decrease following storms, labile organic matter inputs from the surrounding terrestrial system led to a multiday stimulation in R. Thus, variability in ecosystem metabolism was evident on all timescales, and attributable to daily and seasonal influence of light interacting with vegetation, and episodic high flows.

12.1.2 Macrophytes

Estimates of the contribution of macrophyte production to organic matter budgets are too few

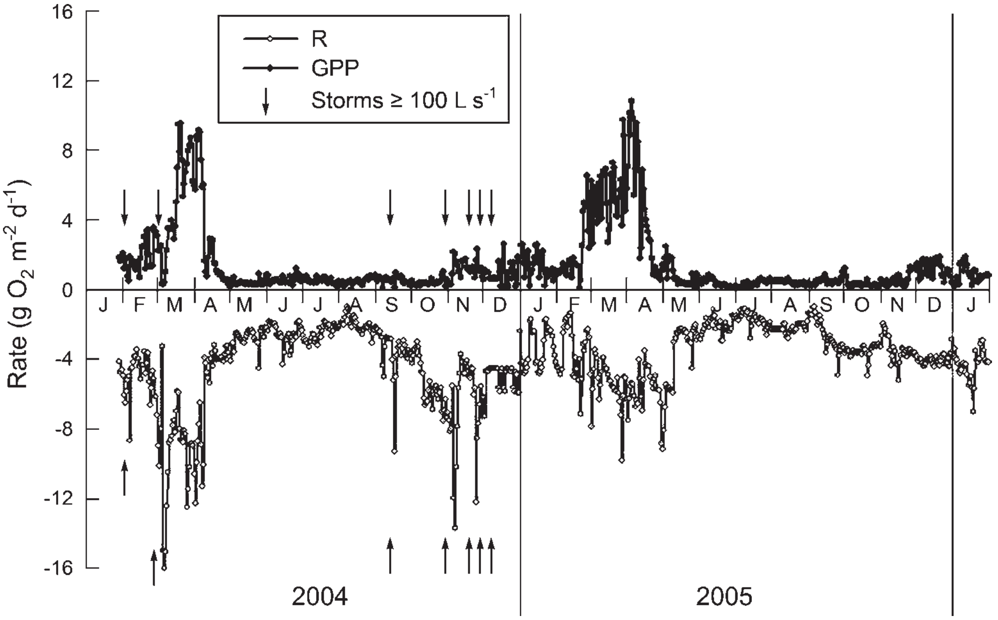

FIGURE 12.2 Daily rates of gross primary production (GPP: positive values, *black line*) and ecosystem respiration (R: negative values, *gray line*) measured in Walker Branch from 28 January 2004 through 31 January 2006. Vertical lines separate years. Arrows indicate storms during which maximum instantaneous discharge was greater than or equal to 100 L s^{-1}. Variance in GPP correlates with seasonal and day-to-day variation in light levels. Variance in ecosystem R correlates with seasonal and day-to-day variation in GPP and autumn leaf inputs. (Reproduced from Roberts et al. 2007.)

to generalize, but at least in some circumstances they are a significant component of system primary production. In the New River, Virginia, production by *Podostemum ceratophyllum* was about equivalent to periphyton production in contribution to the annual organic matter budget (Hill and Webster 1982a, 1983). Macrophytes contributed about 9% of the annual primary production in the Fort River, Massachusetts (Fisher and Carpenter 1976), and about 15% in the Red River, Michigan (King and Ball 1966).

12.2 Allochthonous Inputs

Allochthonous material, which includes all of the organic matter that a stream receives from production that occurred outside the stream channel, often makes up a large fraction of a stream's total inputs of organic matter. Coarse and fine POM derived from the terrestrial ecosystem and DOM from groundwater and adjacent terrestrial soils are important sources of nonliving organic C originating beyond the stream channel. Heterotrophic microorganisms and other consumers utilize these C sources, and in some settings allochthonous detritus dominates stream metabolism. Instream primary production may contribute to DOM pools by extracellular release and enter both DOM and POM pools after sloughing and dieback, and so the separation of allochthonous versus autochthonous sources may sometimes be imperfect, but this is unlikely to be a major source of error in the estimates that follow.

12.2.1 Coarse particulate organic matter

Leaves and wood are the principal inputs of allochthonous coarse particulate organic matter (CPOM), although other plant products and terrestrial invertebrates may occasionally contribute (Wallace et al. 1995, Webster et al. 1995, Wipfli 1997). Leaf litter is the dominant input into forested streams, varying in magnitude with forest productivity, with stream size, and with anthropogenic disturbance. In small streams in Coweeta, logs show neither breakdown nor movement (Webster et al. 1999), and thus are of little importance from the perspective of organic C utilization.

Leaf litter can fall directly into the stream from the riparian vegetation or reach the stream by lateral movements from the bank. The relative contributions of lateral and direct inputs are highly variable depending on wind patterns, bank slope, ground cover, and the distance between the stream and the forest. Lateral inputs were estimated to contribute roughly one fourth of the total based on a review of many streams of eastern North America (Webster et al. 1995). This is consistent with the finding that lateral inputs contributed between 22% and 27% of total litter inputs in Coweeta headwater streams (Wallace et al. 1995), and an estimate of about 30% based on a review of 18 streams from different biomes and continents (Benfield 1997). In the Ogeechee River, lateral inputs were fourfold greater than direct inputs, probably because the width of the river minimized direct litterfall and floodplain inundation maximized inputs from outside the channel.

Highest leaf inputs usually occur during the autumn in the temperate zone, although lateral inputs may occur throughout the year. In an Austrian stream, direct CPOM inputs during the autumn contributed 61–65% of total inputs (Artmann et al. 2003). Similar results were obtained for a forest stream in Hokaido, Japan, where leaf litter during October represented 58% of the annual inputs (Kochi et al. 2004). In the deciduous tropics, inputs are greatest during the dry season (Magana and Bretschko 2003). Additional seasonal variation in leaf fall may occur depending on the type of terrestrial vegetation. In Northern Spain, Pozo et al. (1997) noted that leaf litter input peaked during the summer in a eucalyptus plantation but during the autumn in a deciduous forest. In several small New Zealand streams, inputs of leaf litter peaked in the summer in streams running through native forest, but maxima were observed in autumn in pasture areas. In pine forests, litter inputs were lowest in the winter and peaked during the spring when large inputs of pollen heads were observed (Scarsbrook et al. 2001).

Logging and other activities that disrupt riparian vegetation can affect the magnitude of leaf litter and wood inputs. Following logging in the catchment of a small stream at Coweeta, leaf inputs fell to <2% of previous levels (Webster and Waide 1982). Allochthonous inputs recovered to near reference values after 5–10 years of regrowth and forest succession, but inputs were still detectably below reference levels after 20 years (Webster et al. 1990a). Although litter inputs from early successional trees were less than those observed prior to logging, these leaves were more rapidly broken down. Pest outbreaks, tree diseases, and acid rain are additional disturbances, often human-mediated, that can reduce leaf litter inputs.

Litter inputs expressed per unit area of streambed are expected to decline as stream width increases, and be greater in warmer and wetter climates because of higher forest productivity. Bott et al. (1984) reported lower litterfall inputs at fifth-order sites of a Pennsylvania stream compared with lower-order sites, but the expected downstream decline in CPOM inputs has not been apparent in many comparisons, evidently because differences among sites in climate, floodplain connectivity, and anthropogenic influence are of greater importance. In a comparison of litterfall estimates from 33 sites ranging from 78°S to 75°N and in six different biomes, Benfield (1997) concluded that litter inputs were primarily related to the presence of forested versus non-forested vegetation. Litterfall was positively related to annual precipitation and decreased with increasing latitude, reflecting the influence of climate on overall terrestrial productivity (Figure 12.3). Blackwater streams of the southeastern United States received very high litter inputs as a consequence of floodplain interactions, whereas litter inputs to desert and boreal streams were very low.

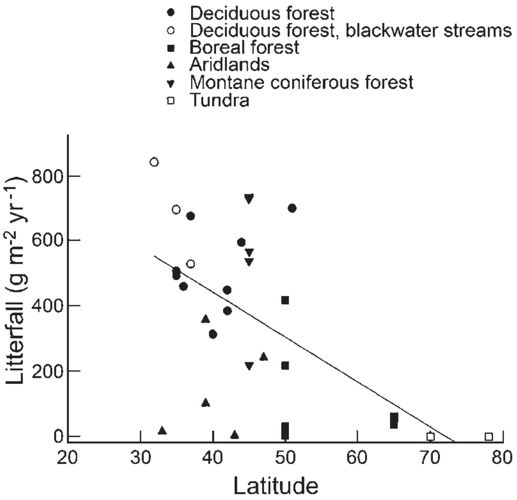

FIGURE 12.3 A linear regression of litterfall versus latitude for 33 stream locations across six biomes. (Reproduced from Benfield 1997.)

12.2.2 Fine particulate organic matter

Fine particulate organic matter (FPOM) is generated within streams from the breakdown of leaf litter and other CPOM, and in some circumstances fecal pellets can be very abundant (Section 7.2.1). In addition, considerable amounts of FPOM enter the channel as a product of the breakdown of vascular plant material from the surrounding terrestrial landscape. FPOM inputs are low during base flow and increase during storms and seasonal high flows (Hedges et al. 1986, Mulholland 1997a), as rising flows entrain particles from stream banks and side channels.

Many studies document variation in the concentration of suspended FPOM with season, surrounding vegetation, and stream flow. A comparison of 31 streams and medium-sized rivers in North America, Europe, the Arctic, and Antarctica found POM to range between 0.14 and 15.30 mg L^{-1} (Golladay 1997). In streams and rivers of eastern United States, POM estimates ranged between 0.5 and 52 mg L^{-1} (Webster et al. 1995); in undisturbed forested catchments, mean annual concentrations often are $< 2\,\mathrm{mg}\ \mathrm{L}^{-1}$ (Fisher and Likens 1973, Naiman and Sedell 1979). Forested streams frequently exhibit higher FPOM concentrations that non-forested streams, as was observed in a comparison of native forest to pasture sites in a New Zealand stream (Young and Huryn 1999), and in the above-mentioned 31 streams from different regions (Golladay 1997). However, high FPOM concentrations also are seen in low gradient streams flowing through agricultural or multiple-use catchments (Malmqvist et al. 1978), and especially in larger lowland rivers (Thames, Berrie 1972b; South Platte, Colorado, Ward 1974). POM concentrations show a positive relationship with regional precipitation, probably due to the influence of precipitation on terrestrial production and thus on the supply of CPOM. Floodplains can be a large source of organic matter to rivers, and higher POM concentrations usually are observed in low gradient streams during inundation (Golladay 1997).

FPOM concentrations are influenced by changes in particle availability, which is influenced primarily by terrestrial production and seasonal changes in biological processes within the stream ecosystem; and by discharge, which varies both seasonally and unpredictably. In streams of the eastern United States during normal flows, FPOM concentrations are higher during spring and summer than during autumn and winter (Figure 12.4), probably because lower biological activity during the colder months results in less instream particle generation (Webster et al. 1995). If the particle supply is relatively constant, then an increase in discharge will cause a dilution effect, even if the total amount of FPOM in transport is greater. In Bear Brook, New Hampshire, POM concentrations were highest in summer but transport was greater in winter (Fisher and Likens 1973), and so dilution is responsible for low winter concentrations. However, in southern Appalachian streams dilution is not the sole explanation for lower winter concentrations, because transport is highest in spring and summer (Webster and Golladay 1984).

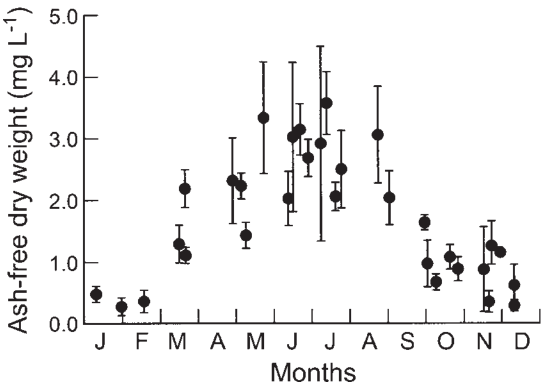

FIGURE 12.4 Seasonal variation in FPOM concentrations in a forested headwater stream in the southern Appalachians. Error bars show 95% confidence intervals. (Reproduced from Webster and Golladay 1984.)

An increase in streamflow in response to a rainstorm results in a corresponding increase in particle concentrations as POM generated during low flows and stored in depositional areas is entrained by rising stream levels (Fisher and Likens 1973, Meyer and Likens 1979). This indicates that the major pool of POM lies in areas already wet or adjacent to the stream's wetted perimeter, where FPOM accumulates during low flows. Inputs of POM from outside of the stream also are likely to be greatest during the rising limb of the hydrograph, due to the erosive effects of rainfall on soil and stream bank litter and generation of flow in previously dry channels. During the descending limb, water enters the stream principally by subsurface flow, and carries little or no POM. Thus, concentrations are highest on the rising limb of the hydrograph (Figure 12.5) and then decline due to exhaustion of the particle supply and dilution of the entrained material.

Just as depletion of benthic POM contributes to concentration differences between rising and falling limbs of the hydrograph, time elapsed since the last storm and seasonal differences in particle generation interact with discharge to determine POM peaks during storms. In a forested headwater stream studied by Wallace et al.

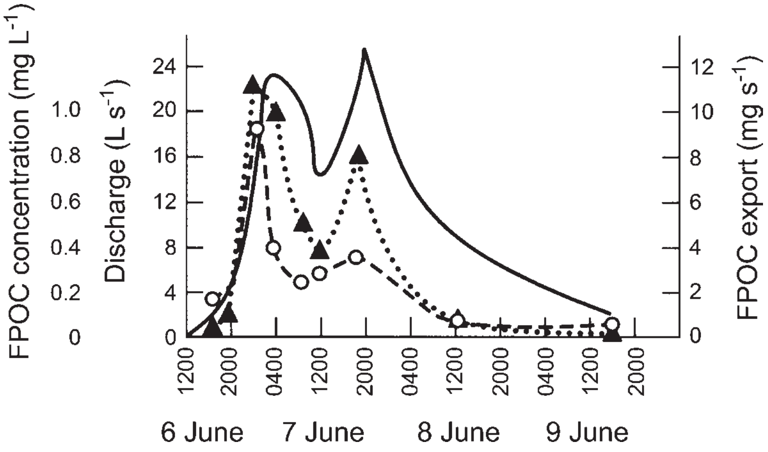

FIGURE 12.5 Changes in discharge, FPOC concentrations, and FPOC transport during a summer storm in a small forested catchment in New Hampshire. Note that FPOC concentrations peak on the rising limb of the hydrograph, indicating rapid entrainment of small particulates. A second hydrograph peak resulted in a much smaller FPOC concentration peak, evidence that washout rapidly depletes the available FPOC supply. — indicates discharge; O--O denotes FPOC concentration and ▲. . . ▲ denotes FPOC export. (Reproduced from Bilby and Likens 1979.)

(1982b), POM concentrations increased greatly with rising discharge during the first autumn storm, apparently due to the availability of abundant FPOM generated by autumn leaf fall, coupled with a lengthy prior period of low flow. A winter storm resulted in a smaller increase, which Wallace et al. attributed to depletion of benthic FPOM by washout during prior fall storms. In larger rivers, the effect of individual storms on POM concentrations is less pronounced, and seasonal variation in flows and floodplain inundation is more important. As is found in smaller systems, POM concentrations in large rivers are highest on the rising limb of the hydrograph, and decline thereafter (Thurman 1985).

Because POM concentrations usually are higher when discharge is greater, most FPOM is transported during episodic and seasonal floods, and thus flow conditions that occur during only a small fraction of the annual discharge cycle can account for a very large fraction of annual transport. High discharges representing just 1% of the annual discharge regime accounted for 20% of water export and fully 70% of annual export of FPOM from a small stream at Hubbard Brook Experimental Forest (Bilby and Likens 1980, Bilby 1981). Some 75–80% of POM transport in small Coweeta streams occurred during storms (Webster et al. 1990), demonstrating the importance of accurately sampling these episodic events. In fact, unless sampling is continuous or captures high flows very thoroughly, total transport may be seriously underestimated.

12.2.3 Dissolved organic matter

DOM includes labile organic compounds that are available to microorganisms for biological uptake as well as refractory material that is less easily assimilated and may be exported great distances (Section 7.3). Groundwater, rainfall and throughfall, and leaching of leaves are primary sources of dissolved organic C. Concentrations vary with terrestrial vegetation, soil flow pathways, and the presence of wetlands, and may be enriched by domestic sewage or agricultural runoff. DOC enters streams primarily through groundwater inputs at low flows, while more DOC enters via lateral flows during storms (Mulholland 1997b). DOC inputs increase during storms due to flushing of locations of DOC accumulation (particularly in organic-rich riparian zones and surface soils on hillslopes), canopy throughfall, and possibly due to leaching of newly entrained material (Meyer and Tate 1983, McDowell and Likens 1988).

The amount of DOM in river water varies on daily, seasonal, and yearly timescales; and spatially, in accord with local geology, vegetation, and rainfall (Table 12.1). DOM concentrations ranged between 0.5 and 36.6 mg L^{-1} in a survey of 33 streams and rivers in the Caribbean, North America, Europe, and Antarctica (Mulholland 1997b). On a worldwide basis, DOC exceeds POC by approximately 2:1, but this depends on type of stream and discharge regime. Based on annual means, reported DOC to POC ratios for North American streams range from 0.09:1 to 70:1 (Moeller et al. 1979). The total export of organic matter from 86 Finnish catchments was dominated by DOC, which made up 94% of total organic C (Mattsson et al. 2005). In headwater streams of British Columbia, DOM also represented a high percentage (84%) of the total organic matter export, and the remainder was mostly FPOM (Karlsson et al. 2005). In larger rivers, however, POC and DOC concentrations are similar, and at high discharge POC can exceed DOC (Thurman 1985).

DOC inputs are influenced by catchment characteristics such as geology, soils, and topography. The size of soil C pool is a strong predictor of stream DOC concentration (Aitkenhead et al. 1999). Water moving through shallow flowpaths has greater contact with the organic horizon of the soils, and so generally has higher DOC concentrations than are found in groundwater (Frost et al. 2006). Shallow flowpaths can be the result of steep slopes, shallow soils, and the presence of infiltration barriers or of saturated soils, such as wetlands and peatlands (Aitkenhead-Peterson et al. 2003). Deeper flowpaths increase the exposure of DOC to microbes and mineral soils, which can assimilate and adsorb DOC, respectively. In the Amazon, differences in texture between oxisols and spodosols, the dominant soil types in clearwater and blackwater river catchments, result in different concentrations of DOC in groundwater and pronounced differences in DOC concentration and composition between these two types of rivers (McClain et al. 1997).

TABLE 12.1 Typical concentrations of dissolved organic carbon (DOC) in running waters and groundwater. (From Thurman 1985.)

	DOC (mg L^{-1})	
	Range	*Average*
Groundwater	0.2–2	0.7
Pristine streams	1–4	2
Major rivers	2–10	5
Swamps, bogs, and blackwater streams	10–30	–

Local circumstances may result in higher values than those given here.

In catchments with a substantial area of wetlands, streams have elevated DOC concentrations due to the accumulation of organic acids that reduce pH, thus slowing bacterial decay (Thurman 1985). The proportion of wetlands in their catchments explained up to 70% of the variation in DOC concentrations of Wisconsin rivers (Figure 12.6), and was a better predictor than riparian wetland extent (Gergel et al. 1999). In catchments of the Adirondack Park of New York state, wetlands contribute 30% of DOC inputs but occupy just 12% of the surface area (Canham et al. 2004). Rivers draining permafrost catchments like the Kuparuk in Alaska also exhibit high DOC concentrations due to surface flowpaths through organic-rich soil layers (Harvey et al. 1997, Mulholland 1997b). Based on radiocarbon analysis, DOC exported from wetlands in Ontario, Canada, was of recent origin despite the fact that peat at a depth of 50 cm had an age between 1,000 and 2,000 years, suggesting that C was exported from wetlands primarily through shallow flowpaths (Schiff et al. 1998).

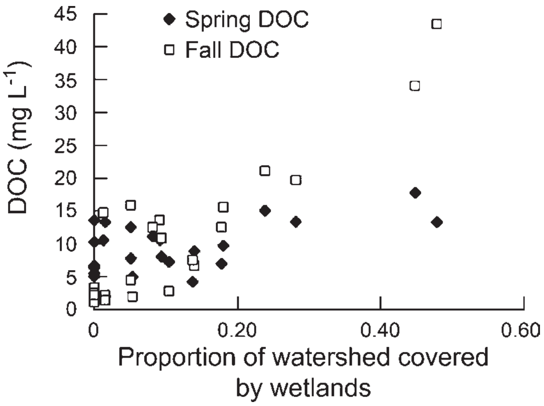

FIGURE 12.6 The relationship between DOC concentrations and the proportion of wetlands in catchments for rivers in Wisconsin. (Reproduced from Gergel et al. 1999.)

Instream DOC sources can be important, including leaf leachate and algal exudates. In a Pennsylvania stream flowing through woodland and meadows, extracellular release of DOM during periphyton blooms elevated stream DOC by nearly 40% on a daily basis, but only in springtime because canopy development reduced instream primary production during summer (Kaplan and Bott 1989). Leaf fall is an important organic C source in woodland streams, and in Roaring Brook, Massachusetts, 42% of stream inputs of DOM during autumn were attributable to leaf leachate (McDowell and Fisher 1976). Meyer and Tate (1983) found DOC inputs to be less in a recently clear-cut stream compared to a forested stream, apparently because successional recovery of the surrounding forest reduced DOC transport from soil water into the stream channel. The exclusion of leaf litter from a headwater stream lowered the concentration and export of DOC in comparison with a reference stream (Meyer et al. 1998), indicating that leaf litter generated near 30% of total daily transport. Although instream sources of DOC are easily assimilated and can be important in some circumstances, quantitatively they are dwarfed by groundwater sources. In a forested stream in Coweeta, 70% of DOC came from groundwater, just over 20% from leaf leachate and about 10% from rainfall and throughfall (Meyer and Tate 1983).

A large fraction of seasonal or annual DOC export often occurs during high flows and thus within a relatively short time interval. This is particularly true when high flow results in water entering streams along shallower flowpaths, resulting in higher concentrations of DOC. In two small catchments in Ontario, DOC transport during storms represented 57–68% of the total during autumn and 29–40% of the total during spring (Hinton et al. 1997). In the Yukon River, Canada, DOC concentrations were highest in May and 50% of annual DOC transport took place during spring under high flow (Gueguen et al. 2006). High DOC concentrations were also observed at the beginning of the snowmelt season in a Colorado headwater stream (Hood et al. 2005). Even when DOC concentrations do not increase with discharge, the total annual transport is strongly influenced by hydrological regime because seasonal variation in discharge usually exceeds seasonal variation in DOC concentrations. In pristine boreal forest streams in Quebec, Canada, DOC concentrations were relatively low and constant during the spring freshet, and higher during the productive summer and autumn (Naiman 1982). Nonetheless, the 2-month stream freshet accounted for roughly half of annual discharge and 50% of DOC exports.

A longitudinal increase in DOC concentrations was reported for first- through seventh-order streams in Michigan and Pennsylvania (Moeller et al. 1979), but this was not corroborated by Webster et al.'s (1995) analysis of streams of the eastern United States. Whether such a pattern exists for unmodified streams, but is frequently masked by anthropogenic influence, is unresolved. As Webster et al. point out, with over 24,000 sewage treatment plants in the eastern United States, natural levels of DOC are largely unknown for rivers of that region larger than third order. As with FPOM, total inputs to a stream reach are difficult to measure, and whether the DOM originated within or from outside the stream is usually unknown.

12.3 Processes

Instream primary production and terrestrial production that enters streams as allochthonous material will either be utilized by stream heterotrophs or exported from the system, usually downstream and possibly to the oceans. Organic matter can accumulate over relatively short periods, on the timescale of weeks to months, and storage on or within the streambed and on banks and floodplains can occur on the timescale of years to decades. Storage of organic matter depends on flow variation, as material tends to accumulate during low flows and be exported by high flows. Averaged over long periods, storage is thought to be negligible, at least for streams of low order. Thus, factors that influence the relative rates of conversion of organic C to CO_2 versus transport largely determine what fraction of organic matter is mineralized within stream ecosystems, and this is expected to differ among organic matter compartments. A high rate of utilization relative to transport indicates that organic matter is contributing to stream metabolism and the stream ecosystem is efficient in its processing of organic C inputs. The opposite result indicates that most organic matter is exported downstream and the stream ecosystem is inefficient.

12.3.1 Benthic respiration

Benthic respiration is the integrative measure of stream metabolism and C utilization from all sources. It includes respiration by primary producers, microbial heterotrophs, and animals, which as mentioned earlier can be visualized as R_A of autotrophs and R_H of heterotrophs. Respiration by microorganisms often is the largest component of R_H, reflecting the important roles of bacteria and fungi in the breakdown of organic matter and their ability to utilize labile DOM from streamwater. Because metabolic processes are strongly temperature dependent, respiration is expected to vary with temperature, as Bott et al. (1984) reported for streams in Michigan and Pennsylvania, and in general to be strongly seasonal. Total respiration should increase with increasing amounts of benthic organic matter (BOM), but the quality of BOM is at least as important as quantity (Findlay et al. 1986a). In a Tennessee woodland stream, respiration was highest in early spring due to high GPP and infall after leaf input, which are periods of moderate temperature, and low during the warmer midsummer period because of low organic matter supplies (Roberts et al. 2007). A downstream increase in benthic respiration might be expected if total C inputs increase, because warmer temperatures stimulate higher rates, or because larger rivers receive greater inputs from domestic sewage or agricultural runoff. Due to the scarcity of data for large rivers, changes in R with increasing river size are poorly documented. However, downstream increases in R have been reported in systems as disparate as the highly autotrophic Salmon River (Minshall et al. 1992) and highly heterotrophic blackwater rivers in Georgia (Meyer and Edwards 1990).

In a cross-biome comparison of 22 streams, Sinsabaugh et al. (1997) analyzed stream benthic respiration rates in relation to BOM, temperature, primary production, and other system variables. Benthic respiration was directly proportional to stream temperature and, presumably due to high rates of utilization, the standing stock of BOM was inversely related to stream temperature (Figure 12.7). Owing to these offsetting trends, specific respiration per gram of benthic organic C was strongly related to temperature. Because the coefficient of this relationship was too high for a simple metabolic response, Sinsabaugh inferred that other factors also must be operating, such as higher quality BOM or greater nutrient availability in streams of

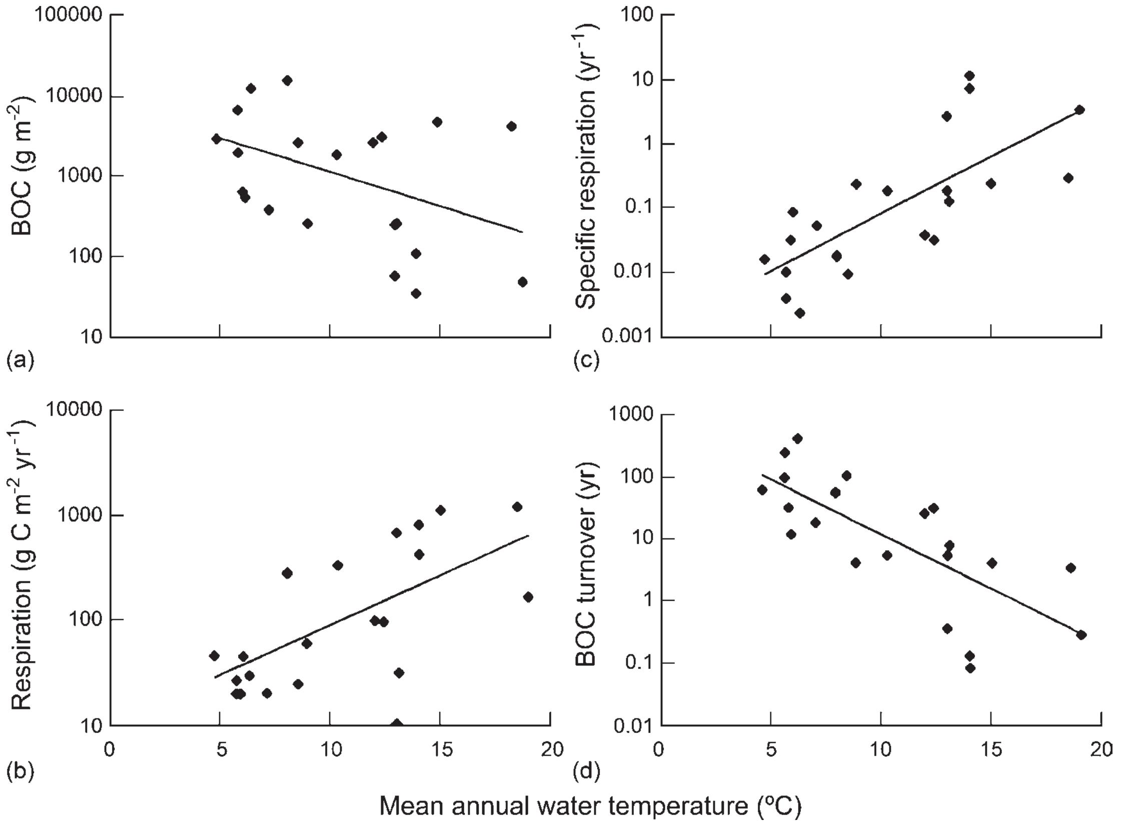

FIGURE 12.7 Relationships of respiration rate and standing stock of benthic organic carbon (BOC) with stream temperature for 22 streams. (a) BOC decreases and (b) respiration rate increases with mean annual water temperature. (c) Specific respiration increases and (d) the turnover time of BOC decreases with increasing temperature. See text for further explanation. (Reproduced from Sinsabaugh et al. 1997.)

warmer climates. The mean respiration rate of 265 g C m^{-2} year^{-1} calculated from the data set analyzed by Sinsabaugh et al. (1997) was considerably lower than the average of 739 g C m^{-2} year^{-1} calculated by Webster et al. (1995) from 61 streams of the eastern deciduous biome of the United States. Differences may be partly attributable to methods and partly to stream type and climate. Neither synthesis found a clear influence of stream order, and it may be that longitudinal studies of a single system rather than cross-system comparisons of streams are better suited to the investigation of downstream trends.

12.3.2 Coarse particulate organic matter dynamics

The breakdown of leaf litter and its conversion into FPOM and DOM are well-studied processes (Section 7.1). Physical abrasion, softening of leaf tissue by wetting and the initial leaching of DOM, colonization by fungi and bacteria, and feeding by consumers all contribute to the conversion of CPOM into FPOM and DOM. Leaf breakdown can occur at very low temperatures, but rates are more rapid as temperature increases, and are influenced by the presence of shredders, availability of nutrients, and whether leaves are buried or exposed. The overriding influence, however, is leaf type (Figure 7.2), which results in a fast-to-slow continuum of leaf breakdown rates. In their synthesis of many studies from 11 streams at the Coweeta Hydrologic Laboratory, the average leaf breakdown rate was found to be 0.0098 day^{-1}, which implies the loss of 50% of initial mass after 71 days (Webster et al. 1999).

Transport rates are expected to vary with POM size, flows, and the retentiveness of the stream channel. High discharges will entrain and transport even large particles, as can be seen from the export versus discharge relationship for a headwater stream in North Carolina (Figure 12.8). Based on a small number of direct measurements, however, the distances traveled by CPOM are surprisingly short. Leaves typically are trapped by obstructions within a few meters of their point of entry to the channel (Webster et al. 1994) and often are broken down in place without further transport, although they can move tens of meters in storms. Using rectangles of waterproof paper, Webster et al. estimated an average distance of about 1.5 m from first entry to the stream, depending mainly on depth and likelihood of encountering an obstacle. Wallace et al. (1995) recorded movements of spray-painted red maple leaves and small pieces of colored plastic transparency sheets for up to 4 years. Although few natural leaves were recovered after about 5 months, no differences were observed between natural and artificial leaves, which, over the 4-year study, moved on average 10-20 m $year^{-1}$. The comparison of leaf breakdown to transport rates makes a strong case that, at least for the small streams where most research has been conducted, CPOM is transformed into other organic matter size classes or mineralized rather than exported.

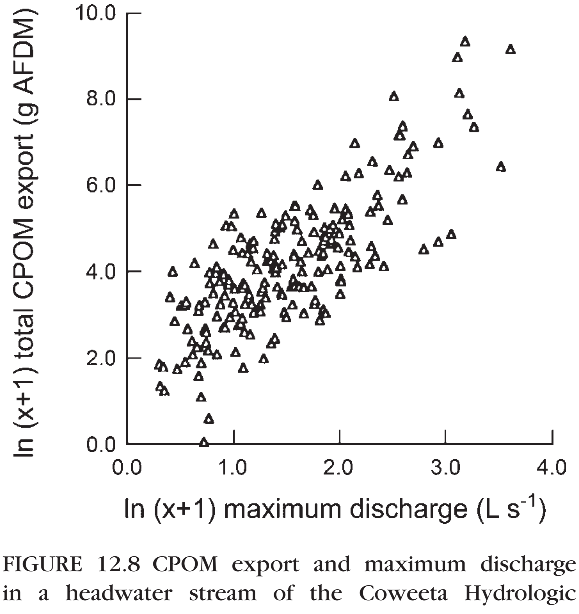

FIGURE 12.8 CPOM export and maximum discharge in a headwater stream of the Coweeta Hydrologic Laboratory, North Carolina. (Reproduced from Wallace et al. 1995.)

12.3.3 Fine particulate organic matter dynamics

The ingestion of particles by collector-gatherers and filter-feeders acts both as retention and utilization, as some fraction of the ingested material is digested and metabolized by the animal consumer. There does not appear to be any estimate of the potential magnitude of this effect owing to benthic collector-gatherers. However, filter-feeders typically consume only a small fraction of transported particles, <1% of annual transport in one estimate (Webster 1983). Thus, microorganisms, mainly bacteria, appear to be responsible for most of the breakdown and remineralization of the organic C of FPOM that occurs within stream ecosystems. However, this interpretation may reflect inadequate study of benthic detritivores. Rosi-Marshall and Wallace (2002) estimated considerable ingestion of amorphous detritus by macroinvertebrates in a mid-order river in North Carolina, but their impact on system-level degradation of benthic FPOM is largely unknown.

Unlike CPOM with its abundance of direct measurements of breakdown rates, the utilization of FPOM is poorly documented, although microbial utilization can be approximated from measurements of respiration rates. Using laboratory measurements of benthic FPOM respiration, Webster et al. (1999) estimated breakdown rates 0.00104 day^{-1}, for a half-life of about 1.8 years. Respiration rates are expected to decline over time as FPOM mass is lost, leaving more refractory material behind, but supporting evidence is weak (Sinsabaugh et al. 1991). Seasonal and latitudinal variation in temperature has a strong influence on respiration rates (Figure 12.7) and thus on the utilization of FPOM (Webster et al. 1999).

FPOM transport distance can be estimated by releasing a known quantity of particles into the stream and measuring water column concentrations at various distances downstream. The decline in particle concentration is fit to an exponential decay equation, and the inverse of the decay coefficient is a measure of average transport distance of a particle before being retained on the streambed. Using corn pollen as a surrogate for FPOM (it is similar in diameter but less dense), Miller and Georgian (1992) estimated mean transport distances of 100–200 m in a second-order stream in New York. Estimated transport distance for natural FPOM labeled with radiocarbon in the Salmon River headwaters of Idaho ranged from 150 to 800 m (Cushing et al. 1993, Newbold et al. 2005). Assuming that particle resuspension occurs every 1.5–3 h and an average transport distance per event of 500 m, Cushing et al. calculate an average downstream transport of $4-8\,\text{km day}^{-1}$. Much greater transport distances, between 3,000 and 10,660 m, were estimated for a sixth-order lowland river, using spores of *Lycopodium clavatum* with a fluorescent label, and distances were greater under faster currents (Wanner and Pusch 2001). Longer transport distances in larger rivers may reflect fewer opportunities for particle entrapment, whereas the extent of water exchange between surface flows and the hyporheic zone has been shown to correlate with transport distances in smaller streams (Minshall et al. 2000).

Owing to the relative slow rate of utilization of FPOM estimated from respiration measurements, and the relatively long transport distances combined with frequent resuspension, export rather than mineralization appears to be the dominant fate of FPOM from studies of smaller streams and rivers.

12.3.4 Benthic organic matter retention

The standing stock of POM is the amount residing within the stream channel, referred to as coarse benthic organic matter (CBOM) and fine benthic organic matter (FBOM). It reflects the balance between the inputs just described and losses due to breakdown and transport. CBOM is expected to decrease with increasing stream order owing to declines in riparian inputs and lower retention. This is supported by data from first- through fourth-order streams at Coweeta (Wallace et al. 1982b), from Hubbard Brook (Meyer and Likens 1979, Bilby and Likens 1980), and from sites in Michigan and Pennsylvania (Minshall et al. 1983). CBOM typically is greatest in autumn after leaf fall and lowest in late summer, whereas FBOM shows less evidence of seasonal variation (Mulholland et al. 1985b). However, interannual variation appears to be small. In Bear Brook, New Hampshire, midsummer leaf and twig BOM varied only twofold over 4 years of measurements (Meyer and Likens 1979). Clearing of the riparian zone can substantially lower CBOM standing stocks (Karlsson et al. 2005), and catchment urbanization is negatively correlated with the amount of FBOM (Meyer et al. 2005).

BOM storage is influenced by the magnitude of terrestrial organic matter inputs and by the retention capacity of the river channel (Jones 1997). BOM is generally dominated by wood followed by coarse and fine materials; however, in some systems FBOM exhibits a greater contribution than CBOM (Newbold et al. 1997, Martinez et al. 1998, Galas and Dumnicka 2003). In first- and second-order streams of the eastern United States, nonwoody BOM ranged between 182 and $855\,\text{g m}^{-2}$, in large measure due to differences in storage and retention among stream habitats and bottom substrate (Webster et al. 1995). FBOM was nearly 60% of the total. Over 80% of BOM was estimated to be buried in a Virginia coastal stream (Smock 1990), and for this reason benthic stocks often may be inadequately sampled. High temporal variability was reported for the Njoro River in Kenya, where BOM accumulation ranged from 97.3 to 6691.8 3 g ash-free dry weight m^{-2}, probably due to variability in litter inputs and discharge.

The retention of BOM is affected by a number of stream features that vary with location and thus potentially determine the efficiency of a stream reach in processing inputs. Retention is likely to be greatest when current velocity is low, when boulders or other channel features create depositional locations and cause accumulation of organic material, when macrophyte beds reduce water velocity, and when floodplain connectivity allows flooding rivers to overflow their banks, slowing the passage of water and material downstream. By increasing the retentiveness of stream reaches, such features should increase the amount of organic matter respired by the consumer community and decrease the amount exported downstream. As retention varies among locations, seasons, or stream types, so should the relationship between processing and export.

Depositional areas, especially pools and around wood accumulations, are important locations of FBOM retention. Logs are a particularly important retention device in low-order streams of forested catchments. Accumulations of organic matter formed when wood becomes lodged against obstructions trap smaller material and leaves into a nearly watertight structure. Sediments and organic matter settle in the pools formed upstream of these dams, creating potential hotspots of detrital processing. Following experimental removal of all organic dams from a 175 m stretch of a small New Hampshire stream, organic matter export increased severalfold (Bilby and Likens 1980, Bilby 1981).

Log dams become less common as stream size increases. An inventory of organic matter standing stock by Bilby and Likens revealed that 75% was contained in log dams in first-order streams, compared to 58% at second-order and 20% at third-order sites. However, the history of logging at the site and maturity of the forest will influence the amount and size of available large wood. This New Hampshire location was in second-growth forest and log dams rarely occurred at channel widths greater than 7 m, whereas much larger log dams were found in streams in Oregon flowing through mature stands of Douglas Fir. There also is evidence that wood dams may be more abundant in conifer compared to deciduous forests (Harmon et al. 1986).

When beaver (*Castor canadensis*) were unexploited they must have contributed greatly to organic matter storage over large areas of the north temperate zone. Where beaver occur at natural densities today, their activities influence 2–40% of the length of second- to fifth-order streams, and increase the retention time of C roughly sixfold (Naiman et al. 1986). In large rivers, the floodplain can be a primary site of POM deposition and storage, and biotic structures such as macrophyte beds are important retention features for POM (Wanner and Pusch 2001).

In addition to organic matter accumulations associated with wood dams, stream channel features including pool–riffle succession and the presence of boulders affect retention of POM, and their influence can vary with hydrology. Retention of CPOM was higher in natural meandering sections than in straightened sections of a third-order stream in New Zealand (James and Henderson 2005). Hoover et al. (2006) documented a number of effects of streambed geometry on leaf retention depending on flow and channel features. Protruding boulders were important in retaining leaves in riffles, but not in pools, where leaves simply settled to the bottom. Leaf retention was greater in locations of greater depth and lower water velocity relative to reference streambed measurements across the river channel. The relative importance of pool versus riffle retention changed seasonally in the Njoro River, Kenya, where more CPOM was retained in pools than riffles during high flows, but the retentiveness of these channel features was similar at low flows (Magana and Bretschko 2003). Nakajima et al. (2006) also noted that CPOM accumulated in pools during periods of high flow, probably due to lower velocities near the streambed in pools.

12.3.5 Dissolved organic matter dynamics

High uptake rates for dissolved organic C are reported for labile molecules including leachate from leaves and highly productive algal mats, and the addition of nutrients often increases DOC uptake (Section 7.3.2). However, the majority of DOC enters streams from soil and groundwater and includes a heterogeneous mix of bioavailable, refractory, and perhaps inhibitory compounds, making total DOC a poor predictor of microbial metabolism. Although the rate of utilization of the DOC pool by heterotrophs is difficult to estimate, the majority of studies point to biological assimilation as the principal removal process, varying with the fraction of DOC that is labile.

By measuring uptake coefficients of DOC using ^{13}C-labeled leaf leachate in mesocosms, Wiegner et al. (2005) estimated that the most readily assimilated DOC fraction would travel 175 m in White Clay Creek before being immobilized, and a second DOC pool they described as of intermediate lability would travel 3,692 m. These distances represented 7% and 150% of the third-order reach length, respectively, suggesting that readily available DOC was an energy input at the reach scale, whereas less available material was exported and potentially served as a subsidy to downstream ecosystems. Because this experiment used fresh leachate rather than material aged by passage through the soil, uptake distances may be underestimated. However, other studies have found that DOC in transport can support 11–55% of the benthic bacterial metabolism in streams and rivers (Bott et al. 1984, Findlay et al. 1993b, Fischer et al. 2002a, Sobczak and Findlay 2002). In the mesocosms studied by Weigner et al., DOC met from one third to one half of the bacterial C demand, depending on the importance of algal production.

Despite many measures of DOC concentrations and a reasonably good understanding of factors that influence spatial and temporal variation, neither input nor utilization rates are well quantified on an areal basis. At least in small streams, downstream transport rather than utilization appears to be the fate of most DOC entering stream reaches. Over the entire length of rivers, however, owing to greater DOC utilization in large lowland rivers, it appears that a substantial proportion of organic C inputs are indeed converted to CO_2. In the lower Hudson River, New York, DOC is the largest pool of organic C, and its concentrations decrease from mile 245, near Albany, toward New York City (Figure 12.9), which implies mineralization owing to heterotrophic activity. Based on an

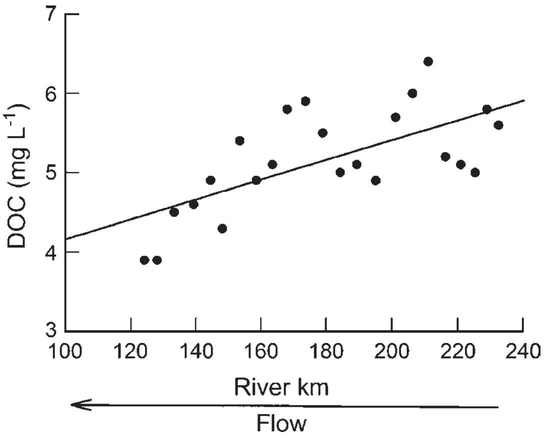

FIGURE 12.9 DOC concentrations along a longitudinal transect in the Hudson River, from Albany, New York, at river kilometer 245 toward New York City at kilometer 0. The downstream decrease in DOC concentrations is consistent with a loss of 100 g C m^{-2} year^{-1} of allochthonous organic C. (Reproduced from Cole and Caraco 2001.)

8-year record, the lower Hudson was almost always supersaturated with CO_2 (Cole and Caraco 2001). Analysis of an additional 46 large rivers worldwide found that the majority of large rivers are net sources of CO_2 to the atmosphere, evidence of considerable metabolic activity. As one example, the Amazon Basin exports 13 times more C as CO_2 to the atmosphere than as DOC or POC to the oceans (Richey et al. 2002). In both the Amazon and the Hudson, the age of organic matter decreases downstream, suggesting that the old C exported from the terrestrial systems is mineralized and replaced by younger C in the lower reaches. Cole and Caraco (2001) estimate that, on average, 43% of the organic C inputs to rivers are converted to CO_2 while in transport. Thus, although headwater through mid-order stream ecosystems undoubtedly export large quantities or organic matter to lower river reaches, large rivers may be capable of mineralizing a substantial amount of the C that enters from terrestrial ecosystems.

12.4 Stream Ecosystem Metabolism

Total respiration provides a single, integrative measure of all metabolic activity within a stream ecosystem, but we also wish to know what fraction is supported by primary production within the stream versus C fixed on land; what fraction of total inputs are respired; and the magnitude of export to downstream ecosystems. Three main approaches have been employed to address these questions. Organic energy budgets, including energy inputs and losses, allow insightful cross-system comparisons and are the basis for calculation of the overall efficiency with which ecosystems use available energy (Webster and Meyer 1997). The P/R ratio and NEP indicate whether an ecosystem is reliant on internal production or requires organic matter subsidies to sustain respiration. The distance traveled by an atom of C in organic form until it is mineralized to CO_2 provides a comparative measure of an ecosystem's efficiency in processing organic material (Newbold et al. 1982b).

12.4.1 Organic matter budgets

A mass balance or budget analysis is an accounting of all inputs of organic matter to and outputs from some delimited area of an ecosystem (Figure 12.10). This can be a stream or river reach, or in the case of small headwater streams, the entire catchment. Organic matter budgets attempt to measure all inputs, including primary production, POM from leaf litter and other sources, and DOM primarily from groundwater; all standing stocks of CBOM, FBOM, and wood; and ecosystem outputs as respiration and export. Budgets can reveal important transformations that occur within the study system (e.g., CPOM might dominate inputs while FPOM dominates outputs), thereby lending insight into the physical and biological processes that alter the quantity and quality of material within the stream. Coupled with measurement of internal fluxes and the processes that are responsible, the budget approach can provide considerable insight into the flow of material through ecosystems.

In their landmark study of a 1,700 m reach of Bear Brook, a small woodland stream in New Hampshire, Fisher and Likens (1973) pioneered the use of organic matter budgets in running waters. Organic matter inputs from litter, throughfall, and surface and subsurface water were quantified. Because impermeable bedrock underlies this drainage basin, all hydrologic outputs could be estimated from streamflow and organic matter concentrations measured at a weir. The amount of stored material in Bear Brook was assumed to be constant, and on this basis respiration was determined from the excess of imports over exports. From the annual energy budget for Bear Brook (Table 12.2), it appears that greater than 99% of the energy inputs were due to allochthonous material (with particulates contributing more than dissolved matter), and about

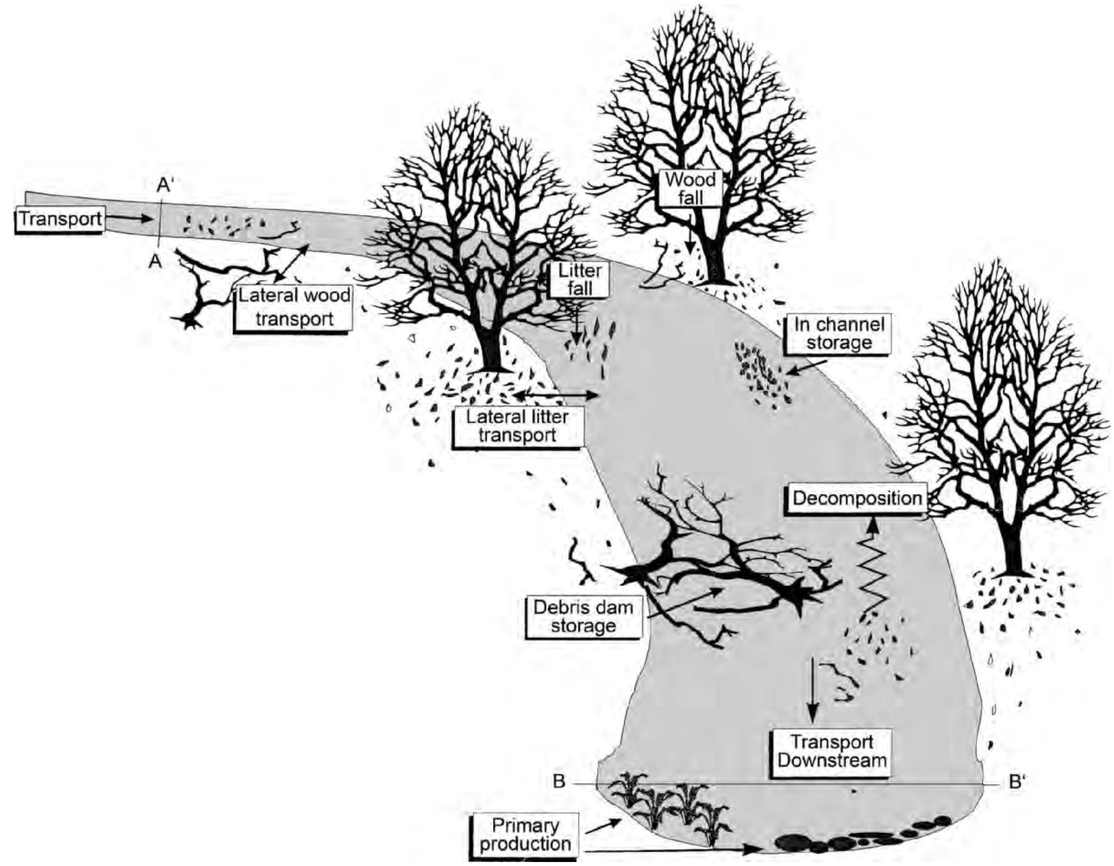

FIGURE 12.10 Inputs, outputs, and standing stocks of organic matter for a forest stream segment defined by the transects A-A′ and B-B′. (Reproduced from Minshall 1996.)

65% of this was exported downstream. More POM was exported from the study segment than entered it from upstream, and this difference was made up by inputs of litterfall. Virtually all internal processing was attributed to microorganisms.

Organic matter budgets have since been constructed for a number of river ecosystems spanning a range of conditions. A predominance of allochthonous inputs seems to be the rule wherever there is ample riparian vegetation. In a first-order blackwater stream in Virginia with a tree canopy along its entire length, litterfall represented 100% of total inputs (Smock 1997). The C budget of the Kuparuk River, originating in the Brooks Range of Alaska and flowing northwards into the Arctic Ocean, is almost totally dominated by allochthonous inputs (Peterson et al. 1986). In this tundra stream meandering through peatland, allochthonous inputs of peat and tundra plant litter exceeded benthic algae primary production by almost an order of magnitude. Although the Kuparuk River is unshaded, cold temperatures and low phosphorus concentrations limit periphyton production. Subsequent estimates show that NPP by mosses is similar in magnitude to benthic algal production, increasing the total contribution of autochthonous C to this river but not altering the main finding that primary production is modest (Harvey et al. 1997).

TABLE 12.2 Organic matter budget for Bear Brook, New Hampshire, in the Hubbard Brook Experimental Forest. Bear Brook is a second-order stream, with a catchment area of 132 ha and a streambed area of $6,377\,m^2$. (Adapted from a compilation of studies by Findlay et al. 1997.)

Organic matter parameters	
Inputs (g AFDM m^{-2} $year^{-1}$)	
Gross primary production	3.5
Litterfall and lateral movement	594
Groundwater DOM	95
Standing crops (g m^{-2})	
Wood > 1 mm	530
CBOM > 1 mm (not including wood)	610
FPOM < 1 mm	53
Outputs	
Autotrophic respiration (g m^{-2} $year^{-1}$)	1.75
Heterotrophic respiration (g m^{-2} $year^{-1}$)	101
Particulate transport (kg $year^{-1}$)	1700
Dissolved transport (kg $year^{-1}$)	514

TABLE 12.3 Organic matter budget for Sycamore Creek, Arizona. Sycamore Creek is a fifth-order stream with a catchment area of 50,500 ha and a streambed area of $33.1\,m^2$. Budget is based on a compilation of studies by Jones (1997).

Organic matter parameters	
Inputs (g AFDM m^{-2} $year^{-1}$)	
Gross primary production	1,888
Litterfall	16.5
Lateral movement	3.1
Standing crops (g m^{-2})	
CBOM > 1 mm (not including wood)	5.2
BOM (not including leaves and wood)	104
Hyporheic FPOM	39
Outputs	
Autotrophic respiration (g m^{-2} $year^{-1}$)	944
Heterotrophic respiration (g m^{-2} $year^{-1}$)	372
Hyporheic respiration (g m^{-2} $year^{-1}$)	3259
Particulate transport-baseflow (kg $year^{-1}$)	11,900
Dissolved transport (kg $year^{-1}$)	506,000

The autochthonous component of organic matter budgets is expected to increase downstream as rivers increase in width and the effects of shading and allochthonous inputs from riparian vegetation diminish. In subarctic streams in Quebec, Canada, allochthonous material contributed over 75% of total inputs in streams of low order (Naiman and Link 1997). In contrast, allochthonous inputs contributed only 6–18% of the total in larger streams of order five and six. The contribution of autochthonous organic matter to total inputs was positively related to stream order in a synthesis of organic matter budgets from 35 streams located in North America, the Caribbean, Europe, and Antarctica (Webster and Meyer 1997). Arid-land streams are an exception because they are open to the sun and receive few litter inputs.

Instream primary production typically dominates organic matter budgets in desert (Minshall 1978, Fisher et al. 1982, Jones et al. 1997) and Antarctic streams (McKnight and Tate 1997). Primary production in Sycamore Creek, Arizona, was sufficiently high that it substantially exceeded community respiration (Table 12.3); the excess was accounted for by accrual of algal biomass and by downstream export. In a meltwater stream in the McMurdo Dry Valleys of Antarctica, primary production by algal mats, composed primarily of filamentous cyanobacteria, was the only C source; unsurprisingly, in a land without terrestrial vegetation, allochthonous inputs were zero. Although autochthonous production may be low in many stream types, Minshall (1978) argued that the role of instream primary production has been underappreciated. Photosynthetic NPP exceeds litter inputs in a number of examples (Table 12.4), and there is a fairly obvious alternation in their relative importance depending upon forest canopy development.

Few organic matter budgets have been constructed for segments of large rivers. Bayley (1989) constructed a C budget for a 187 km stretch (maximum inundated area of $5,330\,km^2$) of the Solimões River (the Amazon above Manaus) that clearly is approximate. Nonetheless, it indicates that only a small fraction of the

TABLE 12.4 Comparison of energy inputs from net primary production (NPP) versus litterfall for a number of spring and running water studies. Additional inputs (e.g., groundwater, transport from upstream) are not considered here. (From Peterson et al. 1986, after Minshall 1978.)

River	*Energy input (g C m^{-2} $year^{-1}$)*		
	Autochthonous NPP	*Allochthonous litter inputs*	*Reference*
Bear Brook, NH	0.6	251	Fisher and Likens (1973)
Kuparuk River, AK	13	100–300	Peterson et al. (1986)
Root Spring, MA	73	261	Teal (1957)
New Hope Creek, NC	73	238	Hall (1972)
Fort River, MA	169	213	Fisher (1977)
Cone Spring, IA	119	70	Tilly (1968)
Deep Creek, ID 1	206	0.2	Minshall (1978)
Deep Creek, ID 2	368	7	Minshall (1978)
Deep Creek, ID 3	761	1.1	Minshall (1978)
Thames River, United Kingdom	667	16	Mann et al. (1970)
Silver Springs, FL	981	54	Odum (1957)
Tecopa Bore, CA[a]	1229	0	Naiman (1976)

[a] Thermal spring

total C supply originates with transport of material from upstream (<1%), or as primary production by river phytoplankton (5.4%) and periphyton attached to macrophytes (1.5%). Production by aquatic and terrestrial macrophytes in the littoral regions and floodplain, and litter inputs from the flooded forest, collectively account for approximately 90% of C production, and so river–floodplain interactions appear to be of far greater consequence than events within the channel. Findings from the Orinoco floodplain were similar: forest litter represented 27% and macrophytes 68% of total C sources, and inputs from phytoplankton and periphyton production together contributed only 2% (Lewis et al. 2001). In a sixth-order blackwater river in Georgia, river channel GPP accounted for only about one fifth of total inputs, which were dominated by floodplain organic matter originating in extensive riparian swamps of up to 1–2 km in width (Meyer and Edwards 1990).

A synthesis of 36 organic matter budgets from six different biomes reveals distinct trends related to landscape controls of inputs (Webster and Meyer 1997). A principal components analysis of major budget components categorized streams along a first axis that was positively correlated with litterfall and BOM, and negatively correlated with primary production; and a second axis that was strongly correlated with POM and DOM concentrations, and thus organic matter transport (Figure 12.11). Small mountain streams cluster in the lower right of Figure 12.11, sharing the characteristics of high litterfall and BOM, and low GPP. Lowland streams have much higher organic matter concentrations and thus greater transport, and arid-land streams fall at the opposite end of the first axis with high GPP and low litterfall and BOM. Thus, climate, terrestrial biome, and position along the elevational gradient can be seen to be important underlying controls on stream organic matter budgets.

The budget approach to organic matter dynamics has been highly informative, but its limitations must be acknowledged. Missing terms are common, particularly DOM sources, POM inputs from floodplains, and storm transport of POM. Inputs, outputs, and storage can vary substantially among years, but because of the effort

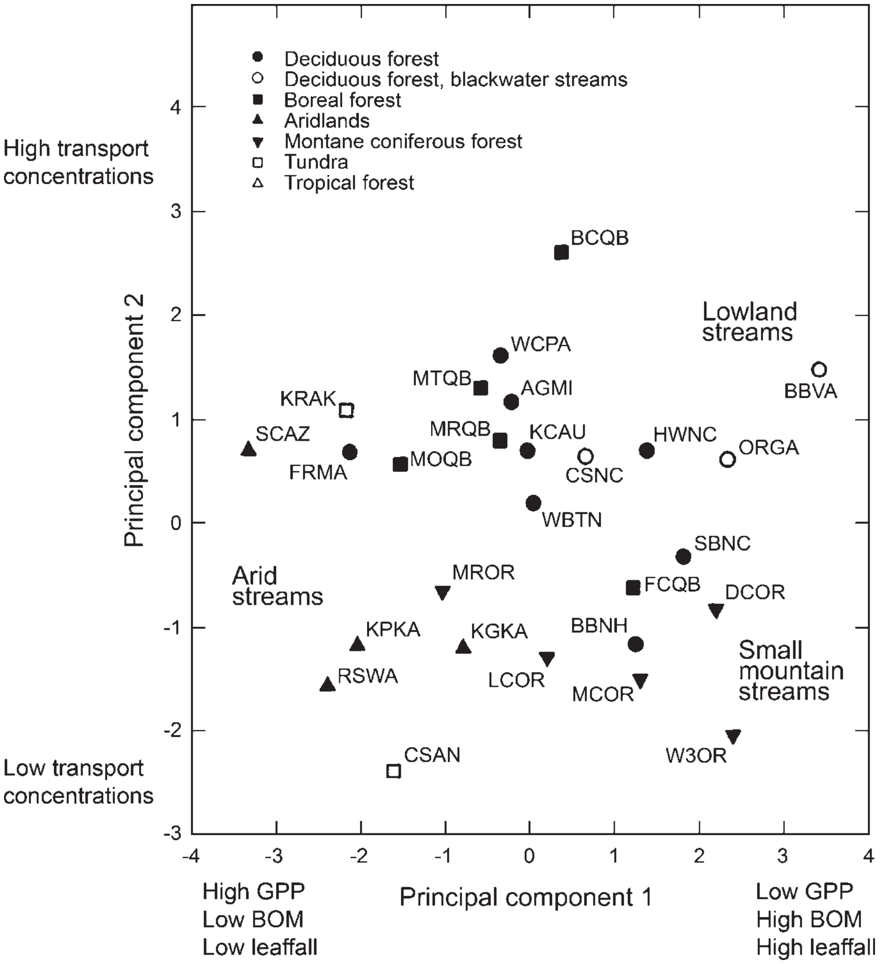

FIGURE 12.11 A principal components analysis of 25 stream energy budgets from six biomes shows that arid streams, small mountain streams, and lowland streams separate along axes determined by energy inputs, benthic organic matter (BOM), and transport rates of organic matter. See text for further explanation. (Reproduced from Webster and Meyer 1997.)

involved, organic matter budgets often are estimated for just 1 year, or pieced together with data from multiple years. In a comparison of 23 organic matter budgets from rivers of various sizes, located in different biomes, only one was in steady state (Cummins et al. 1983). Substantial accrual of stored organic matter occurred in 14 budgets, while exports exceeded imports in the remaining eight. The input–output balance for 17 streams reported by Webster and Meyer (1997) included several cases where outputs exceeded inputs by a large margin. These authors argue that it is unlikely that exports will be higher than inputs in annual budgets, and suggest that underestimation of inputs from groundwater and floodplains may be responsible for the imbalance. In addition, interannual variation in disturbances such as fire, storms, and logging that may occur infrequently are important to ecosystem dynamics, and they are unlikely to be incorporated in a 1-year "snapshot." For example, FPOM export varied fourfold over a 7-year study in a Coweeta stream (Wallace et al. 1997), and Triska et al. (1983) found a similar range over 2 years in an Oregon stream. Ideally, any ecosystem budget should be placed in a historical context in order to capture among-year variation in processing, storage, and export.

12.4.2 The P/R ratio

The ratio of GPP to total ecosystem respiration, the P/R ratio, has long been used as a simple index of the relative importance of energy fixed by primary producers within the stream versus allochthonous organic matter derived from terrestrial plant production. Stream ecosystems at the two extremes are commonly referred to as autotrophic, meaning that energy is supplied through instream photosynthesis versus heterotrophic, where metabolism is based on the utilization of imported dead organic matter and microbial production. According to some interpretations, the ecosystem is supported primarily by autochthonous production when $P/R > 1$. When $P/R < 1$, respiration exceeds production and the stream ecosystem depends on organic matter synthesized outside the stream (Fisher and Likens 1973). The relative importance of autochthonous versus allochthonous basal resources in supporting total ecosystem respiration is a key issue in stream metabolism. There is ample evidence that this balance changes with stream size and shade, and a general expectation of a metabolic transition from heterotrophy to a greater role of autotrophy as one proceeds downstream (Figure 1.7). Although the general concept has validity, interpretation of P/R ratios is more complicated, and $P/R = 1$ is probably not an appropriate transition value (Rosenfeld and Mackay 1987, Meyer 1989).

The problem with using $P/R = 1$ as the metabolic transition value can be illustrated with a simple example of a fully autochthonous system in which the only energy supply is instream primary production, and all production is consumed and thus respired. Such a system will have its $P/R = 1$ and be completely dependent upon autochthonous production. As Minshall (1978) points out, if a small amount of allochthonous matter enters this system, its P/R will decline, even though ecosystem respiration is almost entirely due to autochthonous production.

The central issue is whether stream metabolism, as measured by ecosystem respiration, depends mainly on energy produced within the stream, or on energy imported from outside. For reasons explained below, a $P/R < 0.5$ indicates a community strongly dependent upon allochthonous C (Meyer 1989). A $P/R > 1$ signals an autotrophic ecosystem, and its excess production must be exported downstream or stored in the stream channel. The value of the transitional P/R falls somewhere between.

To better understand the difficulties of interpreting P/R ratios, recall that R is total ecosystem respiration, which is the sum of respiration by autotrophs (R_A) and by heterotrophs (R_H). R_A is often assumed to be 40–50% of GPP (Likens 1975), and the relation $NPP = 0.556 \times GPP$ is frequently used to convert GPP into NPP (e.g., Webster et al. 1995). However, because algae have so little supporting tissue, their respiration may be closer to 25% of GPP (Geider and Osborne 1989), and so NPP would be a larger fraction of GPP. R_H can be further broken down into respiration supported by autotrophic production and respiration supported by allochthonous sources. Whichever is the larger fraction of R_H is the true measure of autotrophy versus heterotrophy. Unfortunately, we cannot separately measure these components of ecosystem respiration, which are combined in the widely used diel oxygen curve method.

As a further caveat, it is not possible to determine what fraction of ecosystem respiration is supported by autochthonous versus allochthonous sources, nor how much is due to C respired by microorganisms versus energy flow through invertebrates and fishes. Thus, microorganisms may derive their energy from both autochthonous and allochthonous sources, and metazoans primarily from autochthonous sources (Thorp and DeLong 1994, 2002). This sort of reasoning may help to explain a striking discrepancy between Bayley's (1989) analysis of C flux in the Rio Solimões, which showed most C originating as detritus from aquatic and floodplain macrophytes, and other investigations directed at the food chain itself. Analysis of the stable isotope of C (^{13}C) in fish tissue and in various plants demonstrates that the food chain supporting an abundant group of detritivorous fishes, the Characiformes, begins with phytoplankton and not macrophyte detritus as might be expected (Araujo-Lima et al. 1986). In the Orinoco floodplain, phytoplankton and attached microalgae again are the main source of C for fishes and aquatic invertebrates, despite the greater abundance of macrophytes and terrestrial litter (Hamilton et al. 1992, Lewis et al. 2001).

Although the P/R ratio should be interpreted with caution, particularly with respect to the value that signals a metabolic transition between autotrophy and heterotrophy, it remains a useful comparative measure. In their longitudinal study of the Little Tennessee River in North Carolina from a headwater site in Coweeta up to a sixth-order reach, McTammany et al (2003) document the downstream increase in P/R and NEP based on single-station, diel oxygen curves (Figure 12.12). By estimating the C budget at all four sites and correcting for R_A, the authors concluded that the stream's metabolic transition occurred at a $P/R = 0.78$, and at a location 52 km below its source. Note that this transition point is for ecosystem metabolism; for secondary production of macroconsumers supported primarily by autotrophic production, the transition may occur at a more upstream location.

A downstream increase in P relative to R is a common finding of streams with forested headwaters (Naiman 1982, McTammany et al. 2003). This is apparent, albeit with local variation, from daily GPP, R, and NEP determined in four rivers located in different biomes (Figure 12.13). Each stream system was located in a relatively undisturbed catchment, had as its uppermost station a forested headwater site, and took for its lowermost station the largest stream site that was relatively undisturbed (up to seventh-order). Oregon sites receive abundant precipitation, mostly as winter rain, and support dense conifer forests. Idaho sites lie in a cold arid region of the northern Rocky Mountains, where forest cover is less than other biomes and runoff is dominated by melt of the winter snowpack. Coniferous forest and scattered deciduous tree species are found at upper elevations, and sagebrush and grass vegetation at lower elevations. Michigan and Pennsylvania sites are in the eastern deciduous biome, with less-pronounced seasonality in precipitation and runoff than either of the western sites (Minshall et al. 1983). NEP was negative in upstream reaches at all sites, and the relative importance of autotrophy increased downstream and varied with biome vegetation. In landscape settings where the headwaters are not forested, including those originating in alpine meadows (Minshall 1978) as well as prairie and pasture streams (Wiley et al. 1990, Young and Huryn 1996), no longitudinal pattern may be apparent owing to high primary production in headwaters.

Comparisons of P and R among ecosystems reinforces the finding from organic matter budgets that differences in terrestrial vegetation and shade profoundly influence the importance of autochthonous versus allochthonous inputs to stream metabolism (Table 12.5). NEP was negative at six of eight low-order streams located in different biomes of North America (Mulholland et al. 2001). Six of the eight streams were forested, so this result is not surprising. P/R ratios from the 35-stream, six-biome, cross-system comparison of Webster and Meyer (1997) ranged from 0 to 1.66, and averaged 0.69. Considering that the transition from allochthony to autochthony occurs at a $P/R < 1$ and nearly half of the streams had a $P/R > 1$, the importance of

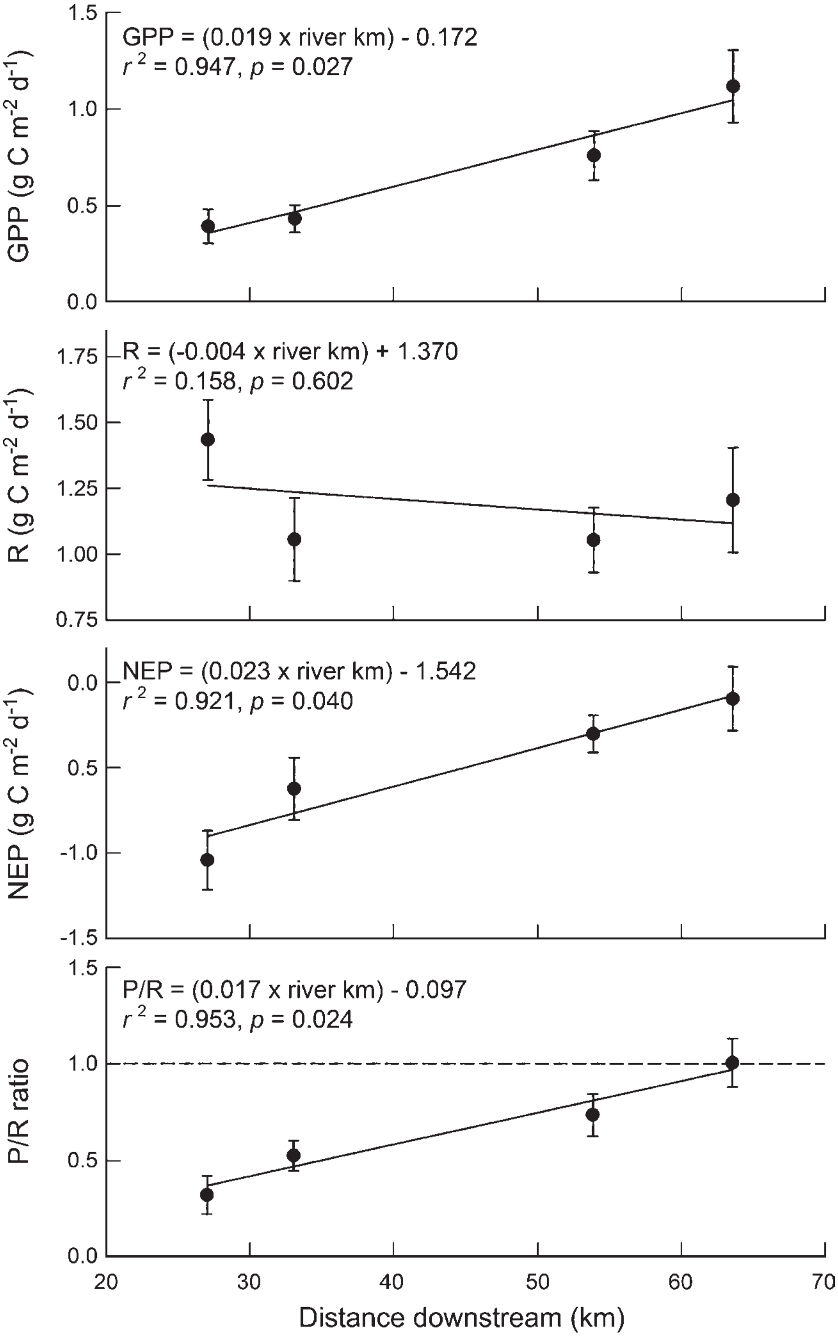

FIGURE 12.12 Relationships between gross primary production (GPP), respiration (R), net ecosystem production (NEP), and the P/R ratio with distance downstream from a forested headwater stream through sixth-order site on the Little Tennessee River, North Carolina. Values are means (± 1 SE). Dashed line represents P/R = 1. (Reproduced from McTammany et al 2003.)

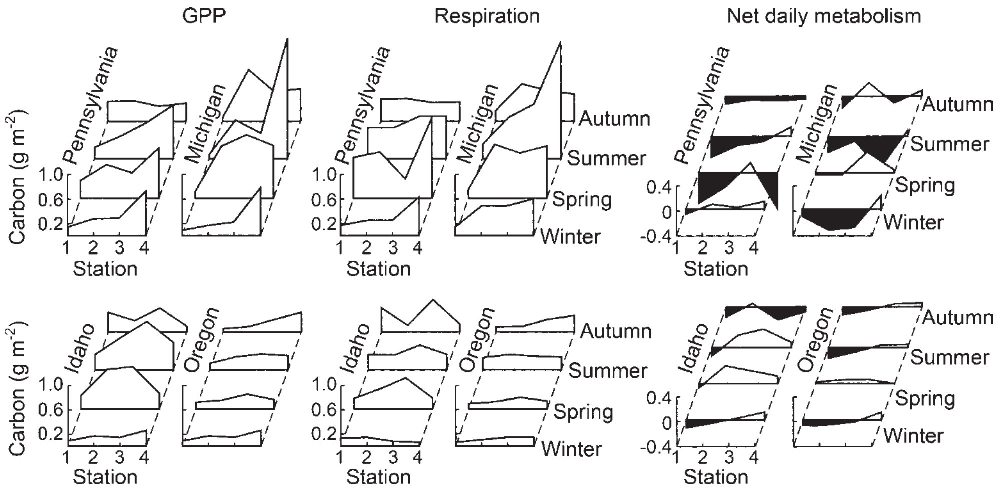

FIGURE 12.13 Rates of gross primary production (GPP), respiration (R), and net ecosystem production (NEP) based on 24 h measurements in benthic chambers containing substrate with periphyton. Four sites (1, uppermost; 4, lowermost) were studied in each region in each season. Note seasonal and regional variation, and a general trend toward increasing NEP at downstream sites. (Reproduced from Minshall et al. 1983.)

TABLE 12.5 Gross primary production (GPP), respiration (R), and P/R values from various stream studies, in g O_2 $m^{-2}day^{-1}$. (Modified from Edwards and Meyer 1986.)

River	*Sampling period*	*GPP*	*R*	*P/R*	*Reference*
Silver Springs, FL	Winter	8–35	2.8–5.0	2.9–7.0	Odum (1957)
Blue River, OK	Annual	3.0–21.5	7.7–12.6	0.39–1.67	Duffer and Dorris (1966)
River Ivel, United Kingdom	Summer	9.6	8.5	1.1	Edwards and Owens (1962a)
Truckee River, NV	August	8.1–9.5	11.4	0.83	Thomas and O'Connell (1966)
Buffalo Creek, PA	August	5.6	2.2	2.6	McDiffet et al. (1972)
Sycamore Creek, AZ	Summer	8.5	5.1	1.7	Busch and Fisher (1981)
Madison River, WY	Summer	4.8	1.6	3.0	Wright and Mills (1967)
New Hope Creek, NC	Annual	0.8	1.3	0.7	Hall (1972)
Fort River, MA	Annual	1.8	3.7	0.5	Fisher and Carpenter (1976)
Bear Brook, NH	Annual	0.01	1.5	0.01	Fisher and Likens (1973)
McKenzie River, OR	Annual	0.4–0.9	0.02–0.07[a]		Naiman and Sedell (1980)
Bayou Chevreuil, LA	Annual	2.1	2.7	0.7	Day et al. (1977)
Salmon River, ID	Annual	0.54–2.53	0.34–1.73[a]		Bott et al. (1985)
Kalamazoo River, MI	Annual	0.13–6.39	0.55–5.79[a]		Bott et al. (1985)
White Clay Creek, PA	Annual	0.46–2.65	0.64–3.81[a]		Bott et al. (1985)
La Trobe River, Australia	Annual	0.15–1.90	2.97–4.61	0.05–0.50	Chessman (1985)
Ogeechee River, GA	Annual	2.2	6.7	0.3[b]	Edwards and Meyer (1987)

[a] For seasonal trends in P/R see Figure 12.13

[b] Seasonal data show P/R $<$ 0.5 throughout year

instream primary production in this data set is notable and perhaps surprising. In accord with expectations of the greater importance of instream primary production as stream size increases, the P/R was positively correlated to stream order (Figure 12.14), and the correspondence was especially clear for river systems in Quebec and Oregon, which had multiple sites spanning a range of stream sizes. Note also that desert streams had high GPP and few litter inputs, reflecting their unshaded condition in unproductive landscapes; in contrast, blackwater streams of the southeastern United States had lower P/R than expected from the overall data set and these are heavily shaded systems that receive high litterfall and floodplain inputs.

In addition to stream size and the terrestrial setting, ecosystem metabolism is likely to vary with hydrologic disturbance and stream channel retentiveness because these influence organic matter storage and thus benthic respiration. Frequent hydrologic disturbance may affect stream metabolism by scouring periphyton and biofilms from stone surfaces, and in more extreme cases through bed transport and up-ending of stones. Measurement of ecosystem metabolism in a sixth-order, gravel-bed Swiss River for 447 days using single-station oxygen curves showed strong effects due to bed-moving spates (Uehlinger and Naegeli 1998). Immediately after spates, primary production and ecosystem respiration both declined, and because production was most strongly affected, P/R ratios declined as well. Primary production recovered more rapidly in summer than in winter, whereas recovery of respiration showed less seasonal dependency. Respiration may be less affected by spates than is primary production because heterotrophic processing of organic matter within the streambed is likely to be less affected than autotrophic activity on the bed surface. Thus, depth of scouring, amount of organic matter storage within the streambed, and magnitude of the disturbance will determine the

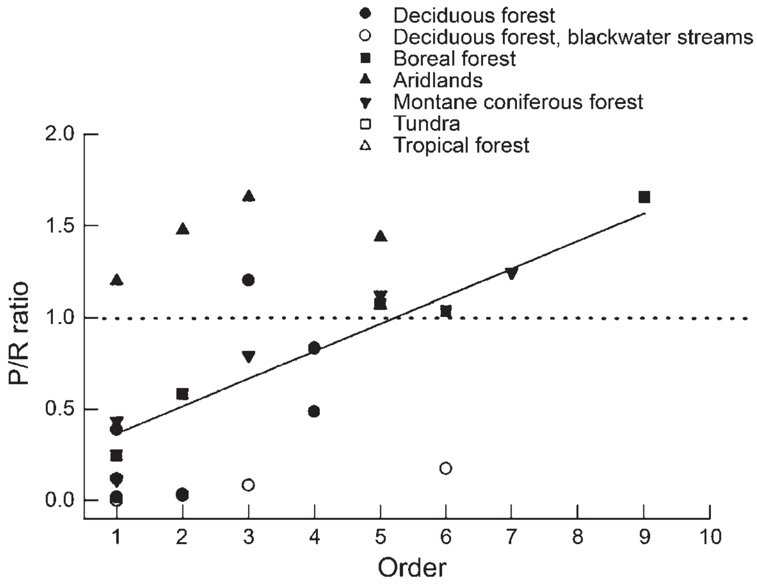

FIGURE 12.14 P/R ratios from 29 streams across six biomes versus stream order. Aridland streams fall well above the trend line, and low-gradient blackwater streams fall well below it. (Reproduced from Webster and Meyer 1997.)

extent to which ecosystem metabolism is altered. Although initially disruptive, organic matter may be deposited within the sediments as the flood subsides, and so the effect on ecosystem respiration may be short-lived. Light, nutrients, and other factors favoring algal growth will of course influence how rapidly the autotrophic community recovers.

12.4.3 Stream ecosystem efficiency

Stream ecosystem efficiency quantifies the extent to which all energy inputs into some areal unit of a stream are converted to CO_2 versus exported downstream. In principle one could measure all inputs and total respiration rate, and if carried out for an entire catchment including its headwaters, this would be an appropriate measure. For any stream reach of perhaps a few hundreds of meters, such a calculation is inappropriate because of the quantity of material that is imported from upstream and exported downstream. Because organic matter transport is such a dominant process in streams, estimates of the travel time or distance of a C atom is a useful comparative measure. Carbon spiraling length includes two components: uptake length, which is the distance traveled in dissolved inorganic form before being immobilized by the biota; and turnover length, which is the distance traveled by an atom of C in organic form before being completely converted to CO_2 by metabolic processes. These terms are also used for nutrient uptake and subsequent mineralization or release (see Figure 1.6 and Equation 11.5). Turnover length is a measure of ecosystem efficiency, and can be estimated from downstream C flux divided by ecosystem respiration (Newbold et al. 1982b, Newbold 1992).

The turnover length (S_p) of different types of POM is estimated from the average particle velocity (V_p) divided by breakdown rate (k):

$$S_p = \frac{V_p}{k} \tag{12.1}$$

This represents the distance a particle travels before entering the next pool of organic matter (for CPOM to become FPOM, or for FPOM to become DOM). The breakdown rate k for FPOM is estimated from its respiration rate in the laboratory. V_p can be calculated as:

$$V_p = \frac{S_w}{T_t + \frac{S_w}{V_w}} \tag{12.2}$$

where S_w is the distance traveled by the particle in the water, T_t is the turnover time or the time that the particle remains on the stream bed, and V_w is water velocity.

In their synthesis of many studies of breakdown and transport in the forested small streams of Coweeta, North Carolina, Webster et al. (1999) compared biological turnover time (a term that also includes physical and chemical breakdown) and transport distance for the four main categories of OM. Breakdown rates ranged from nearly 6 years for sticks to a few months for leaves, and exceeded 1 year for FPOM. Although these estimates are provisional for many reasons, the outcome is reasonable: transport rates were higher than breakdown rates for sticks, leaves, and FPOM. Particle turnover lengths were estimated to be 0.15, 0.11, and 42 km, respectively. Newbold et al. (2005) calculated turnover lengths of 38 and 59 km for two FPOM size categories in an Idaho stream.

Several studies suggest that turnover length is positively related to current velocity and discharge. In the Spree River, Germany, shorter turnover lengths of BOM were observed in an impounded river section (39 km) compared to a free-flowing section (60 km), suggesting that lower current velocity increased the efficiency of use of organic matter (Figure 12.15) (Wanner et al. 2002). The synthesis report by Webster and Meyer (1997) found a significant correlation between discharge and turnover length, implying that small streams are more efficient in the use of organic matter. Webster et al. (1995) noted a downstream increase in C turnover length in

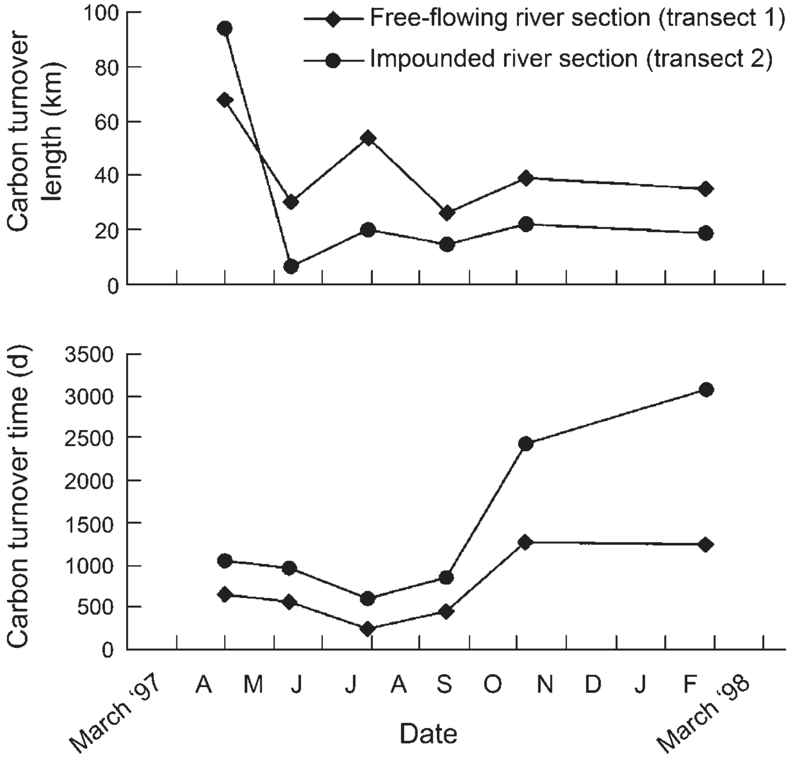

FIGURE 12.15 Temporal variation in turnover lengths and turnover times of organic carbon for free-flowing and impounded sections of the River Spree, Germany. (Reproduced from Wanner et al. 2002.)

streams of the eastern United States, which they related to a downstream increase in concentrations of dissolved and particulate C and in discharge (Webster et al. 1995). In the Taieri River, New Zealand, organic C turnover length ranged between 10 and 98 km, with higher values downstream where discharge also was higher (Young and Huryn 1997). In the Snake River, Idaho, turnover lengths were between 11 and 108 km and were related to patterns in current velocity (Thomas et al. 2005).

12.4.4 The fate of organic matter

Organic matter that enters the channels of streams and rivers can be stored for some time on stream banks and by burial within the channel, but ultimately it is exported to downstream ecosystems or mineralized to CO_2 by the biota. Export is the fate of a great deal of organic matter. An estimated 4×10^{14} g of organic C, roughly 1% of terrestrial NPP, is carried by rivers to the ocean annually (Meybeck 1981, Schlesinger and Melack 1981). This export consists of roughly equal quantities of POC and DOC. Present estimates are that 25% of C entering the world's rivers is processed within the system, 25% is stored as sediment POC, and 50% is transported to the oceans (Meybeck 1982, Mulholland and Watts 1982, Thurman 1985).

Headwater streams that are dominated by allochthonous inputs of organic matter clearly are inefficient at processing this material, typically exporting more than is metabolized (Webster and Meyer 1997). As is evident from estimates of transport distances reported earlier in this chapter, more material is exported as refractory FPOM and DOM than is metabolized to CO_2. The ultimate fate of this organic matter of terrestrial origin is less certain, however, as chemical evidence indicates it is decomposing on the continental margins, in river deltas, and perhaps in the lower reaches of rivers before reaching the oceans (Hedges et al. 1994). Coupled with the downstream decline in DOC concentrations in the lower reaches of some large rivers and the common finding of supersaturation of water in lowland rivers with CO_2 (Cole and Caraco 2001), utilization rather than export may dominate in lower reaches of large rivers.

12.5 Summary

Sources of organic C and thus energy to lotic ecosystems include autochthonous production by algae and aquatic plants, and allochthonous inputs of dead organic matter from terrestrial primary production. Studies of stream ecosystem metabolism address two central questions: (1) the relative magnitude of internal versus external energy sources, including their variation along a river's length and with landscape setting; (2) the efficiency of the stream ecosystem in metabolizing those energy supplies versus export to downstream ecosystems and possibly to the oceans. Principal approaches include the comparison of GPP to ecosystem respiration, mass balance estimation of all inputs and exports, and measures of the efficiency with which organic C is utilized.

Organic C budgets are based on the estimation of all inputs, standing stocks, and losses within a stream reach or, ideally, a catchment, although the latter is practical only for headwater streams. Budget studies demonstrate the overwhelming importance of climate and the terrestrial biome on the relative magnitude of allochthonous versus autochthonous inputs. Inputs of coarse, fine, and DOM from terrestrial primary production typically dominate the energy supply in small, forested streams where algal primary production tends to be light-limited, but primary production is of greater importance in open locations that receive sufficient light. Thus, longitudinal position and landscape setting determine the relative magnitude of sources of organic C to stream ecosystems. Aridland, meadow, and prairie streams have high primary production relative to detrital inputs, forested streams are the converse and highly dependent upon external energy inputs, and lowland streams have large quantities of DOC and POC in transport.

The relationship between GPP and ecosystem respiration, expressed as the P/R ratio or NEP, indicates whether an ecosystem is reliant on internal production or requires organic matter subsidies to sustain respiration. Wherever GPP is low relative to ecosystem respiration, a stream clearly is dependent upon external energy inputs, either from the adjacent terrestrial ecosystem or from upstream sources. Stream ecosystems where P exceeds R are likely to export organic matter to downstream locations. Although a $P/R < 1$ has often been used to indicate a stream ecosystem dependent upon microbial production fueled by the breakdown of allochthonous material, the transition value at which stream metabolism depends equally on autochthonous and allochthonous production likely falls between 0.5 and 1. The numeric value of the metabolic transition is difficult to ascertain because ecosystem respiration includes the activities of heterotrophs as well as autotrophs. Nonetheless, P/R and NEP both show the influence of longitudinal and landscape position, increasing downstream from forested headwaters and exhibiting low values in forested locations and high values in aridland and other open locations.

Stream ecosystems are relatively inefficient at mineralizing their inputs of organic C, as indicated by comparisons of processing rates to transport rates, of outputs to inputs, and of C turnover lengths. Globally, rivers export significant quantities of organic C from terrestrial primary production to downstream locations and the oceans. Streams of low order unquestionably are inefficient, exporting large quantities of FPOM and DOM. Large rivers also have substantial POM and DOM in transport, but declines in DOC concentrations in lower reaches of large rivers and their supersaturation with CO_2 provide evidence of substantial metabolic activity, indicating that significant mineralization takes place near the lower terminus of rivers.

Chapter thirteen

Human impacts

Although the human footprint is appreciable in all but the most inaccessible regions of the planet, freshwater ecosystems are especially subject to multiple pressures: water abstraction, industrial and domestic effluents, the spread of invasive species, altered hydrology, habitat degradation, and overharvest of resources. Over half of the accessible freshwater runoff is already appropriated for human use, more than one billion people lack access to safe drinking water, and approximately half of the world's six billion people lack basic sanitation services (Jackson et al. 2001, Postel et al. 1996). The demand for freshwater resources creates an urgent need to ensure sufficient freshwater for human well-being, while minimizing declines in biological diversity, the deterioration of freshwater ecosystems, and loss of ecosystem services.

The biological diversity of freshwater ecosystems is experiencing much greater declines than is seen in the majority of terrestrial ecosystems (Sala et al. 2000, Dudgeon et al. 2006), and if human pressures continue to rise and biodiversity continues its downward trend, the prospects for freshwater ecosystems are alarming and perhaps catastrophic. The freshwater biota is experiencing a biodiversity crisis (Revenga and Kura 2003), brought about by multiple interacting threats. Habitat degradation is pervasive, the result of instream alterations including dams, dredging, and channelization, harmful activities along the water's edge that destabilize banks, and changes in land use that affect hydrology with secondary consequences for physical processes and the biota. Pollution from diffuse and end-of-pipe sources is widespread, and in many areas of the world the water is not safe for humans or for aquatic life. Although significant advances have been made in treating wastewater and reducing point source pollution in more developed nations, sewage spills continue to occur because of aging infrastructure and the rapid pace of development. Invasive species, spread by accident and design, often have devastating effects on native species via predation, competition, habitat alteration, and as conveyers of diseases. Overexploitation does not affect all species or areas, but turtles, mollusks, some crayfishes, and many fishes have been or are being forced into decline by capture rates that are unsustainable. Finally, climate change has direct impacts by changing temperature and runoff patterns, and has indirect effects on many aspects of lotic ecosystem function. Individually and through their interactions, these five categories of threats demand urgent action to reverse the course of biodiversity and ecosystem decline.

Rivers provide numerous benefits to humankind, some of them irreplaceable. These ecosystem services include water supply for domestic, industrial, and agricultural uses, harvestable organisms, hydropower, waste disposal, navigation, recreational enjoyment, and spiritual fulfillment. Impaired lotic ecosystems may fail to provide these services, and instead of contributing to human well-being become the source of water-borne diseases including diarrhea, river blindness, schistosomiasis, and malaria. The great utility of rivers results in conflicts between types of uses, especially between those uses for which an economic value can easily be assigned, and other uses that have historically been excluded from any explicit valuation.

This chapter reviews the imperiled state of river ecosystems and their biota, examines the threats, and explores the science-based knowledge that can help us manage, restore, and conserve streams and rivers. It is all too easy to catalog the harm and perhaps take away too bleak a message. Scientific knowledge, citizen awareness, and new policies are growing rapidly. There is hope that ecosystem-based management within a framework that recognizes both human and environmental needs for freshwater will underpin a new era of improving ecological conditions for rivers and their biota.

13.1 Freshwater Biodiversity

Freshwater ecosystems, occupying approximately 0.8% of the earth's surface (Gleick 1996), support at least 100,000 known species (LéVêque et al. 2005, Strayer 2006), about 6% of the 1.8 million described species. In an ambitious effort to catalog the number of animal species in all major freshwater groups by continent or major ecoregion, LéVêque et al. (2005) compiled lists from literature, web sites, museums, and by consulting specialists for their best estimates. Freshwater plants, algae, and fungi were not included in the original compilation, which is an ongoing effort. Although the numbers are provisional, a brief accounting of diversity in major groups of freshwater invertebrates is of interest. The best current estimate of the total number of invertebrates that are either truly freshwater or are dependent on freshwater is about 90,000 species in about 570 families in 17 phyla (Strayer 2006). The true total, including currently undescribed species, may be twice that number. Insects, crustaceans, mollusks, and mites are the most numerous invertebrate groups (Figure 13.1). Numbers of species in some major groups of aquatic insects are Ephemeroptera, 2,100; Plecoptera, 2,000; Odonata, 5,500; Trichoptera 10,000; Diptera, >20,000; and Coleoptera, at least 6,000 (LéVêque et al. 2005). Protozoans, nematodes, annelids, and many small-bodied taxa likely contain many more species than are presently described, and major geographic regions such as South America, Africa, and Asia are understudied, so this compilation is unquestionably incomplete.

About 25,000 fish species are known worldwide, including at least 10,000 freshwater species and approximately 500 that are diadromous (Berra 2001, LéVêque et al. 2005, Nelson 2006). Fish diversity is much higher in tropical freshwaters than in temperate regions, and many species undoubtedly have yet to be described. At the continental scale, Africa contains at least 3,000 species, South America 3,500 to over

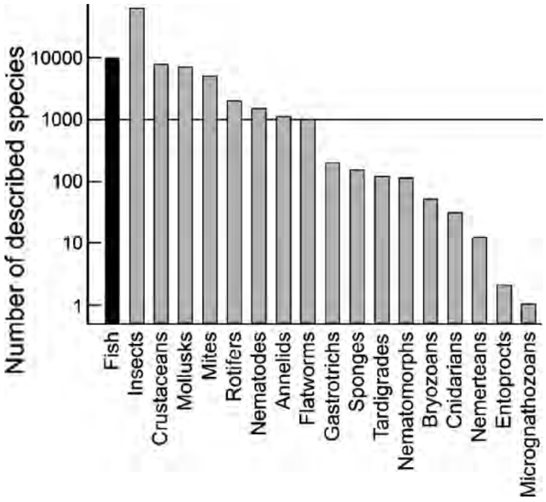

FIGURE 13.1 Numbers of described species of freshwater invertebrates. The black bar shows the number of described species of freshwater fishes for comparison. (Reproduced from Strayer 2006.)

5,000, and tropical Asia 3,000–3,500. All vertebrate classes have freshwater representatives, although dependency on freshwater environments varies, as all amphibians include an aquatic phase and no birds are exclusively aquatic. Approximately 300 new fish species are described or resurrected from synonymy annually (Stiassny 1999), and almost one third of the total known amphibian species have been described in the past decade (Dudgeon et al. 2006). This is evidence that the true totals are much higher.

13.1.1 Species imperilment

The number of endangered and extinct freshwater invertebrates is not reliably known. The World Conservation Union (IUCN) Red List includes 1,369 species (from all fresh waters), of which 77% are mollusks, decapods, and odonates (Strayer 2006). Small, inconspicuous invertebrates and understudied geographic regions of the world are seriously underrepresented. Strayer offers the following approximation: if 8% of the three best-studied taxa are imperiled and there are perhaps 150,000 freshwater invertebrate species worldwide, then 12,000 freshwater invertebrates are now imperiled or have gone extinct.

As is generally the case, the estimated number of extinctions is considerably greater than the numbers that have been documented. Some 123 freshwater animal species have been recorded as extinct since 1900, but such counts are conservative due to incomplete knowledge of the taxonomy and historical distributions for much of the biota. Whenever the imperilment for major freshwater animal groups has been estimated by expert panels and from "red list" summaries and the Natural Heritage Central Database of The Nature Conservancy, the results have been alarming (Figure 13.2). Ricciardi and Rasmussen (1999) modeled the proportional species loss per decade for North American terrestrial and aquatic fauna based on known extinctions since 1900, and then projected future rates from the number of currently imperiled taxa. By this admittedly

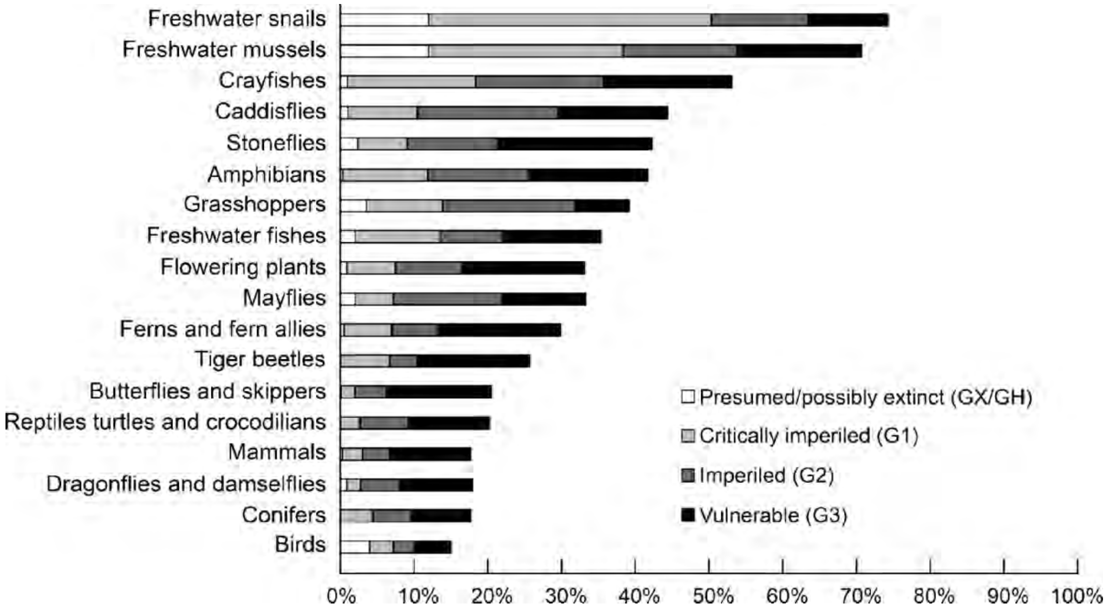

FIGURE 13.2 Extent of imperilment of major groups of US species. Note that the most imperiled species groups are entirely or primarily freshwater species. (Modified from Master et al. 1998.)

approximate approach, projected mean future extinction rates are five times higher for freshwater than terrestrial fauna, and the freshwater rates are similar to those projected for tropical rain forest assemblages.

13.1.2 Imperilment of major groups

Historically, the status of freshwater biodiversity has been assessed from knowledge of a few animal groups, such as fishes, mollusks, and crustaceans, or by focusing on well-known species such as salmon. The extent of the endangerment of North American freshwater fishes is well summarized by Williams et al. (1989), who categorize 103 species and subspecies as endangered, 114 as threatened, and 147 as deserving of special concern. This total of 364 taxa represents roughly one out of three species and subspecies of North American fishes. In Canada, 71 of the 205 native freshwater fishes are assessed as being at risk (Dextrase and Mandrak 2006). Some 63% of the 115 native fishes of California are extinct or imperiled, including eight species that are extinct within the state and 15 that have state or federal recognition as in danger of extinction (Moyle 1995). Most declines have multiple causes, but water projects, invasive species, and habitat degradation are thought to be most important. Because 60% of California's native fishes are endemic to the state (and 80% to the region), this loss of California's fish species is potentially of global significance.

Although knowledge of the status of freshwater fishes from different regions of the world is uneven, there is ample evidence of widespread imperilment. Moyle and Leidy (1996) estimate that some 20% of the world's freshwater fishes are imperiled or already extinct, and that estimate may be low due to undetected extinctions (Stiassny 2002). Imperilment unquestionably is greater in some areas than others, such as the historically rich, endemic ichthyofauna of Madagascar, clearly in decline on an island undergoing massive deforestation (Stiassny 1999).

The nonmarine mollusks of the world are members of a highly diverse phylum that includes an estimated 7,000 described and 3,000–10,000 undescribed species occurring in freshwater. Worldwide, 708 freshwater species appear on the 2002 IUCN Red List of Threatened Species (Lydeard et al. 2004). The North American molluscan fauna, and particularly that of the southeastern United States, is globally rich with an exceedingly high diversity of snails (family Pleuroceridae) and mussels and clams (family Unionidae). This fauna now faces a catastrophic level of extinction. Approximately two thirds of the nearly 300 unionid species of North America are classified as extinct, imperiled, or vulnerable by the Natural Heritage Network, and 37 US species are presumed or possibly extinct (Master et al. 2000). In the Mobile Basin of the southeastern United States, in what was once the most diverse molluscan fauna in the world, one third of the species have disappeared due to habitat and flow alteration (Table 13.1).

North America harbors the greatest diversity of crayfish worldwide, with 308 species and 30 subspecies for a total of 338 recognized taxa (Taylor et al. 1996). Crayfishes can be strong interactors in aquatic ecosystems, consume substantial quantities of vegetation and leaf litter, and are a critical food resource for popular sport fishes such as bass. Both wild and cultured populations are an economically important food resource, and are also harvested as bait for recreational fisheries. Although only two species are considered likely to be extinct and formal listings under the Endangered Species Act are few, nearly half of the North American crayfishes merit some level of conservation protection (Taylor et al 1996). The restricted range of a number of species combined with habitat degradation and species invasions are primary causes. The latter includes North American species that aggressively displace indigenous species and are greatly expanding their ranges, such as the rusty crayfish *Orconectes rusticus*.

TABLE 13.1 The aquatic fauna of the southeastern United States is characterized by high diversity, endemism and imperilment, and inadequate protection, as seen for the State of Alabama. (From Lydeard and Mayden 1995.)

	Number of native freshwater species	*Percent of the North American fauna (%)*	*Endemic to region[a] (%)*	*Imperilment[b] (%)*	*Listed under US Endangered Species Act (%)*
Fishes	303	38	41	10	40
Gill-breathing snails	147	43	77	65	1
Mussels	171	60	34	69	32
Turtles	23	52	22	43	20

[a] Alabama and a neighboring state

[b] Considered extinct, endangered, threatened, or of special concern

Other groups of vertebrates also are highly imperiled. The global decline of amphibians, attributed to climate change, disease, and habitat loss amongst other causes, threatens an estimated one third of all species worldwide (Stuart et al. 2004). Dudgeon et al. (2006) summarize evidence for the imperiled status of crocodilians, turtles, and other reptiles, particularly in tropical rivers. The freshwater dolphins, arguably the most endangered mammals still alive, number fewer than 100 individuals in the case of the Yangtse Dolphin. Because recent surveys of this species, also known as the Baiji, have failed to record any sightings, it may have recently become extinct; if confirmed, this represents the loss of an entire family (the Lipotidae).

Finally, although much attention rightfully focuses on rarity and extinction, many species within modern-day assemblages frequently have restricted ranges and reduced abundances relative to their historical condition. Using historical records to establish the original ranges of 25 fish species native to the lower basin of the Colorado River, Fagan et al. (2005) found that on average, species ranges had diminished >45% relative to their historical distribution, and fully one third of species had lost at least half of their occurrences. Of the 15 species, one is extinct (*Cyprinodon arcuatus*), and of the remaining 14, eight are considered endangered, two are vulnerable, and four are at lower risk. As this example illustrates, even when the majority of the original fauna still survives, their restricted and fragmented distributions are evidence of a functionally altered biological community.

13.2 Threats to Rivers

Modern-day threats to rivers have been reviewed by a number of authors (Allan and Flecker 1993, Pringle 2000a, Malmqvist and Rundle 2002, Dudgeon et al. 2006, Strayer 2006). Causes of the imperilment of river ecosystems and their biota are diverse, and are discussed below under the headings of habitat alteration, invasive species, pollution, overexploitation, and climate change (Table 13.2). Ultimate causes can be found in the conflicting demands on fresh water, changing land use, and the many unsustainable practices that characterize growing populations and expanding economies throughout the world. Most human activities that harm river ecosystems show an upward trend throughout the 20th century, and although some aspects of pollution have ameliorated in recent years, other pressures, including species invasions and climate change, are expected to worsen.

13.2.1 Habitat alteration

Alteration of physical habitat is the most significant threat to biodiversity and ecosystem function in the majority of human-impacted river systems. The consequence of many different

TABLE 13.2 The primary threats to streams and rivers. (Modified from Malmqvist and Rundle 2002.)

	Proximate causes	*Abiotic effects*	*Biotic effects*
Habitat alteration	Damming, water abstractions and diversions	Loss of natural flow variability, altered habitat, severing of upstream–downstream linkages	Reduced dispersal and migration, changes to water quality and assemblage composition
	Channelization	Reduced habitat and substrate complexity, lower base flows	Reduction in biological diversity favoring highly tolerant species
	Land-use change including deforestation, intensive agriculture, urban development	Altered energy inputs, increased delivery of sediments and contaminants, flashy flows	Changes in assemblage composition, altered trophic dynamics, can facilitate invasions
Invasive species	Aquaculture, sports fishing, pet trade, ornamental plants	Some invasive species modify habitat, otherwise minor	Declines in native biota, biotic homogenization, can result in strong ecosystem-level effects
Contaminants	Nutrient enrichment from agriculture, municipal wastes, atmospheric deposition	Increased N and P, altered nutrient ratios	Increased productivity, algal blooms, altered assemblage composition
	Acidification from fossil fuels (SO_2, NO_x), mines	Reduced pH, increased Al^+, metals	Physiological and food chain effects
	Toxic metals from mining, industrial gaseous emissions, waste disposal	Increased trace metal concentrations (e.g., Hg, Cu, Zn, Pb, Cd)	Toxic effects through biomagnification
	Organic toxins	Increased levels of PCB, endocrine disruptors, some pesticides	Physiological and toxic effects
Overexploitation	Commercial harvest for food, pet trade recreational fisheries	Usually none	Changes in assemblage composition, altered trophic dynamics, can facilitate invasions
Climate change	Temperature changes	Milder winters, altered evapotranspiration patterns and flow regimes	Range shifts in accord with physiological tolerances, increased productivity
	Precipitation changes	Altered flow regimes, greater flashiness	Greater role for disturbance

human activities, for the purpose of discussion human impacts on habitat can be grouped under altered flows, altered channels, and altered land use. Flows are affected by impoundments, water abstraction, and changing land use. The effects range from imposed constancy, to enhancement of floods and droughts, and even to dewatering. River channels are straightened, widened, realigned, and stabilized for flow conveyance, habitat-forming wood is removed, and levees are imposed to reduce flooding, all of which result in simplification and homogenization of habitat. Changing land use includes all aspects of forest harvest, agricultural intensification, and the spread of urban areas, and so has indirect and diffuse effects on flow, habitat, and contaminant levels.

13.2.1.1 Altered hydrology

The extent of alteration of river flow and loss of river connectivity due to dams and impoundments is staggering. Worldwide, it is estimated that there are >45,000 large dams >15 m in height or of large reservoir capacity (Figure 2.1) and perhaps a million smaller dams. The United States has >75,000 dams >2 m in height and approximately 2.5 million smaller water control structures (Hart and Poff 2002). As a consequence, most river systems are impacted and few free-flowing sections of any size remain. Within the 48 contiguous US states, only 42 high-quality rivers contain free-flowing sections >200 km in length (Benke 1990). Most of the largest river systems of North America, Europe, and former USSR are highly or moderately affected by fragmentation of their main channels (Dynesius and Nilsson 1994). Only tundra rivers in the northern hemisphere and some large tropical rivers, particularly in South America, remain predominantly undammed (Nilsson et al. 2005). The pace of dam construction increased steadily throughout the 20th century, reached a peak between 1970 and 1975 during which roughly 5,000 large dams were constructed, and now has slowed to approximately 2,000 large dams per decade (Gleick 2000). This slowing is due partly to a declining number of suitable sites, and partly to growing appreciation of the resultant social and ecological disruptions.

Dams vary widely in their size, purpose, and mode of operation and these differences influence their impact upon river ecosystems (Petts 1984). Dams also differ in whether water is released from the surface of the dam, near the bottom, or both. Water supply impoundments require a large storage volume to meet projected needs and outlast droughts. Dams constructed for irrigation must store as much water as possible during the rainy season for release during the growing season. Flood control reservoirs maintain only a small permanent pool in order to maximize storage capacity, and draw down as soon as possible after a flood event to restore their capacity. Navigation requires water storage in upper reaches to offset seasonal low flow conditions, and may be complemented by a system of locks and dams. Hydroelectric dams store water for release to meet regional energy demands, which can vary seasonally or over the course of 24 h. “Run-of-the-river” dams release water at the rate it enters the reservoir, usually are of low height, and are thought to have few adverse effects on hydrology, although they may still impair longitudinal connectivity. “Peaking” hydropower dams meet daily fluctuations in energy demand by allowing water to flow through turbines only at certain times, usually from midmorning through early evening. Changing water levels create unstable habitat conditions that can be especially disruptive to juvenile fishes and limit spawning opportunities for adults (Freeman et al. 2001). Finally, reservoirs may also serve recreational purposes including fisheries, but typically, this is a secondary function of a multipurpose facility.

The river environment below an impoundment is affected by changes in flow, sediment load, temperature, and water quality of the outflow (Stanford and Ward 1979). Effects on channel shape and substrate conditions are varied and can be especially serious. Dams that release very high discharges may cause scouring of fine materials and armoring of the streambed, a process in which the surface substrate becomes tightly compacted. Because of the loss of the river’s normal sediment load, the result of deposition in the slow waters of the impoundment, the discharge immediately below a dam is “sediment-starved.” This can lead to substantial channel and bank erosion and down-cutting of the streambed as the river adjusts to the altered balance between the amount of water and sediments that it is transporting. Where fine sediments are available, the absence of flushing flows can result in their accumulation within the streambed, reducing habitat space for invertebrates.

A river's temperature regime is altered to varying degrees by impoundments, strongly so in the case of large reservoirs with deep-release dams located on temperate rivers, which release water of cool and relatively constant temperature throughout the year (Figure 13.3). The new thermal regime facilitates the replacement of warm-water by cool-water fish species, which often are introduced trout in the western and southeastern United States. A moderated thermal regime has been shown to cause dramatic reductions in macroinvertebrate diversity at high latitudes, where exposure to near-freezing temperatures followed by a spring temperature rise is necessary to break egg diapause. In the Saskatchewan River, Canada, a fauna that originally included 12 orders, 30 families, and 75 species was reduced to only the midge family Chironomidae following construction of a deep-release dam (Lehmkuhl 1974).

Because impoundments trap sediments, water clarity typically increases below dams, resulting in a greater abundance of periphyton or higher plants than is found elsewhere in the river. For example, a dense growth of the aquatic moss *Fontinalis neo-mexicana* developed in riffle habitats of a regulated reach of an Idaho river (Munn and Brusven 1991), and this in turn

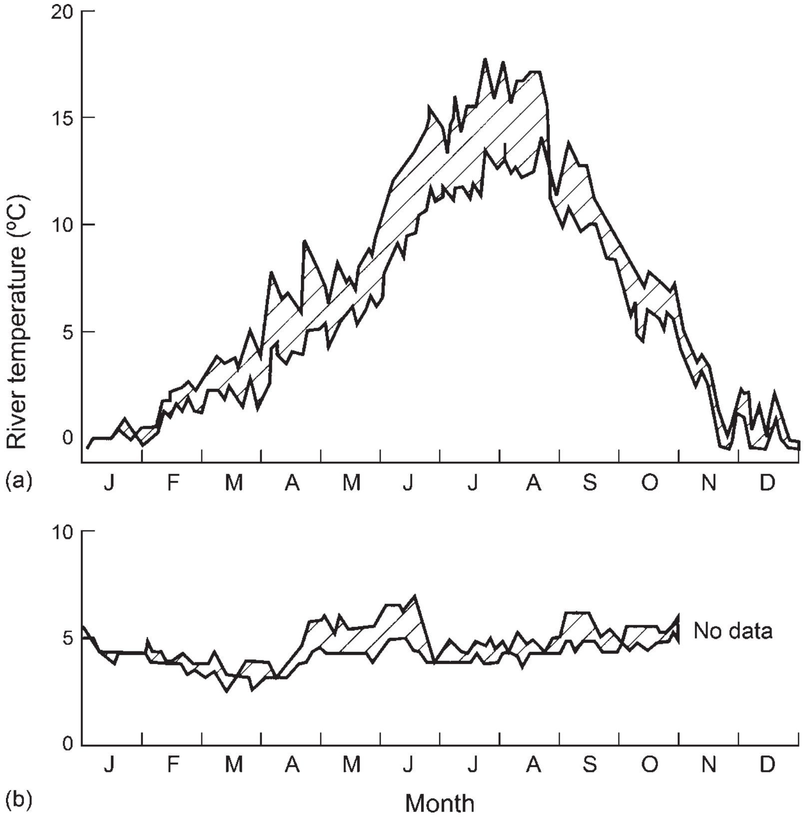

FIGURE 13.3 Thermal regimes of the (a) unregulated Middle Fork and (b) regulated South Fork of the Flathead River, Montana, during 1977. The shaded area approximates the daily temperature range. (Reproduced from Ward and Stanford 1979.)

appeared to be responsible for substantial changes in the benthic fauna. Sediment loads normally limit the diversity and abundance of benthic algae in the Colorado River, but in the tailwaters below Glen Canyon Dam, transparency exceeds 7 m, and the filamentous green alga *Cladophora glomerata* is abundant. Although *Cladophora* enters the food web primarily as detritus, it provides epiphytic diatoms and habitat for invertebrates, including the amphipod *Gammarus lacustris*, and thus helps to sustain a blue-ribbon fishery for nonnative trout (Shannon et al. 1994, Blinn and Poff 2005).

The benthic invertebrate community immediately below dams often shows a reduction in species richness. In the Gunnison River, Colorado, the greatest number of species of Trichoptera (Hauer et al. 1989) and Plecoptera (Stanford and Ward 1989) are found in unregulated reaches, and the lowest species richness occurs in the tailwaters below deep-release dams. Often the faunal changes are fairly predictable from knowledge of habitat requirements. From a survey of the effects of dams on mayflies, Brittain and Saltveit (1989) report that low flows usually cause a shift from lotic to lentic species such as *Cloeon*, *Paraleptophlebia*, and *Siphlonurus*, whereas high flows and fast currents favor other species including *Baetis*, *Rhithrogena*, and *Epeorus*.

In addition to the specific and local-scale effects of individual dams on the impounded river section and downstream reach (which may extend for tens or even hundreds of km), dams sever the upstream–downstream connectivity that is a core characteristic of river ecosystems. The consequences of this loss of connectivity is readily apparent for the many freshwater species from shrimp to river dolphins to migratory fishes that use different habitats at different stages of their life cycles and so require unrestricted movement both upstream and downstream. Dams on the Yangtse River in China have contributed to declines of sturgeons and paddlefish, blocking migrations of the potamodromous (migrating within river systems) *Acipenser sinensis* in the Yangtse River, fragmenting populations of the endemic Yangtse sturgeon (*A. dabryanus*) and contributing to the decline of the paddlefish *Psephurus gladius* (Dudgeon 2000). Many aquatic species that dwell in the streams of tropical islands migrate between rivers and coastal zones (March et al. 2003). Although some shrimp, fish, and snail species have impressive abilities to overcome obstacles such as waterfalls, large dams without spillways totally block migrations, causing the extirpation of species that may play important roles in headwaters (Pringle 1996). Experimental exclusion of freshwater shrimps from sections of headwater streams of Puerto Rico has shown effects on sediments, algal and insect assemblages, and on litter processing (Pringle et al. 1999, March et al. 2003), suggesting that the elimination of shrimp may have significant consequences.

The influence of dams on migrating salmon of the Pacific Northwest of North America may be the best known yet still controversial example of biological impacts on migratory species. The total number of individuals of all species of salmon returning from the sea to spawn in the Columbia River prior to development is conservatively estimated to be 6.2 million, of which spring- and summer-run Chinook were most abundant. By the close of the 20th century, numbers of naturally produced salmon had declined to about one eighth of their predevelopment abundance (NRC 1996). Some 19 major hydroelectric facilities were constructed between the 1930s and 1970s, impeding and in some cases completely blocking upstream migrations of returning salmon. Juveniles that once passed swiftly downstream with the river's current now must expend more energy in swimming through slack-water impoundments, risk damage from passing over spillways or through turbines, and run a gauntlet of predatory fish and birds that congregate below dams. Despite the well-documented declines of salmon runs

(Figure 13.4) and the obvious negative effects of dams, other factors including deteriorating habitat in nursery streams, commercial and recreational harvest, and varying ocean conditions all affect salmon survival (Ruckelshaus et al. 2002). Because it is uncertain how much salmon would recover by the removal of just one of these threats, and hydropower provides 90% of the energy needs of the Pacific Northwest, the breaching of Columbia and Snake River dams to restore salmon has failed to gain widespread support. In other instances where dams block access to extensive salmon spawning area and generate only modest hydropower, such as on the Elwha River in Washington State, advocates for dam breaching have met with greater success.

Floodplains are a natural feature of large lowland rivers, a fact that is easy to forget in North America and Europe due to construction of dams, dikes, and levees to control flooding and permit agricultural use and human settlement in former floodplains. Natural floodplains are highly imperiled ecosystems, with over 90% under cultivation in Europe and North America (Tockner and Stanford 2002).

The ecological benefits of flooding are evident from studies of the Missouri River subsequent to catastrophic floods of the mid-1990s. A partially tamed river due to six mainstem reservoirs on the middle river and channelization and levee construction along the lower river, the Missouri historically experienced March and June flood pulses that inundated the extensive bottomland forests, occasional prairies, oxbow lakes, and shallow, temporary wetlands of its active floodplain (Galat et al. 1998). By 1990, approximately 50 species of plants and animals of the regulated river were of conservation concern. When record flooding occurred along the lower Missouri River in 1995 and 1996, reconnection of the lower Missouri River with its floodplain benefited numerous species. Emergent and floating-leaved macrophytes that rely on vegetative reproduction and are adapted to flooding recovered quickly, and more and different fish species were observed, particularly in flood-connected water bodies where turtle species richness also was highest. Although it is infeasible to advocate periodic flooding of all of the Missouri's floodplain, these postflood findings demonstrate the resiliency of floodplain communities and the restorative potential of recurrent controlled flooding in suitable areas.

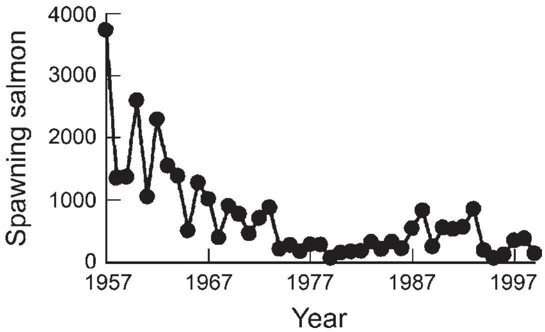

FIGURE 13.4 Decline in spawning populations of Chinook salmon (*Oncorhynchus tshawytscha*) since the construction of four dams on the lower Snake River, western United States (Reproduced from Kareiva et al. 2000.)

Some great rivers remain largely unregulated and flood regularly over vast areas of forest and wetland, including the Amazon, Orinoco, and Mekong. Many fishes in the Mekong make upstream breeding migrations during the wet season, spawning in inundated areas (the pelagic "whitefish" species), or move laterally into flooded forest (the benthic "blackfish" species) (Dudgeon 2000). Because fish production in tropical rivers is positively correlated with extent of flooded area and fluctuates among years with the size of flood peaks (Welcomme 1979), fish production and human livelihoods are likely to be harmed by river regulation. Recently completed hydropower dams as well as others under construction on the Mekong are expected to decrease seasonal inundation around Tonle Sap Lake, and almost surely will diminish its productive fishery on which many depend (Campbell et al. 2006).

13.2.1.2 Channelization

From small drainage ditches that return water to a river a short distance downstream, to interbasin diversions that connect historically distinct river systems, to massive plumbing schemes that alter drainage patterns of large regions, canals and water transfers have had an effect upon rivers rivaling that of dams. Indeed, diversion projects typically are combined with impoundments and dams, either to bring water to the impoundment for added hydropower, or to send water though pipes and canals for irrigation and navigation. The extent of canal construction and channelization is considerable. Within the United States, some 26,550 km of channelization work had been completed by 1977, and a further 16,090 km were proposed (Leopold 1977). Surveys conducted in the United Kingdom and Denmark also document extensive channelization (Brookes 1989). Quinn (1987) counts 54 interbasin diversions in Canada scattered across nine provinces whose total volume, if consolidated, would be the third largest Canadian river, after the St. Lawrence and McKenzie. Nearly all of the Canadian diversions are attributable to hydro-development (Bocking 1987).

The channelization of small streams, primarily to improve conditions for agriculture, is widespread. More than 90% of all lowland stream reaches in Denmark, Holland, and Britain have been channelized, mainly during an intensive period of stream modification between 1920 and 1970 (Pedersen et al. 2006). This practice is also widespread in agricultural areas of the Midwest (Landwehr and Rhoads, 2003). Eight states in the Great Lakes and cornbelt regions, with soils that are highly productive when drained, account for nearly 80% of the agricultural production of the United States (Fausey et al. 1995), and so the economic benefits are uncontested. Agricultural fields often are underlain by an extensive network of subsurface drainage tiles, which help to drain the soils but also result in faster runoff. Consequently, stream channels must be made wider, deeper, and straighter in order to convey greater stormflows. Channelization dramatically alters the shape and dimensions of the stream system (Brookes 1988) and these ditches often are managed by weed cutting, wood removal, and dredging of sediments to ensure flood conveyance. Unsurprisingly, both the fish assemblages (Moyle and Leidy 1996) and the macrophytes of highly managed systems have been shown to be strongly affected by these practices.

Whereas small streams are widened and straightened for water conveyance, larger rivers commonly are modified for navigation, flood control, and utilization of floodplain land. The period 1750–1900 marked an era of ambitious regulation schemes for most of the large rivers of Europe (Petts 1989); changes in the channel of the Rhône (Figure 13.5) are typical. The United States had a particularly compressed history of canal construction during this era, as little of substance was constructed before 1800, and the railroads largely outcompeted barge traffic within 60 or so years. In between, however, some 7,000 km of artificial waterways were hand-dug, with only blasting powder as an aid. In countless rivers, removal of snags and deepening of the main channel have occurred to improve navigability for trade and transport. As Sedell and Froggatt (1984) document for the Willamette River in Oregon, the resulting loss of riverine channel structure has been great (Figure 13.6). The snags themselves provide important habitat for invertebrates, and in rivers with soft bottoms, snags are major sites of secondary production (Table 5.2). Shoreline length is a useful measure of habitat simplification owing to channel modifications. In rivers that still maintain a complex and dynamic interaction with their floodplains, such as the Tagliamento in Italy (Tockner and Stanford 2002), shoreline length can be as high as 25 km per kilometer of river length: in channelized rivers, that value can be as low as 2 km of shoreline per river kilometer.

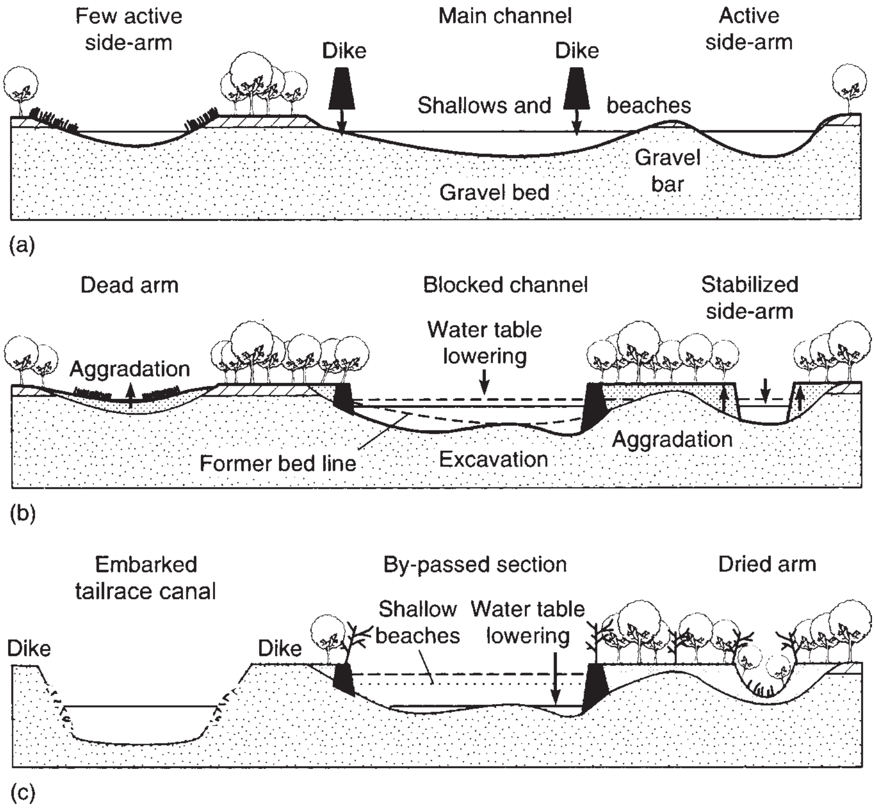

FIGURE 13.5 Changes in the lower River Rhône from 1870 to the present. (a) In 1870, the natural river was braided with a tendency to meander. Construction of levees beginning in the mid 19th century and excavation confined the river to a single, deep channel, improving navigation and protecting riverside residents from flooding. (b) The channelized braided riverbed in 1971. Hydroelectric developments and channelization since the 1960s have largely dewatered the old main channel and furthered the drying of old side channels. (c) The regulated braided riverbed in 1980. The stippled areas represents gravel, the unshaded area represents silt. (Reproduced from Fruget 1992.)

At an even larger spatial scale, interbasin water transfers to supplement water supplies are a common solution in water-thirsty regions. The California State Water Project transfers water from northern to southern parts of the state, Israel's National Water Carrier pumps water from the Sea of Galilee to supply the southern half of the country, and the Lesotho Highlands Project supplies Johannesburg, South Africa. Water shortages in China's Yellow River, which supports the industrial and agricultural activities of over 100 million people, are becoming severe, with days of no measurable flow occurring in 22 of the 28 years spanning 1972–1999 (He et al. 2005). The duration of desiccation has increased from an average of 8 days in the 1970s, to 11 days in the 1980s and 82 days in the 1990s, with the 1997 event lasting 226 days in the Lower Yellow River. With 3,382 dams providing the capacity to store fully 91% of the mean annual discharge, management of the available supply can be optimized, but water transfers to supplement the Yellow River are inevitable. Ten major diversion projects currently are planned, the largest of which is a south to north transfer from the Yangtse to the Yellow River.

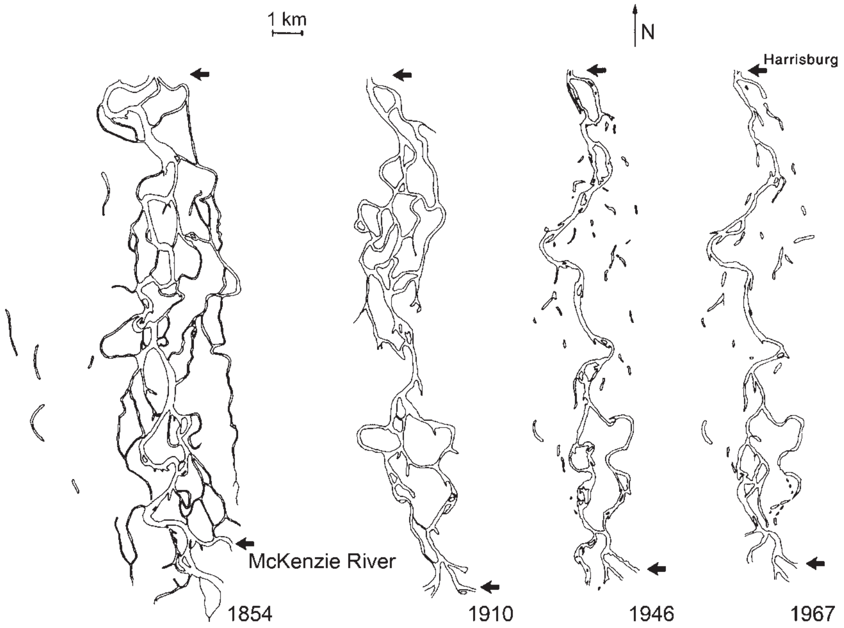

FIGURE 13.6 Historic change of the Willamette River, Oregon. Early settlers commented on the extensive floodplain 1.5–3 km in width, the thick underbrush, and multiple shifting channels filled with snags. Snag removal for steamboat travel beginning in 1868, followed by expansion of agriculture on the old floodplain and construction of 11 major dams since 1946, have transformed the Willamette into a very different river than it was less than 150 years ago. The estimated length of shoreline in a 25 km stretch was 250 km in 1854, 120 km in 1910, 82 km in 1946, and 64 km in 1967. (Reproduced from Sedell and Froggat 1984.)

Within North America, one has only to look to the Colorado River and the waterscape of California to see the effects of large-scale water diversion. The sprawling metropolis of Los Angeles was made possible by the 1913 completion of an aqueduct system nearly 400 km in length, bringing snowmelt from the Sierra Nevada mountain range to the city of Los Angeles and economic ruin to the ranching communities of the mountain valleys. Today, approximately 90% of water use in California is for irrigated agriculture, and roughly half of all water used in southern California comes from outside the state, in aqueducts and canals diverted from the Colorado River. The Imperial Valley, now the largest expanse of irrigated agriculture in the western hemisphere, was aptly named the Colorado Desert until it was developed with diversions from the Colorado River and a network of irrigation canals (California Water Atlas 1979). None of this was practical so long as the flow of the Colorado River varied with the seasons and spring floods were allowed to escape to the sea. Regulation of the Colorado River's flow became imperative not just for hydropower, but to ensure year-round water supply for diversion. Nine major storage reservoirs, anchored by Lake Mead in the Lower Basin and Lake Powell in the Upper Basin, have a collective storage capacity of roughly four times the long-term average virgin flow of 18.5×10^9 m^3 (15 million acre-feet). Practically no flow has entered the Gulf of California since 1961 (Figure 13.7), and today the mighty Colorado ends in a pipe in Tijuana, 225 km north of its natural terminus, according to an agreement that allots Mexico a final share of the river.

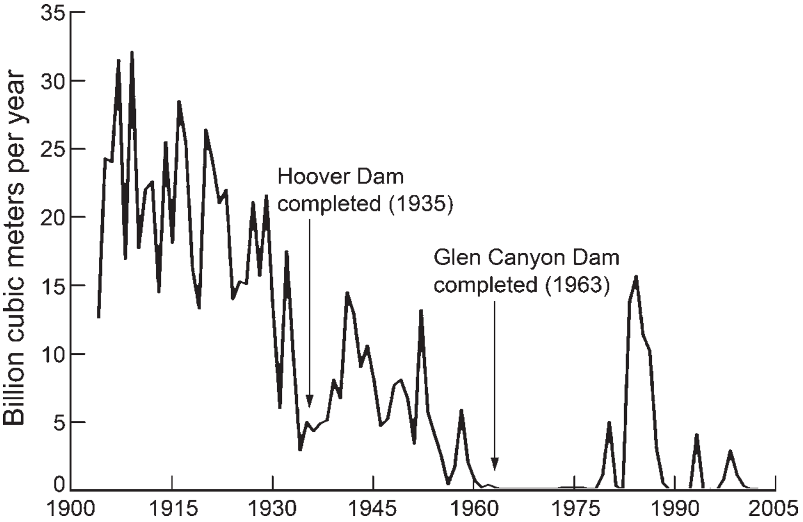

FIGURE 13.7 Flows of the Colorado River below all major dams and diversions, 1904–2004. (Reproduced from Postel 2005.)

13.2.1.3 Land use

Land-use change is an integrator of many human activities that have a negative impact on stream ecosystems. Flow variability and sediment delivery to streams are strongly influenced by the impervious surfaces and storm drains of urban areas, the channelized streams and field tiles of agricultural areas, and logging practices and road building in areas of forest harvest. Habitat degradation is likely to be manifested in changes to flows, benthic habitat conditions, and riffle-pool integrity. In regions that naturally have a vegetated riparian, the presence of vegetation stabilizes banks, moderates water temperature, filters nutrients and sediments, and strongly influences energy pathways by influencing the availability of light and inputs of particulate organic matter (Gregory et al 1991). Typically the loss of riparian vegetation is accompanied by bank erosion, silt deposition, warmer water, and altered food webs; and as human presence encroaches to the stream edge contaminant loading often increases (Lowrance et al. 1997, Hickey and Doran 2004). Although the pathways are less obvious, land use patterns and human presence throughout the catchment often serve as good indicators of a stream's condition, acting as a general index of human disturbance (Table 13.3).

Most settled regions of the world have seen extensive transformations of their landscapes. In New Zealand, over 80% of the land was forest before agricultural expansion; today, pasture for sheep is the dominant land use in the middle and lower catchment areas of most of New Zealand's streams and rivers (Quinn 2000). Agriculture is the dominant land use in many developed watersheds in the United States, comprising >40% of the land area of the Lower Mississippi, Upper Mississippi, Southern Plains, Ohio, Missouri, and Colorado River basins (Allan 2004). Urban land use typically makes up a lower percentage of total catchment area, and for large basins urban land is usually <5% of catchment area. Because urban stressors have a disproportionate influence on aquatic ecosystems (Paul and Meyer 2001) the influence of urbanization can be important even at low values. When small catchments of low-order streams are the focus,

TABLE 13.3 Principal mechanisms by which land-use activities influence stream ecosystems. (From Allan 2004.)

Environmental factor	*Effects*
Sedimentation	Increases turbidity, scouring, and abrasion; impairs substrate suitability for periphyton and biofilm production; decreases primary production and food quality causing bottom-up effects through food webs; in-filling of interstitial habitat harms crevice-occupying invertebrates and gravel-spawning fishes; coats gills and respiratory surfaces; reduces stream depth heterogeneity leading to decrease in pool species
Nutrient enrichment	Increases autotrophic biomass and production, resulting in changes to assemblage composition, including proliferation of filamentous algae, particularly if light also increases; accelerates litter breakdown rates and may cause decrease in dissolved oxygen and shift from sensitive species to more tolerant, often nonnative species
Contaminant pollution	Increases heavy metals, synthetics, and toxic organics in suspension, associated with sediments, and in tissues; increases deformities; increases mortality rates and impacts to abundance, drift, and emergence in invertebrates; depresses growth, reproduction, condition, and survival among fishes; disrupts endocrine system; physical avoidance
Hydrologic alteration	Alters runoff–evapotranspiration balance, causing increases in flood magnitude and frequency, and often lowers base flow; contributes to altered channel dynamics, including increased erosion from channel and surroundings and less-frequent overbank flooding; runoff more efficiently transports nutrients, sediments, and contaminants, thus further degrading instream habitat. Strong effects from impervious surfaces and stormwater conveyance in urban catchments and from drainage systems and soil compaction in agricultural catchments
Riparian clearing/ canopy opening	Reduces shading, causing increases in stream temperatures, light penetration, and plant growth; decreases bank stability, inputs of litter and wood, and removal of nutrients and contaminants; reduces sediment trapping and increases bank and channel erosion; alters quantity and character of dissolved organic carbon reaching streams; lowers retention of benthic organic matter owing to loss of direct input and retention structures; alters trophic structure
Loss of large wood	Reduces substrate for feeding, attachment, and cover; causes loss of sediment and organic material storage; reduces energy dissipation; alters flow hydraulics and therefore distribution of habitats; reduces bank stability; influences invertebrate and fish diversity and community function

land use can vary from nearly 0–100% coverage of urban, agricultural, or forested land.

When streams that drain catchments under different land use are compared, the influence of landscape setting is apparent. Quinn et al. (1997) compared water quality, habitat, and biota in 100 m reaches of New Zealand streams draining pasture, native (podocarp–broadleaf) forest, and exotic pine forest that previously was pasture. Pasture streams received much more light, were warmer, had higher nutrient levels, and much higher algal biomass. Both pine and pasture streams had more fine sediment stored in the streambed than native streams; pine streams had the most wood, and pasture streams the least. Community composition differed most between pasture and native forest, with more midges and snails in the former, and more mayflies, stoneflies, and caddisflies in the latter.

Many studies have shown that habitat quality and biological diversity (often assessed using metrics of biological integrity, see Section 13.3.1) correlate with various measures of land use either along the river corridor or throughout the stream's catchment (Allan 2004). Based on a comparison of 30 streams in the Etowah River basin, Georgia, Roy et al. (2003) found that number of taxa and other biotic indices were negatively related to urban land cover and positively related to forestland cover. Urban land cover correlated negatively with streambed sediment size and positively with nutrient concentrations and turbidity, suggesting that environmental conditions affecting the biota reflected land use. A similar study of 134 stream sites throughout Wisconsin found that habitat quality and biotic integrity were negatively correlated with the amount of agricultural land and positively correlated with the amount of forested land (Wang et al. 1997).

There is ample evidence that poorly regulated forest harvest has resulted in substantial degradation in habitat and fish populations (Bisson et al. 1992). Changes in streamflow and increased sediment production are among the most serious consequences of logging activities because they have long-term effects on channel and habitat features. Major sources of sediments include landslides from deforested slopes, surface scour from logging roads, and erosion of sediments stored on stream banks or within the streambed itself due to greater flooding (Scrivener and Brownlee 1989, Bruijnzeel 2004). As more of the basin is logged, pools fill with sediments, pool-forming large wood is lost, and the frequency and size of pools decline (Bisson et al. 1992). In general one observes a reduction in species diversity, attributed to habitat simplification, and an increase in standing crop biomass, attributed to greater light penetration and autotrophic production. Surveys of streams in logged versus unlogged watersheds in the Pacific Northwest found that salmonid species diversity was lower in logged areas regardless of underlying geology (Figure 13.8). Aquatic invertebrates also are adversely affected by clear-cut timber harvest. Corn and Bury (1989) compared amphibian abundances in headwater streams in uncut forests to streams in second growth forests that had been logged between 14 and 40 years previously. Species richness was lower and the percentage of fine sediments was greater in previously logged streams, demonstrating the long-term consequences of timber harvest.

How effectively a riparian buffer strip can lessen the adverse impacts of land use on aquatic ecosystems, and what width is required, continue to be debated. The recommended width of buffer strips varies from <10 to 100 m, and will likely depend on protection goals and context (Lee et al. 2004). Attempts to distinguish between the importance of riparian versus catchment land use to stream condition and the effectiveness of riparian buffers of various widths have produced mixed results, in part because land cover variables are often correlated (Roth et al. 1996). By selecting sites with uncorrelated forest cover values and developing a model relating buffer width to stream variables, Jones et al. (2006) demonstrated that the reduction in buffer width from 30 to 15 m results in

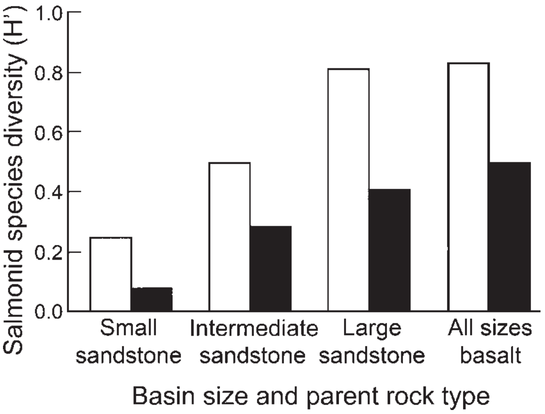

FIGURE 13.8 Diversity of salmonid fishes in logged (shaded bars) and unlogged (unshaded bars) Oregon coastal streams with different parent rock types. Diversity is expressed as H' ($-\Sigma \rho_i \log \rho_i$, where ρ_i is the frequency of the *i*th species). (Reproduced from Bisson et al. 1992.)

elevated stream temperatures and reduced trout populations in Georgia streams. Even when a riparian buffer exists, its effectiveness can be counteracted by stormwater drainage pipes, subsurface drainage tiles in farm fields, and gullies in eroded landscapes, which rapidly convey water, sediments, and pollutants into stream channels. In urban streams in Melbourne, Australia, invertebrate populations were more highly impacted when storm drains conveyed runoff directly into streams, compared with urban areas that had considerable impervious surface but lacked direct connection (Walsh et al. 2005a, b).

13.2.2 Nonindigenous species

Nonindigenous, exotic, and alien are terms applied to species that colonize a region where they do not naturally occur. Nonindigenous species that become abundant in new environments are referred to as invasive, implying harm to the recipient community. Alien species are of concern for several reasons. Once established in a new environment, they usually become permanent residents and often are capable of reproducing and dispersing far beyond the point of origin. In contrast to chemical pollutants that can be eliminated at their source, or habitats that might potentially be restored, species introductions usually are impossible to reverse. Natural enemies may be lacking, and the impacts of introduced species in new habitats are highly unpredictable because of differences in the nature of species interactions under novel ecological conditions.

Introductions are well documented for a wide variety of freshwater plants, invertebrates, and fishes. A compilation of international introductions of inland aquatic species as of 1988 recorded a total of 1,354 first introductions of 237 animal species, primarily fishes, into 140 countries (Welcomme 1988). The majority of occurrences are of limited extent. Most species have been introduced to ten or fewer countries, and 40% have been recorded from only one country. At the other extreme, nine species have been introduced into more than 30 countries, including three popular sports fish (rainbow and brook trout, largemouth bass); *Gambusia affinis*, used in mosquito control; and two tilapias and three species of carp popular for aquaculture and weed control. Nonindigenous species often are additions to the receiving community, which may retain all or most of its complement of native species. However, whenever the majority of the biomass consists of introduced species, changes in food web structure and ecosystem function are highly probable. At least 72 nonindigenous species have been successfully introduced in the Colorado River system, which originally held 49 native species (Blinn and Poff 2005), and within the Grand Canyon National Park, over 85% of individual fish are nonnative (Minckley 1991).

Invasive plants including aquatic macrophytes and riparian species also take their toll of aquatic ecosystems by reducing recruitment of native plants and modifying ecosystem processes and disturbance regimes (Gordon 1999). The water hyacinth *Eichornia crassipes*, originally from South America and introduced into the United States in the late 1800s as an ornamental, is considered one of the world's worst aquatic weeds in subtropical freshwaters. It occupies large areas of the Florida everglades, where its extensive floating mats impede flow, eliminate native plants, and reduce oxygen levels (Schmitz et al. 1993). Salt cedar (*Tamarix* spp), native to southern Europe and Eurasia, has colonized extensive riparian areas of the US southwest, where it displaces native riparian species and increases water loss due to its high transpiration rates (Cleverly et al. 2006).

13.2.2.1 Causes of species invasions

Freshwater species are purposefully transported and released in new environments to enhance sports fishing, for aquaculture, and as agents of biological control. Indeed, stocking of nonnative fish remains a cornerstone of management efforts to provide the most desirable species for sport or commercial fisheries. Of the 110 documented invasions of fish species into California, 45% were introduced for food or sports fishing and 15% as forage for sports fishes (Moyle and Marchetti 2006). Although relatively few species are extensively used in aquaculture (Welcomme 1984), these are among the most widely transferred fishes. Introductions associated with fish culture expanded considerably in the 1960s, as international development agencies promoted aquaculture to provide protein for rapidly expanding human populations and to benefit local economies. Fishes also have been introduced as biological control agents to combat disease vectors and noxious aquatic weeds. Mosquito control has been a frequent objective, using species such as mosquitofish (*Gambusia affinis*) and guppies (*Poecilia reticulata*). Control of aquatic weeds, many of which themselves are exotic, is another frequent objective (Shireman 1984), with tilapia and carp the most commonly promoted species.

Unintentional introductions occur in a number of ways, including escapees from fish farms, the release of aquarium pets, unnoticed species that "hitch-hike" with a planned introduction, and those carried in ballast water or dispersed through canal systems. Of the 1,205 introduction records for aquaculture purposes listed in FishBase (an encyclopedic database of finfish biology), about half are reported to have become established in the wild (Casal 2006). Over 1,200 species of tropical aquarium species are shipped to various parts of the world, and as many as 6,000 species may ultimately be of interest to the pet trade overall (Welcomme 1984). Most tropical fish introductions have occurred since 1960, when techniques greatly improved for the live transport of fish. About 10% of international transfers of exotic fishes have been the result of truly nonpurposeful introductions, such as accidental transfers of small cyprinids included with shipments of juvenile carp species. Recently, ballast water introductions have been a focus of concern, illustrated by invasions into the Laurentian Great Lakes of the ruffe (*Gymnocephalus cernua*), the zebra mussel (*Dreissena polymorpha*), and the mitten crab (*Eriocheir sinensis*) (Ricciardi and Maclsaac 2000). Intercatchment water transfers have contributed to species translocations in southern Africa because almost all of that region's major river systems are connected by tunnels, pipes, and canals (Bruton and van As 1986). At least five fish species have invaded the Orange River from the Great Fish River, which prior to their connection had distinct faunas with high numbers of endemics.

13.2.2.2 Invasion success

Invasion success is expected to be influenced by traits of the invading species and characteristics of the receiving environment, including "environmental resistance" from the invaded community. The successful establishment of an alien species can be viewed as a succession of probabilistic events, beginning with transport or dispersal and followed by establishment and further spread, until finally becoming fully integrated into the community (Figure 13.9). Lastly, its impact on native species and ecosystem processes determines whether the novel species qualifies for nuisance or invasive status.

Marchetti et al. (2004a) undertook a detailed analysis of invasion success for freshwater fishes of California, which has 68 native species and 110 documented nonnative invasions. Because 43% of these invasions were failures, it was possible to explore correlates of the successes. The best statistical predictors of a species' invasion success included a past history of successful invasion, broad environmental tolerance, ability to thrive in human-altered environments, similarity of source and recipient environments, and large propagule size (at least 100 individuals, multiple releases, or both). Prior success was a particularly good predictor of the ratio of success to failure, which was near 1:1 for species

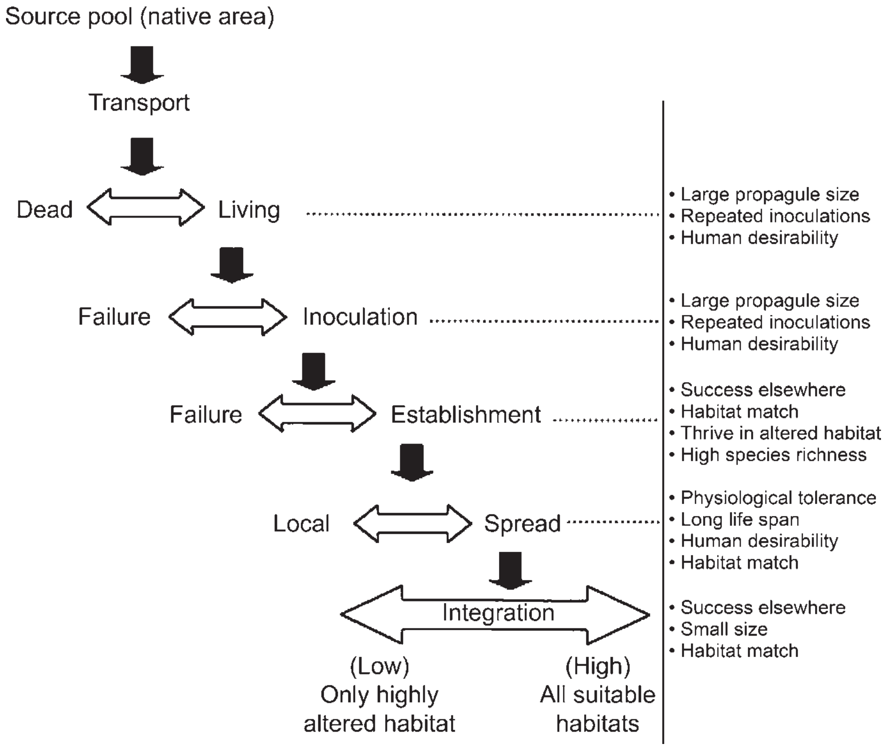

FIGURE 13.9 The species invasion process as envisioned for fishes in California: at each step, invading individuals encounter factors that restrict some or all from proceeding to the next step. Successful invasion requires surviving each stage of the process. Once a species is established, a combination of biotic and environmental factors determines whether it will spread and eventually be integrated into the existing assemblage of species. (Reproduced from Moyle and Marchetti 2006.)

with no previous record of successful establishment in a new environment, rising to 4:1 for alien species established in ten or more countries. Success rates were high for game and forage fish, with a 2:1 success to failure ratio. In contrast, unintentional releases of aquarium pets, fish carried in ballast water or moving through constructed waterways, and escapees from fish farms had a 28% success rate. High physiological tolerance was found in 66% of all successful invasions in California (Marchetti et al. 2004b), but was no guarantee of success as 47% of failures had similar high tolerances. What is clear, of course, is that species invasions fail when environmental conditions exceed their tolerances, as is the case for many tropical aquarium fishes in temperate waters. At least some invaders appear to be successful due to novel traits, such as feeding on underutilized resources, high aggressiveness, or timing of reproduction. Species with wide native distributions might be expected to be more successful colonists but this was reported to be at best a weak indicator, and other candidate characteristics such as small body size, fast life cycle, and generalist trophic position met with even less success in the California case study. At this time we can say that some traits are known to predispose a species to become invasive, but predictive models have their limits and so it is advisable to err on the side of caution in risk assessments (Moyle and Marchetti 2006).

Environments that are highly similar to those found within the native range of the invading species are expected to offer the greatest opportunity for successful establishment. The rainbow trout is an excellent model to evaluate environmental factors that might influence colonization success because it is widely introduced (Figure 13.10) and good records of introductions often are available (Fausch et al. 2001). They have been highly successful in the southern Appalachians, but most introductions to Scandinavia, central Europe, the United Kingdom, and the main island of Japan have failed. In other areas, including the Rocky Mountains, the Andes, Australia, and New Zealand, rainbow trout introductions have met with moderate success. By extensive analysis of flow records, Fausch et al. (2001) make a strong case that the coincidence of the timing of fry emergence with a low probability of flooding characterizes their native environment and strongly predicts success at establishment; in other words, the match between the native and receiving habitats is critical.

Habitat alteration can facilitate species invasions by creating novel environmental conditions to which native species are not well adapted. When free-flowing rivers are transformed into lakelike impoundments by dams and river regulation, native species may decline because of these changes and successful invaders will likely be those best suited to the altered ecosystem. A survey of 128 species of introduced freshwater fishes across 125 major drainages in North America found that large drainage basins with many impoundments and fewer native species contained the greatest number of introduced species (Gido and Brown 1999). Working with an extensive suite of morphological, behavioral, and life history traits for all fish species (28 native, 62 nonnative) of the Lower Colorado basin, Olden et al. (2006) found that rapidly spreading invasive species tended to occupy "vacant" niches, particularly with regard to life history traits, and the displaced species tended not to overlap in life histories with successful invaders. Thus the opportunity to invade previously unoccupied niche space, most likely arising from long-term environmental changes

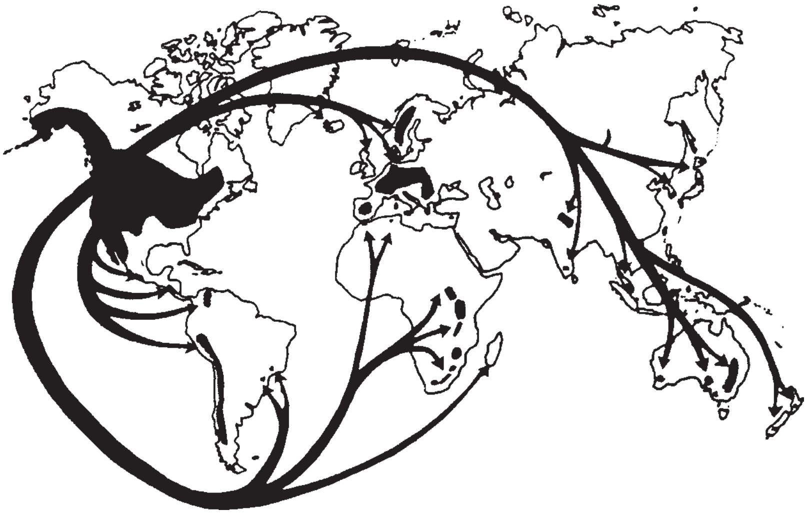

FIGURE 13.10 Transfer of rainbow trout (*Oncorhynchus mykiss*) from its original range in western North America (shaded area) to every continent but Antarctica. (Reproduced from Petersen et al. 1987.)

and particularly the establishment of lentic conditions in impoundments, has played a major role in the establishment of invasive species in the Colorado River Basin.

Finally, the three most successful invaders of freshwater worldwide, the common carp (*Cyprinus carpio*), rainbow trout (*Oncorhynchus mykiss*), and a tilapia (*Oreochromis mossambicus*), provide interesting contrasts in the degree to which invasive species duplicate the ecological role of a native species, or add a novel dimension to the assemblage. Rainbow trout (and brown trout as well) often displace another salmonid or a troutlike form. On the other hand, both carp and tilapia have been successful in regions where it appears that the ecological or life history traits of the invading species differs from all members of the recipient assemblage. Based on a comparison of species traits of carp to abundant native fishes in Australia, Koehn (2004) argued that carp were clearly different in their resource use and behavior, as detritivorous fishes are lacking in most freshwater fish assemblages in Australia. The success of *Oreochromis* is attributed to its broad physiological tolerance, extended reproductive season, protection of young, mouth-brooding behavior that allows them to reproduce in all habitats, omnivorous feeding, and predation upon young of coexisting fish species (Canonico et al. 2005).

13.2.2.3 Impacts of invasive species

The impact of nonindigenous species on the native biota is highly variable. Evidence to date suggests that many, perhaps the majority, of invading species have little impact, do not become abundant, and are assimilated into the existing assemblage without causing significant change. On the other hand, some invasive species clearly are harmful, and their contribution to species imperilment in freshwater is perhaps second only to habitat loss (Harrison and Stiassny 1999). Some 167 of Mexico's roughly 500 species of freshwater fishes are listed as being at some degree of risk, and 76 of these are attributed at least in part to the influence of invasive species (Contreras-Balderas et al. 2002). A survey of 31 case studies of fish introductions to stream communities in Europe, North America, Australia, and New Zealand found that 77% of the cases documented a subsequent decline in the native species (Ross 1991). Examples included the decline of native species in the southwestern United States following the introduction of mosquitofish, and declines of the native brook trout following the introductions of brown and rainbow trout. Trout and galaxiid fishes in New Zealand are incompatible; formerly widespread populations of galaxiids are now fragmented into remnant populations restricted to regions above barrier waterfalls inaccessible to trout (Townsend and Crowl 1991). In addition, nonindigenous species may cause a variety of indirect effects via food web interactions. In New Zealand, introduced trout exert greater top-down control over invertebrates than the native galaxiids, resulting in a reduction in benthic grazing and an increase in algal biomass (Flecker and Townsend 1994).

Declines in native species following fish introductions occur via a number of mechanisms, including species interactions, habitat alterations, introductions of diseases or parasites, trophic alterations, and hybridization (Taylor et al. 1984). Predation appears to be a common cause of the replacement of native species by exotics. Of ten studies reviewed by Ross (1991) where resource use was examined, habitat shifts following fish introductions were observed in half. For example, a variety of native species including the Sacramento sucker, rainbow trout, California roach, and three-spined stickleback shifted patterns of habitat use in the presence of the Sacramento squawfish, a predatory cyprinid introduced into the Eel River of California (Brown and Moyle 1991). Invading species also affect native species by hybridization, which Miller et al. (1989) found to be a factor in 38%

of the recorded extinctions of North American fish species. In most instances some other factor apparently resulted in the initial decline, and hybridization was the final blow. Examples include at least two subspecies of native cutthroat trout that have gone extinct because of interbreeding with stocked rainbow trout, the Snake River sucker, which hybridized with the Utah sucker, and the blue pike, which hybridized with the walleye.

A host of diseases and parasites are associated with alien species (Hoffman and Schubert 1984, Bruton and van As 1986), posing yet another threat to the invaded community. A fungal parasite causing crayfish plague decimated native crayfish throughout Europe following the introduction of resistant crayfish species from North American (Reynolds 1988). The cestode *Bothriocephalus acheilognathi*, which originated in China and the Far East and has been introduced worldwide with grass carp, has the potential to affect a wide variety of species (Bruton and van As 1986). Whirling disease, caused by *Myxobolus cerebralis*, was introduced to the United States from Europe in the 1950s and now affects wild fish and fish hatcheries in 23 states (Bartholomew and Reno 2002).

The worldwide spread of invasive species coupled with the decline or extirpation of native species results in a fauna that is becoming progressively more similar across regions, which in turn lessens the uniqueness of local faunas. This is the phenomenon known as biological homogenization, and freshwater fishes are a prime example. Using historic and present distributions of fishes of the 48 contiguous American states, Rahel (2000) compared the fish faunas for all states (1,128 pair-wise combinations), finding a clear increase in faunal similarity. On average, pairs of states have 15 more species in common than historically, and the 89 state pairings that originally had no fish species in common now have an average of 25 shared species. Introductions of sports fish and for aquaculture were primarily responsible and extirpations were few, a common finding with fish introductions (Gido and Brown 1999, Moyle and Marchetti 2006).

Few invasive species can match the impact of the zebra mussel *Dreissena polymorpha* in North America, which has become so abundant in some river and lake habitats that native species are directly imperiled and ecosystem function has been greatly affected. Rarely common in small streams except below the outlets of infested lakes, they can reach very high densities (100–10,000 m^{-2}) in larger rivers, where they have strong negative effects on native mollusks by fouling their shells and outcompeting them for food (Strayer 1999a). As zebra mussels continue their spread, the loss of many species of native mussels is a serious possibility. Their influence over ecosystem function is a result of very high filtering rates, in the range of 10–100% of the water column per day, such that feeding by zebra mussels rather than downstream export becomes the dominant fate of transported food particles (Strayer et al. 1999). First observed in the Hudson River in 1991, zebra mussels had spread to all of the lower river's freshwater regions by 1992, having reached a biomass that exceeded all other heterotrophs in the freshwater tidal Hudson. Phytoplankton and small zooplankton declined precipitously, as did benthic consumers including native bivalves. However, macroinvertebrate populations increased, apparently benefiting from pseudofeces as a food supply and the mussels themselves as structural habitat. Light penetration increased greatly due to the filtering of the water column, and soluble reactive phosphorus (P) increased, presumably due to the reduction in algal populations. There is also evidence that macrophytes increased greatly following the zebra mussel's invasion, representing a shift in productivity from the river to its vegetated shallows. These effects also extended to the fish assemblage: open-water fish species declined in zebra mussel-infested river sections whereas littoral fishes increased substantially (Strayer et al. 2004). Zebra mussels and a few other bivalves may rank amongst the most influential of invaders of freshwater ecosystems, diverting resources from the water column to the benthos and to vegetated shallow margins.

13.2.3 Pollution

Declines in water quality result from industrial, municipal, residential, and agricultural sources that generate a wide variety of contaminants. Point source pollution comes from a single source and is often delivered through a pipe from an industry or municipal wastewater treatment plant, whereas nonpoint source (NPS) pollution comes from diffuse sources, such as fertilizer runoff and acid rain. The former can more readily be monitored and regulated, and in many developed countries considerable progress has been made toward reducing industrial and municipal waste. This is not true everywhere, of course. In China an estimated 80% of rivers and of drinking water supplies are reported to be polluted due to that country's recent and rapid economic development (Wang 2004). NPS pollution is much more difficult to manage, and in the United States is considered a more serious problem (USEPA 2000). Most NPS pollution consists of nutrients and sediments and is attributed to agriculture, but timber harvest, road building, and suburban sprawl all contribute as well.

Declining water quality due to many different pollutants unquestionably is an important aspect of the deterioration of aquatic ecosystems. Often the effects are local, but contamination of a river reach can block fish passage as effectively as a dam. Biodiversity is most likely to be threatened when the affected area is critical habitat to an already rare and endangered population, as with some fishes of the Yangtse River (Dudgeon et al. 2006), or when a large area is contaminated, as in the case of freshwater acidification and the reportedly widespread contamination of China's rivers.

13.2.3.1 Point source contaminants

Many North American rivers, although gradually improving, have experienced some degree of pollution and show regional variation in the types and sources of contaminants. In the Delaware River near Philadelphia, significant pollution was noted as early as 1799, low levels of dissolved oxygen were reported in 1915, and workers at river docks during World War II complained about the stench (Jackson et al. 2005). Sediments of the Connecticut River are burdened with a complex brew of metals and organic compounds including polychlorinated biphenyls (PCBs) and polycyclic hydrocarbons (PAHs), resulting in fish and shellfish advisories; in the middle Hudson River, commercial and sports fisheries are restricted due to PCB contamination.

The important point source discharges in urban areas are from wastewater treatment plants (WWTPs) and industry (Paul and Meyer 2001). Improvements in WWTP technology have resulted in significant reductions in chemical constituents in many countries. However, in many older cities, storm and sewer drains are combined in a single system, and so during high flows the volume of water exceeds the capacity of the WWTP, forcing it to bypass untreated wastewater directly into receiving waterways. Combined sewer overflows are reported from one fourth to one third of cities in the United States and United Kingdom, and the problem is further exacerbated by aging and leaking sewer systems and the proliferation of septic systems in exurban areas.

13.2.3.2 Runoff from the land

Contaminants transported in urban and agricultural runoff are primary sources of nonpoint pollution to waterways, transporting sediments, nutrients, agricultural pesticides and herbicides, and various harmful substances (Table 13.2). More than one third of the river miles in the

United States are officially listed as impaired or polluted, and various categories of NPS pollution are considered leading causes (EPA 2002). Agricultural sources are responsible for 46% of the sediment, 47% of total P, and 52% of total nitrogen (N) discharged into waterways within the United States (Gianessi et al. 1986). Sedimentation affects the distribution of fish species, which vary widely in their tolerance for silted conditions. Agriculture increases nutrient levels due to fertilizers and animal waste, and also by increasing soil erosion, which particularly affects the transport of phosphorus. Urban areas can also be significant nutrient sources due to municipal wastes and fertilizers. In the Salt Fork River, an agricultural catchment in east-central Illinois that includes two substantial urban areas, urbanization was at least as important as agriculture in controlling instream nutrient concentrations (Osborne and Wiley 1988). This was true for soluble reactive P throughout the year and for nitrate-N during half of the year. During winter and spring, N fertilization of agricultural fields was the main determinant of instream concentrations.

Mass balance studies (Boyer et al. 2002) and analysis of fertilizer usage over time (Goolsby et al. 2001) show clearly that fertilizer usage is the primary driver of nutrient concentrations in rivers draining agricultural landscapes (Section 11.4). This is apparent from trends in nutrient concentrations in rivers (Figure 13.11) and in sources of N inputs (Figure 13.12). Nitrate concentrations in the Mississippi River doubled between the 1950s and 1980s, coincident with steady growth in the application of fertilizers over the same period (Turner and Rabalais 1991). The Mississippi's greatly increased export of nitrate is responsible for a substantial area of low oxygen within the Gulf of Mexico, the result of enhanced algal productivity and decay (Rabalais et al. 2001), and for changes to food web structure, owing to altered nutrient ratios (Turner et al. 1998). This is occurring in a region that supports 25% of US fish landings, and so has serious consequences for the regional fishing economy. Export of dissolved inorganic N by rivers is expected to continue to increase worldwide, due to increased fertilizer use and atmospheric deposition. Kroeze and Seitzinger (1998) forecast that by 2050, 90% of the DIN load of the world's rivers will be anthropogenic in origin.

A gradient of increasing urbanization has numerous impacts on stream ecosystems, including flashier flows from impervious surfaces and storm drains, nutrient and organic matter enrichment from lawn fertilizers and pet waste, altered channel morphology, and increased delivery of sediments and various toxins (Paul and Meyer 2001). Water entering streams can be significantly warmed during its passage over paved surfaces, and new construction is an important source of sediments. As a consequence of what has become known as the "urban stream syndrome" (Walsh et al. 2005), biotic richness is reduced while dominance by tolerant species is

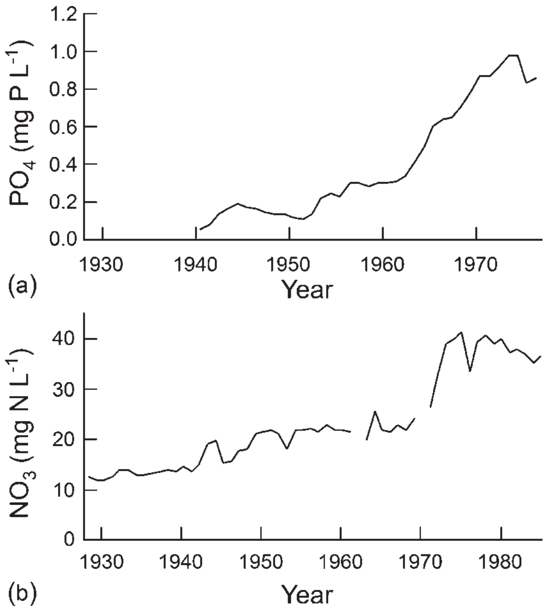

FIGURE 13.11 Historical trends in (a) phosphate and (b) nitrate concentrations in the River Thames, UK (Reproduced from Heathwaite et al. 1996.)

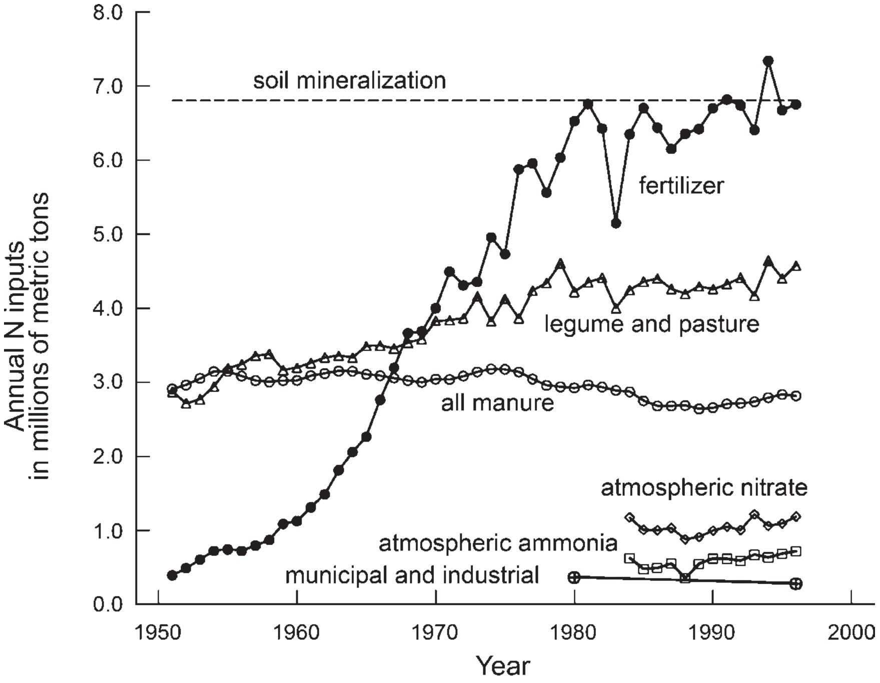

FIGURE 13.12 Annual nitrogen inputs to the Mississippi-Atchafalaya River Basin, 1951–1996. (Reproduced from Goolsby et al. 1999.)

greater. Stream macroinvertebrate assemblages generally show a reduction in diversity in response to increasing urbanization, but variable changes in abundances, as moderate levels of nutrient and organic enrichment can increase numbers of invertebrates whereas toxins, temperature change, and siltation generally cause declines. Although macroinvertebrates can be abundant in locations of organic pollution, the assemblage typically is dominated by midges (Chironomidae) and worms (Oligochaeta) (Wright et al. 1995). Improved drainage design to counteract the direct effects of storm drains that connect impervious surface to stream channels is likely to be among the most effective management actions for streams draining urban catchments (Walsh et al. 2005).

Individual large mines are point sources, but in areas of the southern Rocky Mountains, thousands of dispersed, abandoned mines from the 19th century silver and gold rush are so scattered they act more like NPS inputs. Because heavy metal concentrations were the best predictor of macroinvertebrate communities at 78 Rocky Mountain sites (Clements et al. 2000), it is likely that the legacy of historic mining activity influences the distribution and abundance of aquatic invertebrates throughout the region.

13.2.3.3 Atmospheric deposition

Acid rain and mercury deposition result in widespread and diffuse pollution to surface waters, even at considerable distance from sources. Acidification of freshwaters is a serious threat in regions of poor buffering capacity that have high levels of oxides of sulfur and N in the atmosphere, resulting in acid rain and snow (Section 4.4.3). Acidification of rivers and lakes in Scandinavia, Northern Europe, and the northeastern and some areas of the western United States has been most evident since the 1960s due to the accelerated inputs of pollutants to the atmosphere from the burning of fossil fuels. Sulfur deposition has declined in response to regulatory changes over the past several decades (Driscoll et al. 2001), but N deposition has not (Stoddard et al. 1999). Acidification of streams first affects acid-sensitive species, but when pH falls below 5 most species are affected (Section 4.4.3). Liming of streams to counteract acidification has met with only limited success; acid-sensitive species are observed from time to time but fail to persist (Bradley and Ormerod 2002). Reductions in SO_2 emissions in response to clean air legislation in the United States clearly has had beneficial effects, resulting in steadily increasing pH of rain and streamwater in the Hubbard Brook Experimental Forest in New England (Figure 13.13).

Elemental mercury as a gas is efficiently transported around the world, so that even remote areas experience mercury pollution originating from coal combustion, waste incineration, and other industrial processes (Morel et al. 1998). Methylmercury (MeHg), a form of organic mercury, is produced from inorganic mercury by biological and chemical processes, primarily due to the activities of sulfate-reducing bacteria in anoxic waters and sediments. Because MeHg is bioconcentrated in aquatic food chains, its concentration in fish often reaches or exceeds levels considered safe for human consumption, even in remote areas. The causes of bioaccumulation of MeHg are complex, but involve its solubility in algal cells and lipids and ready absorption through the intestinal wall of fishes, rather than direct uptake of mercury from the water. Because inorganic mercury does not readily enter food chains, its conversion to MeHg is critical to mercury accumulation.

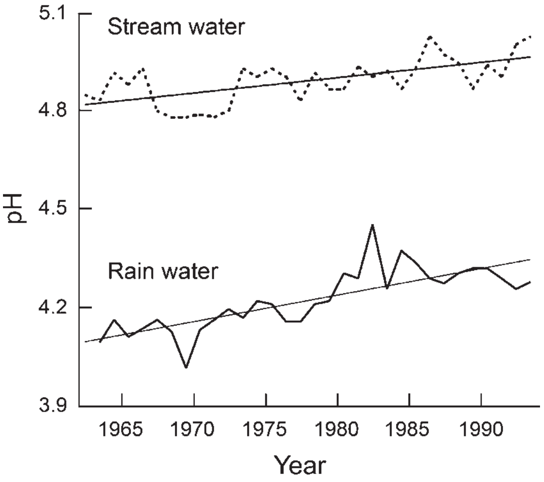

FIGURE 13.13 Recent trends in stream and rainwater pH in the Hubbard Brook Experimental Forest suggesting that streamwater pH has increased alongside the pH in precipitation. (Reproduced from Malmqvist and Rundle 2002 after Driscoll et al. 2001.)

The construction of reservoirs results in increased methylation of inorganic mercury by microbes. The amount of MeHg produced increases in relation to the quantity of organic carbon (C) stored in flooded vegetation and soils, showing an initial pulse and elevated levels in the water for years (Hall et al. 2005). Thus atmospheric deposition and dam construction can act synergistically to increase the human health risks of fish consumption.

13.2.4 Overexploitation

Overexploitation is of primary concern for fishes and some other vertebrates including amphibians, turtles, crocodilians, and certain water-associated birds and mammals; and for mollusks and some decapod crustaceans. Its importance relative to other causes of imperilment can be difficult to assess, partly due to lax record keeping, and partly because exploited stocks commonly face multiple threats including dams, habitat degradation, and pollution. Few freshwater invertebrates are imperiled due to direct harvest (Strayer 2006). However, mussels, valued for their shells, pearls, and meat since prehistoric times, have been extensively harvested in Europe and North America. Some reports describe quantities that would be unimaginable today, such as the >13 million kilograms of shells taken from the waters of Illinois in 1913 (Claassen 1994). These harvests were directed at abundant species, but the consequences of the bycatch for rare species may also have been significant (Strayer 2006). Today, freshwater mussels are harvested for their shells, which are cut into small spheres and used as seed pearls in saltwater oysters for the development of cultured pearls in Japan, China, and Australia. Regulated commercial harvests presumably are sustainable, but illegal harvests of mussels have been reported in the Midwestern United States, and so poaching poses an additional risk.

Overexploitation of freshwater turtles is the single most important threat to the turtles of Asia, where the majority of individuals are sold as food but most species are also sold for traditional medicine and as pets (Cheung and Dudgeon 2006). Almost one million individuals comprising 157 species, including 72 globally threatened species, were encountered in a market survey of three cities in south China, the world's largest consumer of turtles. Because some trade is covert, these may be underestimates. Little is known of the ecology of most Asian turtles, making it difficult to assess the ecological consequences of this harvest. All turtle species in and around Tonle Sap Lake, Cambodia, are seriously threatened by trade, as are seven species of water snake (Colubridae: Homalapsinae). Market surveys indicate that in excess of 8,500 water snakes are sold daily, primarily for crocodile and human food, in what may be the most intensively harvested snake assemblage in the world (Campbell et al. 2006).

Commercial and recreational fisheries have each been responsible for serious declines of highly valued freshwater fishes. Many of the large, long-lived species of river fishes around the world are endangered, with overfishing a contributory cause, including several carp, catfish, sturgeon, paddlefish, and a whipray of Asian rivers (Dudgeon et al. 2006). As the commercial fishery of the Peruvian Amazon has become more technologically advanced, high harvest pressure appears to be driving that fishery toward smaller fish and greater effort to achieve full capacity catches, classic signs of overfishing (De Jesus and Kohler 2004). Recreational overfishing deserves more attention, as substantial numbers of people are involved in some countries, fishing effort may be less likely to decline when stocks approach collapse levels, and even in catch-and-release angling, there can be postrelease mortality and sublethal effects on growth and fitness (Muoneke and Childress 1994, Cooke et al. 2002). Four important recreational fisheries in Canada experienced significant but largely unrecognized declines over the last decades of the 20th century (Post et al. 2002). The reason why this "invisible collapse" has not attracted more attention are speculative, but Post and colleagues suggest that anglers have come to expect less (the "shifting baseline") and have adapted by switching to different and less valued prey. In addition, recreational fishing and aquaculture are the most important reasons for the spread of nonindigenous species, and thus have a very important but indirect influence on freshwater biota (Cambray 2003, Cowx and Gerdeau 2004).

Overfishing has often been the first in a historical sequence of threats to fish populations, followed over time by pollution, habitat degradation, introduced species, and climate change (Jackson et al. 2001). This is well illustrated by the history of the Murray cod *Maccullochella peelii* of the Murray-Darling River, Australia's largest (up to 114 kg) freshwater fish (Rowland 1989). Based on records from railroad consignments and the markets in Melbourne, a large fishery had developed by the 1860s, with sales in urban markets peaking in the early 1900s, followed by a decline. Fishing became unprofitable by the 1930s, and then the Depression and World War II may have helped to end this period of overfishing. A second expansion of the fishery occurred from 1940 through 1955, followed by a second decrease to much lower levels by the early 1960s. By this time, however, the cumulative impact of dams, increased pollution, a growing recreation fishery, and the impacts of Eurasian perch on young cod combined to prevent the now reduced cod populations from recovering. Bringing this historical sequence to the present, hatchery stockings are contributing to the recovery of the Murray cod, and although the giants of the past are unlikely to be seen again, a recreational fishery has benefited.

Worldwide, the total freshwater commercial catch has been recorded since the 1950s, and these data show a steady increase with a possible plateau since the late 1990s (Figure 13.14). The 2002 freshwater catch of 8.5 million tons, about one tenth of the marine capture, is dominated by Asia and Africa, and is approximate because both under- and overreporting are suspected (Allan et al. 2005a). It is difficult to know whether overfishing is occurring because catch data for individual species rarely are available and many fisheries target entire assemblages in species-rich environments, often employing an impressive diversity of fishing gears (Welcomme 2001). The phenomenon known as "fishing down the food web" (Pauly et al. 1998), in which large individuals and species are removed first,

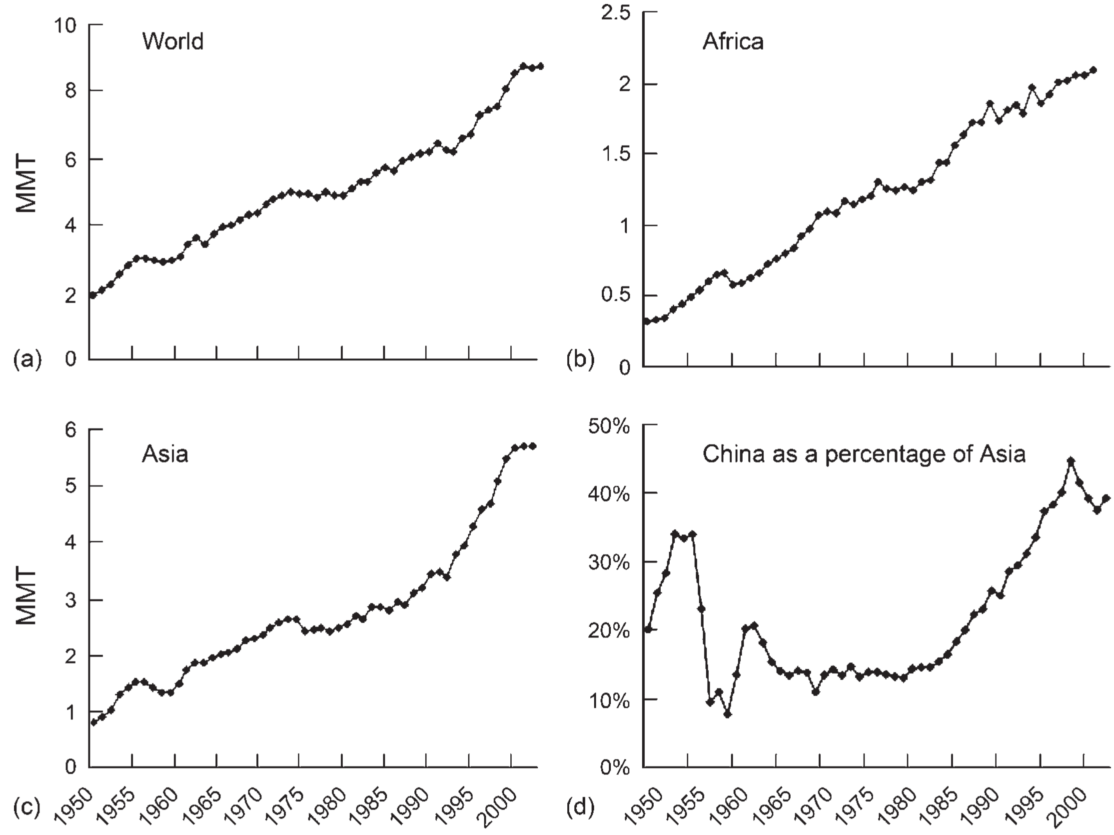

FIGURE 13.14 Fisheries landings from inland waters, 1950–2002, in MMT (million metric tons): (a) world, (b) Africa, (c) Asia, and (d) China as a percentage of Asia. (Reproduced from Allan et al 2005a.)

followed by smaller individuals, undoubtedly occurs in freshwater fisheries. However, inland waters often are dominated by small-scale commercial and subsistence fisheries that provide seasonal employment and protein for local consumption, and preferences for small fish in many African cuisines and the use of fish pastes and sauces in Asia encourage harvest of small species. As a consequence, freshwater fisheries may experience a mix of fishing down and fishing for all size classes. Changes in fishing gear are one indicator of overfishing, as nets of finer mesh are more time consuming and expensive to make than coarser mesh sizes, and will be adopted by fishers only out of necessity. In the foothill rivers of the Venezuelan Andes, local fishers use cast-nets to catch migrating *Prochilodus*, a member of the most widely harvested freshwater fish family in South America. Net mesh is measured by the width of several fingers of the hand, and over the last 20 years net mesh has declined from "four fingers" to "two fingers" to accommodate the decreasing size of the target (Taylor et al. 2006).

Overfishing of inland waters threatens the well-being of tens of millions of fishers who rely on this resource for income and food. It also threatens ecosystem health due to the loss of apex predators and influential species. Declines in Pacific salmon, attributable partly to overexploitation, have demonstrated the importance of marine-derived nutrients that these migrants transport into unproductive freshwater environments and the wide variety of consumers including birds and mammals that relied on this predictable food supply (Willson and Halupka 1995). The flannel-mouth characin *Prochilodus*, declining in Venezuelan rivers in part due to overfishing, has profound effects on ecosystem processes as described in Section 10.5.

13.2.5 Climate change

There is a broad consensus that rising levels of carbon dioxide (CO_2) and other greenhouse gases in the atmosphere have contributed to an approximately 0.6°C temperature increase over the past century (IPCC 2001). Further changes in greenhouse gases and other atmospheric pollutants are expected to result in significant additional warming by 2100, particularly at latitudes between 40°C and 70°C, as well as substantial regional and seasonal variation in precipitation. Climate change undoubtedly will have important consequences for aquatic ecosystems, having proximate effects due to changes in temperatures and flow regimes and more subtle effects due to changes in riparian vegetation, disturbance intensity and frequency, water chemistry, and species interactions (Meyer et al. 1999, Allan et al. 2005b). Some future impacts have a high likelihood of occurring but much uncertainty remains, partly because future climate conditions at regional and local scales are uncertain (Stainforth et al. 2005), and partly because of the complexity that results from climate change acting through multiple pathways. In addition, climate change will interact with other threats to lotic ecosystems, enhancing some regional water shortages, favoring species invasions, and acting as an additional stressor on the biota.

Most freshwater organisms are adapted to a particular temperature range (Section 5.3.1), and so poleward distributional shifts under warmer climate scenarios are highly probable. Studies predict a northward latitudinal shift of approximately 500–600 km for both macroinvertebrates (Sweeney et al. 1992) and fishes (Shuter and Post 1990) in response to a warming of 3–4°C. However, dispersal ability varies among taxa and few rivers are barrier-free, and so some species may face limited opportunities. For example, fish in the southern Great Plains and the desert southwest of the United States cannot move northward because those streams and rivers tend to run west and east. Because summer water temperatures now approach the upper limit for a number of species, just a few degrees of warming poses serious risk of extinction for native fishes in these regions (Matthews and Zimmerman, 1990). In mountainous areas, organisms can shift to cooler temperatures by moving to higher elevations, but the species' range will contract, as Keleher and Rahel (1996) illustrate for trout in the Rocky Mountains under a 3°C future warming scenario. Because streams are coolest in the headwaters, small streams are effectively like the tops of mountains, in that once these cool-water refuges are warmed there is no escape route for individuals or populations that are trapped there. Temperature also sets the northern range limit for harmful invasive species such as the zebra mussel (Strayer 1991), and so their expansion northward seems highly probable.

The amount and timing of runoff are expected to change significantly under future climate scenarios due to changes in evapotranspiration and precipitation. However, it is difficult to predict at regional scales whether changes in precipitation or evapotranspiration will be greater, and thus whether surface water levels and runoff will increase or decline. When two contrasting General Circulation Models were used to predict changes in runoff for 18 water resource regions of the United States, predictions were the same direction in only nine of the regions, and where the direction was similar, often the magnitude was not (Frederick and Gleick 1999). However, some outcomes are expected with reasonably high certainty. Glacier-fed streams are expected to experience an increase in discharge for years to decades, followed by declines as glacier ice is depleted. In regions that formerly accumulated a winter snowpack, warming temperatures will result in earlier runoff, or a shift to a variable winter flow regime driven by rain events (Barnett et al. 2005). Because winter snowpack is a natural storage reservoir, much of this winter runoff will be lost to the oceans. Due to the important influence of hydrologic disturbance on stream communities (section 10.3.3), a greater frequency and intensity of flooding is likely to be a widespread and important consequence of climate change for lotic ecosystems.

The most probable ecosystem response to climate change is an increase in biological productivity. Ectotherms typically increase their metabolism by a factor of 2–4 with each 10°C increase in water temperature, until very near their upper temperature tolerances (Regier et al. 1990). Thus, while changes in species composition may be complex and unpredictable, an overall increase in system productivity is likely to be a common response to climate warming. Riparian vegetation will almost certainly change under future climates, affecting the nature, timing, and supply of allochthonous inputs, and this is likely to affect the processing of detritus and functioning of the microbial–shredder food web linkage in complex ways. Altered C/N ratios of the leaves likely will reduce palatability, temperature changes will affect leaf processing rates, and floods may export leaf matter before it can be processed (Rier and Tuchman 2002, Tuchman et al. 2002). Figure 13.15 illustrates that these interactions are complex and potentially offsetting, making the overall impact of climate on this important energy supply difficult to predict.

The ability of the stream biota to disperse to more favorable environments will vary among taxa and locations. Fishes, winged invertebrates, and microorganisms that disperse with the wind or are transported by mobile taxa such as birds likely have dispersal rates that will allow them to keep pace with climate change. Other taxa such as mussels may not be as fortunate. Idiosyncrasies in drainage patterns and geography will determine whether suitable dispersal corridors and new habitats are available. Organisms that are aquatic in all life stages obviously must disperse along stream corridors, and so dams, inhospitable habitat, and other potential barriers can limit dispersal within basins, and catchment boundaries can be absolute barriers. Insects with an aerial adult stage are better able to disperse, and although the majority of their movements may occur along river corridors, dispersal across watersheds also occurs (Bilton et al 2001, Bunn and Hughes 1997). The majority of ^{15}N labeled

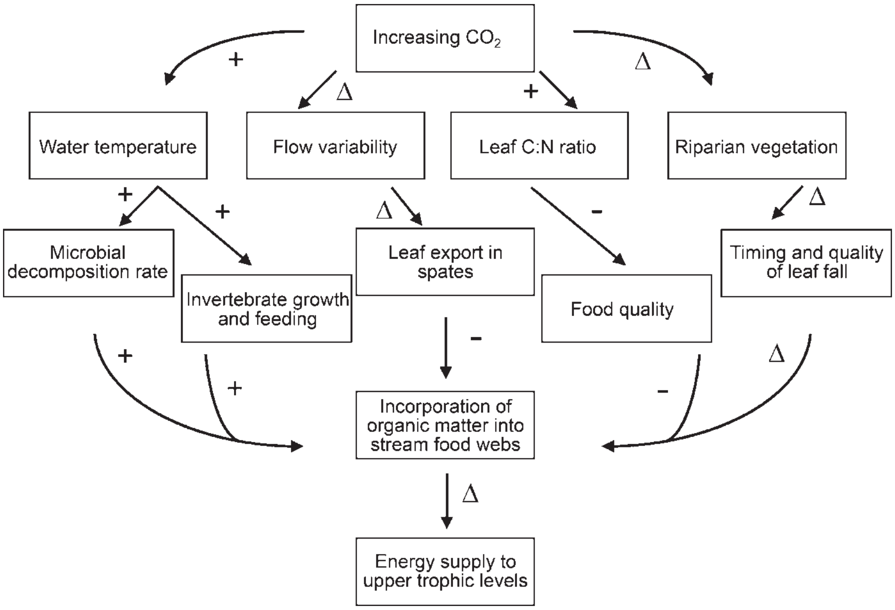

FIGURE 13.15 A rise in atmospheric CO_2 is expected to have complex effects on organic matter inputs, especially leaf fall, which is a principal energy supply to small streams. A warmer climate will increase most rate processes, increased hydrologic variability may adversely affect the retention and thus processing of organic matter, a higher C/N ratio of leaves is expected to reduce palatability, and climate change may cause shifts in the composition of riparian species. +, positive influence; −, negative influence; Δ, direction of change is uncertain. Based on studies by Rier and Tuchman (2002) and Tuchman et al. (2002a, b). (Reproduced from Allan et al. 2005b.)

stoneflies (*Leuctra ferruginea*) dispersed along the stream corridor with the preponderance of individuals moving in the upstream direction, but some dispersed >500 m across a forested landscape to an adjacent stream (MacNeale et al. 2005). Cross-catchment dispersal indicates the potential for range expansion as new environments become available. However, owing to geographic differences among locations in dispersal opportunities, and differences among species in rates of dispersal, it is highly unlikely that entire assemblages will shift together. There will be exciting research opportunities as ecologists work to understand the novel communities of stream ecosystems in transition.

Finally, it is important to note that climate change has the potential to worsen the impact of other threats. Increases in stream temperature due to riparian clearing will be exacerbated by a warming climate, and become particularly acute if hydrologic changes lead to low summer flows. Flooding may become more severe in many areas due to climate change, but will be more extreme if forest harvest, wetland loss, and impervious surfaces also play a role. As Figure 13.15 illustrates, some pathways are sufficiently complex that even predicting the direction of overall change is extremely difficult.

13.3 River Management

There is no doubt that rivers face serious threats, and although some stressors are moderating in their influence, others continue unabated. While there are many concerns, there also is much reason for hope. Rivers have enormous restorative powers, advances in science are beginning to point the way toward holistic, ecosystem-based management, and public awareness and concern are growing rapidly. In plain language, in order to manage, restore, and conserve lotic ecosystems, we have to understand how they function, we need to assess their condition over time in order to identify status and trends in river health, we need tested and proven management practices, and we need the will and organizational structure to put good intentions into action. The following sections will briefly examine some of these issues, which offer many opportunities for new partnerships among scientists, practitioners, and policy specialists to begin to reverse the many negative trends documented in the preceding section.

13.3.1 Bioassessment

Monitoring the status and trends of freshwater biota and ecosystems is essential in order to quantify human impacts and evaluate the effectiveness of management actions. Biological indicators of water quality have been in use for at least 100 years, and initially relied on the use of suites of species that were sensitive to organic enrichment and low oxygen levels. Known as Saprobic Indices, these were in wide use in Europe by the 1950s (Wright 1995). In the United States, water quality measures such as low dissolved oxygen, species diversity metrics such as the Shannon-Weaver Index, and a few indicator species known to be intolerant of pollution were the primary tools for monitoring stream condition into the 1970s. The 1972 amendments to the Clean Water Act called for maintaining and restoring the biological integrity of freshwaters, and that language is now reflected in widely used integrative ecological indices based on the biota and on aspects of habitat (Karr et al. 1986, Plafkin et al. 1989) including Karr's Index of Biological Integrity (IBI). The goal of these indices is to measure river condition, and increasingly this is referred to as "river health," in the very broad sense that a healthy river is one in good condition (Karr and Chu 1999).

The IBI is a multimetric index, meaning that it is the sum of 10–12 individual metrics, including species richness and composition, local indicator species, trophic composition, fish abundance, and fish condition. Because it is based on multiple metrics, which are considered to be sensitive to different levels and types of environmental stress, the IBI should be a useful integrator of multiple stressors affecting biological assemblages (Figure 13.16). Biotic integrity has been shown to vary within a region in relation to land-use measures and other indicators of environmental conditions (Section 13.1.3). The IBI has subsequently been adapted for use with macroinvertebrates (Kearns and Karr 1994) and periphyton (Hill et al. 1999).

Standardization of biological assessment faces a number of methodological challenges. The number of species in a sample increases with sampling effort and stream size, and varies across regions owing to differences in the regional species pool (Section 10.1). These are difficult but resolvable problems, and have led to prescriptions of sampling effort (such as a stream length equal to 25 times its width), different cut-off levels for metrics based on stream size (five darter species may be necessary for the highest score in a third-order stream, versus 1–2 species at a first-order site), and regional IBIs (including different scoring systems for warm water and cold water fish faunas) (Karr and Chu 1999).

Another approach that is gaining favor uses statistical models to predict the expected set of species from environmental site characteristics. Known as Rivpacs (River Invertebrate Prediction and Classification System) when first developed in the United Kingdom (Wright et al. 1984, Moss et al. 1987), and Ausrivas for its application in Australia (Marchant et al. 1997), it uses a multivariate model developed using undisturbed reference sites to predict which species have a high probability of occurring based on environmental measurements that characterize the site. When a test site is to be evaluated, its environmental conditions are used to predict the expected

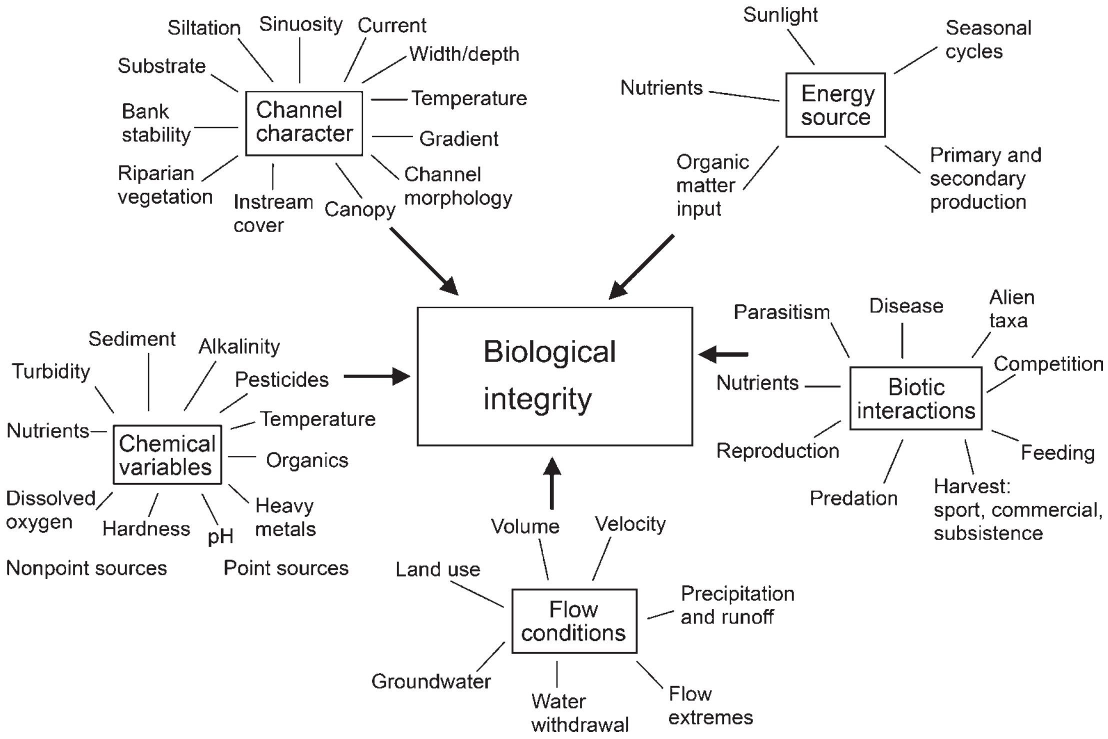

FIGURE 13.16 The Index of Biotic Integrity measures changes to stream health in response to human alterations to physical, chemical, and biological components of the five principal factors depicted. (Reproduced from Karr and Chu 2000.)

assemblage if the site is unaltered, and then the observed assemblage is compared to the expected (O/E). Not for the statistically faint-of-heart, O/E predictive models have proven to provide a sensitive measure of disturbance in southeastern Australia (Marchant et al. 1997) and are under development in other countries, including the United States (Hawkins 2006). In principle this method requires a substantial number of undisturbed streams to use as reference sites, but in some areas all streams may be moderately or substantially disturbed. This has led to the use of "least-disturbed" and "best-available" sites for scoring purposes (Stoddard et al. 2006), which is useful for comparison of sites within a region but makes difficult any comparison of index values across regions.

Analyses that are based on species traits represent yet another approach that holds promise for biological assessment. In one example, Usseglio-Polaterra et al. (2000) assembled data on 22 traits for 472 benthic macroinvertebrate taxa of the Loire River, and then employed multivariate ordination techniques to examine longitudinal changes in the assemblage. Because they were able to detect changes linked to dams, urban zones, and tributary inputs not detected with faunal data alone, they suggest that trait analyses may prove a useful additional method of bioassessment.

Although bioassessment is widely and successfully used to determine impairment of streams and compliance with water quality standards, the ability to combine state assessments into regional or national assessments of ecological integrity has been hindered by the lack of a common interpretative framework. To address this issue, Davies and Jackson (2006) proposed a model of biological response to a gradient of environmental stress within a framework of six tiers that describe how closely a water body resembles its natural state (Figure 13.17). By associating narrative descriptions of the response of ten ecological attributes to increasing levels of stressors, this model intends to provide more uniform and consistent assessment of the status of aquatic ecosystems.

13.3.2 Restoration and recovery of lotic ecosystems

Relatively intact streams and rivers can be managed to maintain a full complement of species and the natural range of ecosystem processes that characterize a healthy system, and degraded systems can be improved and restored. There is general agreement that emphasis should be placed on maintaining and restoring physical and biological processes that create healthy ecosystems and high-quality habitat, and on designing site-specific activities within a whole-catchment context (Roni et al. 2002). Specific activities are diverse and vary with stream type, the nature of the problems, and the goals of managers (Table 13.4). In the Pacific Northwest and other areas where salmonid enhancement is the primary goal, efforts commonly focus on improvements to habitat through the placement of boulders and wood, on restoring connectivity by replacement of poorly sited road culverts and reconnecting the stream channel to off-channel habitats such as beaver ponds, and on protecting the riparian zone as a source of shade, cover, and allochthonous inputs (Roni et al. 2002). Especially for rivers that now lack a mature riparian as a source of wood, the addition of large wood to streams has become a widely used method to enhance stream habitat worldwide (Reich et al. 2003). In physically unstable systems, bank stabilization to reduce slumping and sediment inputs often is a major goal, accomplished

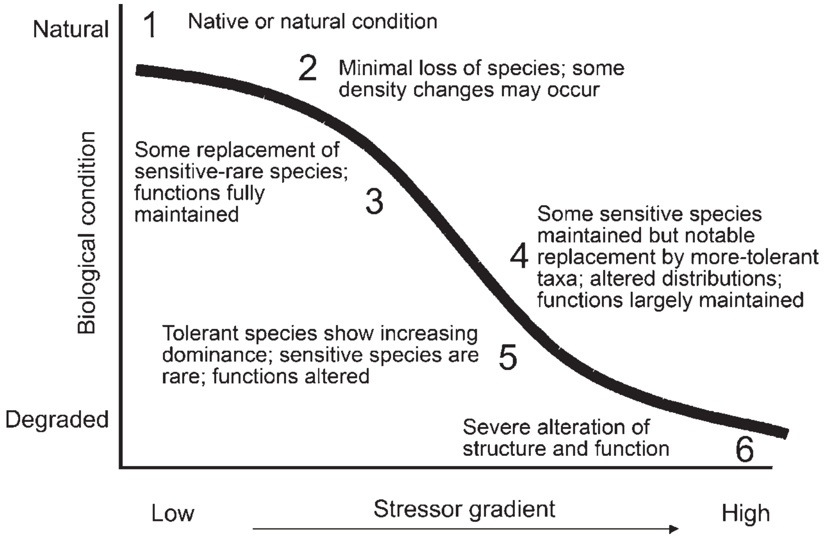

FIGURE 13.17 Conceptual model depicting changes in biological condition of a stream in response to an increasing gradient of anthropogenic stress. Numbers 1 through 6 refer to six tiers of river condition from fully natural and unaltered to that which is highly degraded. (Reproduced from Davies and Jackson 2006.)

with riparian plantings, addition of stone or wood at the toe of the bank, and by reductions in flow extremes when feasible (Shields et al. 1995). Wherever dams regulate flows, the objective is to provide necessary low, high, and flushing flows, with appropriate seasonal timing, to provide critical habitat and maintain ecosystem and geomorphic function (Figure 13.18). In short, the challenge is to identify the best suite of site-specific activities and integrate them into a catchment-wide plan.

To evaluate the extent of stream restoration in the United States, Bernhardt et al. (2005b) assembled over 37,000 cases from governmental databases, grey literature, and contacts from seven regions of the coterminous 48 states, classified into the 13 categories of Table 13.4. Goals and activities were distinguished because it was

TABLE 13.4 Common goals and activities undertaken to manage and restore streams. BMP refers to best management practices, LWD to large woody debris. Median costs were developed as part of a mainly US-based survey of river restoration. (From Bernhardt et al. 2005.)

Goal	*Median cost (US $)*	*Example activities*
Aesthetics/ recreation/ education	63,000	Cleaning (e.g., trash removal), revegetation, agricultural best management practices (BMPs), bank or channel reshaping, education
Bank stabilization	42,000	Revegetation, bank grading, rip-rap, large woody debris (LWD) added, deflectors, rootwads
Channel reconfiguration	120,000	Bank or channel reshaping, revegetation, rip-rap, riparian buffer creation/ maintenance, meander creation
Dam removal/ retrofit	98,000	Dam removal, revegetation, flow regime enhancement
Fish passage	30,000	Fish ladders installed, LWD removed, pools created, LWD added
Floodplain reconnection	207,000	Bank or channel reshaping, reinstating/maintaining hydraulic connections, revegetation, wetland construction, bank grading
Flow modification	198,000	Flow regime enhancement, water level control/maintenance, revegetation, boulders added, flow monitoring
Instream habitat improvement	20,000	Boulders, LWD added, sand traps, deflectors, revegetation
Instream species management	77,000	Native species reintroduction, bank or channel reshaping, revegetation, flow regime enhancement
Land acquisition	812,000	Land acquisition or purchase
Riparian management	19,000	Livestock exclusion, riparian buffer creation/ maintenance, eradication of weeds/nonnative plants, revegetation
Stormwater management	180,000	Wetland construction, riparian buffer creation/ maintenance, bank or channel reshaping, rip-rap, revegetation
Water quality management	19,000	Riparian buffer creation/maintenance, livestock exclusion, revegetation, fencing, agricultural BMPs

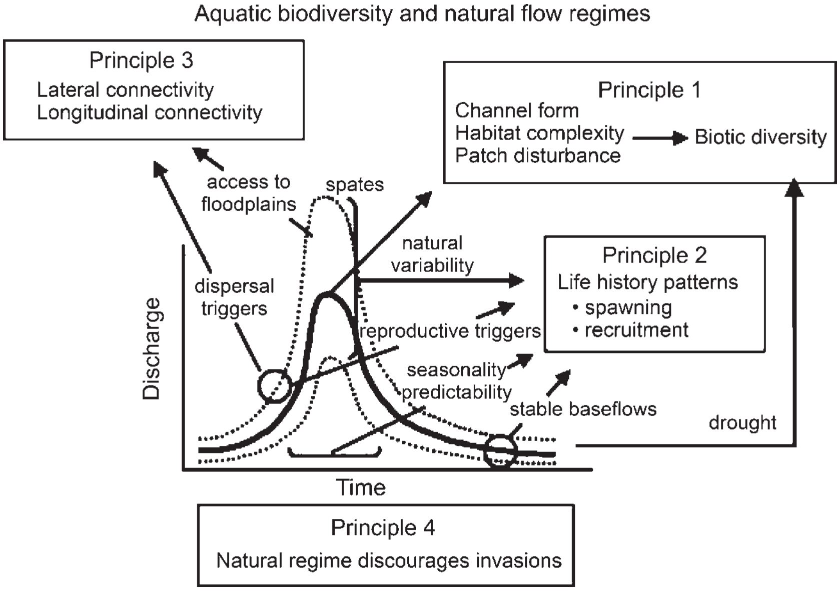

FIGURE 13.18 Diagrammatic representation of the natural flow regime of a river showing how it influences aquatic biodiversity via several, interrelated mechanisms (Principles 1–4) that operate over different spatial and temporal scales. (Reproduced from Dudgeon et al. 2006, after Bunn and Arthington 2002.)

apparent that the same activity could be employed for more than one purpose. The four most common goals were to improve water quality, manage riparian zones, improve instream habitat, and stabilize banks, which are typically small-scale projects that are relatively inexpensive. Using available cost data and extrapolating to the entire data set, Bernhardt et al. estimate expenditures of US $14–15 billion since 1990, or an average of US $1 billion annually. Moreover, their estimates excluded large projects on the Missouri, Columbia, and Colorado Rivers, and the Kissimmee and Everglades in Florida. Clearly, a great deal of stream restoration is taking place.

Individual case studies of river restoration include successes and failures. When artificial structures were added to sections of Austrian streams that had experienced river straightening, riffle–pool habitat variability was enhanced and fish communities improved significantly within 3 years (Jungwirth et al. 1995). Meander construction in a channelized Indiana stream resulted in improvements in habitat quality, algal abundance, and macroinvertebrate density in restored reaches, although neither macroinvertebrate diversity nor fish abundance benefited (Moerke et al. 2004; Moerke and Lamberti 2003). Streams in Finland that had been channelized for timber floating and were restored with boulder dams, flow deflectors, and channel reconstruction showed improvements in the extent of moss cover, habitat structure, and macroinvertebrate communities (Muotka et al. 2002). The addition of stone, riparian plantings, and installation of channel structures to a deeply incised sand-bed channel in Mississippi had positive effects on pool habitat and woody vegetation cover, resulting in increases in abundance, size, and diversity of the fish assemblage (Shields et al. 1995).

Other restoration projects have seen less positive results or have been counteracted by unmanaged stressors. In the Indiana example just described, continued sedimentation throughout the catchment was thought to be an important impediment to recovery (Moerke and Lamberti 2003). The addition of artificial riffles and flow deflectors to agricultural streams in the United Kingdom benefited habitat and flow, but neither macroinvertebrates nor fishes improved, which the authors attributed to problems with water quality and overall system flashiness (Pretty et al. 2003, Harrison et al. 2004). A comparison of riparian buffer zones in North Island, New Zealand, between reaches that had been fenced and planted 2–24 years earlier versus unbuffered control reaches found improvements in visual water clarity and channel stability in buffered reaches, but nutrient and fecal contamination responses were variable, and macroinvertebrate communities showed little change (Parkyn and Davies-Colley 2003).

It should not be a surprise that some restoration projects work better than others, and the study of successes and failures provides the opportunity to learn and improve practices. From its beginnings, the young field of restoration ecology has emphasized the opportunities to put ecological theory into practice and thus test ecological theory in the real world (Jordan et al. 1987). The amount of money spent in the name of stream restoration obviously calls for a better understanding of what constitutes successful restoration, and examples of restoration failures just described underscore the urgent need to evaluate restoration projects. Only about 10% of the projects surveyed by Bernhardt et al. (2005b) included monitoring, and although inadequate reporting likely contributes to this low percentage, that survey reinforced the view of many professionals that opportunities to learn from both successes and failures are being foregone. A subsequent and more detailed survey of 317 projects revealed a much greater extent of monitoring, perhaps because these were projects for which a manager could be found and contacted, and so were mostly agency professionals (Bernhardt et al. 2007). In these instances, however, monitoring rarely was carried out within the framework of an experimental design with well-formulated questions, and so it is doubtful that learning opportunities were maximized.

The success of a restoration project can be judged by a variety of criteria: whether it was built as designed and withstood subsequent floods, whether the design is aesthetically pleasing and results in its use and enjoyment, whether practical lessons were learned, and perhaps whether the project built enthusiasm for subsequent projects. Palmer et al. (2005) put forth five criteria by which to evaluate the ecological success of a restoration project. These include a guiding image of the dynamic healthy river that could exist at a site, measurable improvement of ecological condition, a self-sustaining outcome that requires little maintenance, an implementation phase that does no lasting harm from heavy machinery or other intervention, and the completion of pre- and postassessment studies with dissemination of findings. Jansson et al. (2005) suggest adding a sixth criterion, requiring that specific hypotheses and a conceptual model of mechanisms be made explicit. However, it is neither realistic nor necessary that all projects be monitored or even that most be monitored. Careful evaluation of restoration is justified when there is reason to suspect ecological harm may occur, when we have limited understanding of the outcomes, or when projects are large and complex. For many routine types of restoration, it is preferable to perform sufficient evaluation to have confidence in standard practices, and then invest only sparingly in monitoring.

In the future, the greatest challenge facing stream restoration will be to understand how best to expend limited funds along a river and throughout a catchment. Present practice is to restore streams “one reach at a time” (Bernhardt et al. 2007), and although over one third of the over 300 practitioners surveyed by Bernhardt et al. replied that individual projects were carried out as part of a catchment plan, the setting of priorities throughout a catchment remains largely opportunistic, and monitoring for the cumulative benefits of a number of discrete projects is largely unexplored. Indeed, scaling from the site to the catchment is a common problem that also affects conservation planning, the topic we turn to now.

13.3.3 Protected areas

The downward trend in freshwater biodiversity, coupled with the many threats reviewed in Section 13.2, demonstrates the need for freshwater conservation strategies. In addition to management and restoration of human-impacted systems, it is important to identify areas that have the greatest potential to conserve freshwater biodiversity and the best strategies to accomplish that goal. To date, rivers have been largely neglected in the discussion of protected areas (Abell et al. 2007). It is not possible to say what fraction of the world's rivers is currently protected, as they are not explicitly included in world databases of protected areas. Rivers located within parks have experienced contaminant spills and invasive species, and often are affected by dams even within park boundaries. Typically such parks are not designed with biodiversity protection as a goal, and so whether their boundaries include species of concern is likely to be accidental. In France, all mainland national parks are located at high elevations, whereas most imperiled fishes are present downstream (Keith 2000).

Authors agree that the catchment scale is appropriate for freshwater conservation (Saunders et al. 2002, Dudgeon et al. 2006), but problematic in practice because the area required can be impracticably large and the exclusion of people rarely is feasible. Although small areas may be set aside with freshwater conservation as their sole priority, and even some larger-scale river systems may be protected in their entirety in remote regions, human use of freshwater resources will need to be accommodated in most instances. When one considers the need to protect the entire upstream drainage network, the riparian zone and much of the surrounding landscape, and to avoid dams, pollution, or other activities that might prevent passage of migratory species, the challenges of whole-catchment conservation are apparent.

Abell et al. (2007) argue that the solution requires looking beyond the protection of individual sites, and instead developing a spatially distributed set of conservation strategies intended to protect specific populations or target areas (Figure 13.19). A freshwater focal area is the location of a feature requiring protection, such as a biodiversity hotspot or spawning area for a threatened species. Critical management zones are those areas whose management is essential to the functionality of a focal area, such as an intact river segment for passage of migrants, or a wetland that moderates flow extremes. The catchment management zone is the entire catchment upstream of the focal area, which might encompass a significant human presence but nonetheless would be governed by principles of basic catchment management. This need not be excessively restrictive: the management of New York State's Adirondack Park to maintain water quality for downstream users would fit well within such a model.

Future protected areas are likely to be more integrative by considering land, freshwater, and coastal oceans (Stoms et al. 2005), as well as in recognizing the presence of people in and near protected areas, and the flux of organisms across protected area boundaries. The disconnect between river and land protection is made obvious by the observation that rivers often form park boundaries, and the boundaries of land reserves rarely coincide with catchment divides (Pringle 2000b). Priority-setting and design strategies for the freshwater component currently lag well behind terrestrial and marine conservation work, and are hampered both by inadequate knowledge of the biota, especially those other than vertebrate animals, and insufficient understanding of ecological relationships.

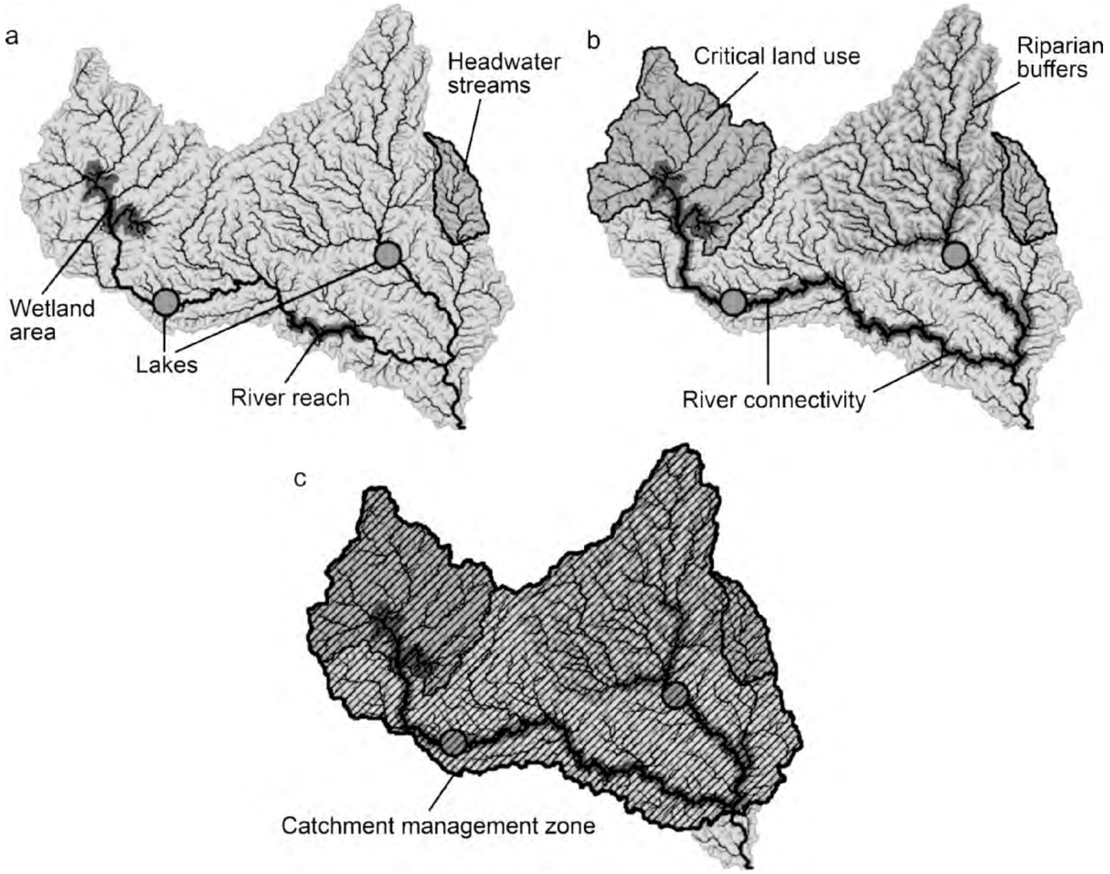

FIGURE 13.19 Diagrammatic representation of a freshwater protected area strategy that relies on spatially distributed actions to protect a target area from remote as well as local threats. (a) *Freshwater focal areas*, such as particular river reaches, lakes, headwater streams, or wetlands supporting focal species, populations, or communities; (b) *critical management zones*, like river reaches connecting key habitats or upstream riparian areas, whose integrity will be essential to the function of freshwater focal areas; (c) a *catchment management zone*, covering the entire catchment upstream of the most downstream freshwater focal area or critical management zone, and within which integrated catchment management principles would be applied. (Reproduced from Abell et al. 2007.)

All fields suffer these deficiencies to varying degrees, however. Much can be done using landscape analysis to identify lightly impacted areas, well-known taxa to recognize areas of diversity and endemism, and bioassessment methods combined with our knowledge of species–habitat relationships to select high-quality sites. A proactive approach to river conservation that targets an achievable percentage of representative river ecosystems worldwide is a worthy goal and challenge for the next generation of river ecologists.

Finally, we should recognize that ecological goals are most likely to be met when incorporated into water development planning from the outset, and conservation goals are most likely to be met when human needs are incorporated into conservation planning (Richter et al. 2003).

Conservation and management will complement one another in seeking acceptable compromises among protecting biodiversity, sustaining ecosystem function, and providing for human livelihoods and well-being (Moss 2000, Dudgeon et al. 2006).

13.4 Summary

Running waters are dynamic systems, ecologically and geomorphologically. Variation in the earth's geology and climate profoundly affect the biological functioning of rivers through their influence on valley vegetation and also on slope, hydrologic flowpaths, and channel characteristics. A principal goal of this book is to explain, as best we can, the enormous diversity among streams and rivers that is associated with stream size, landscape, and longitudinal position. Unfortunately, few rivers today are truly pristine, and many have been highly altered by various human activities. Habitat alteration, invasive species, contaminants, overexploitation, and climate change are major threats facing rivers today.

Freshwater ecosystems occupy <1% of the earth's surface but support at least 100,000 known animal species, including over 10,000 freshwater fishes and 90,000 invertebrates. There is no reliable estimate of the fraction that is imperiled, but data for major North American plant and animal groups provide evidence that a high proportion of the freshwater biota is at risk. Even when species persist, recent surveys often reveal reduced abundances and restricted distributions compared with historical occurrences, pointing to profound functional alteration of the remaining assemblage.

Alteration of physical habitat is likely the single most significant threat, and is due to many different human activities that affect flows, channel morphology, and land use. Due to construction of dams around the world, most river systems are impacted and few free-flowing sections of any size remain. Most of the largest river systems of North America, Europe, and former USSR are highly or moderately affected by dams, and dam construction on the rivers of Asia is of growing concern. Effects on rivers include changes to flow, sediment load, temperature, and water quality, as well as loss of upstream–downstream and lateral connectivity. Small streams are widened and straightened for water conveyance, whereas larger rivers commonly are modified for navigation, flood control, and utilization of floodplain land; both result in significant degradation and loss of habitat. Changing land use, including forest harvest and the spread of agriculture and urban areas, has pervasive but diffuse effects on river habitat by altering flows, increasing sediment inputs, and influencing energy supplies, temperature, and bank stability through changes to the riparian vegetation.

Invasive species pose a significant risk by dominating biomass and space, resulting in declines in native species and changes in trophic structure and ecosystem processes. Although a great many species have been introduced by accident or design, only a modest number become established as assemblage dominants, and so qualify as invasive or nuisance species. At the other extreme, nine species have been introduced into more than 30 countries, including three sports fish, a species used in mosquito control, and two tilapias and three species of carp popular for aquaculture and weed control. The successful establishment of an alien species can be viewed as a succession of probabilistic events, beginning with transport or dispersal and followed by establishment and further spread, until finally becoming fully integrated into the community. Invasion success is best predicted by a past history of successful invasions, broad environmental tolerance, ability to thrive in human-altered environments, similarity of source and recipient environments, and large propagule size. Although many nonindigenous species appear to have little impact on the recipient community, trout competitively displace native species and the zebra mussel has substantially modified ecosystem processes where it has become abundant in North America.

Declines in water quality result from contaminants that reach surface waters at specific locations, which is often true of industrial and municipal wastes, or from diffuse sources, as runoff from agricultural and urban land or atmospheric deposition. Harmful water quality conditions are widespread in developed countries, where nutrients and sediments from agriculture affect many streams and rivers and toxic contaminants vary in importance depending on present-day and legacy sources. In many developing countries, with less effective use of pollution control technologies, problems can be much worse. Acidification of surface waters from atmospheric deposition of SO_2 and NO_x has affected rivers and lakes in Scandinavia, Northern Europe, the northeastern and some areas of the western United States.

Overexploitation is of primary concern for fishes, other vertebrates including turtles and crocodilians, and for some mollusks and decapod crustaceans. Its importance relative to other causes of imperilment can be difficult to assess because exploited stocks commonly face multiple threats including dams, habitat degradation, and pollution. Overexploitation of freshwater turtles is the single most important threat to the turtles of Asia, and many tropical fisheries are harvested at such high levels that their sustainability is in question. The overfishing of inland waters is a concern not only because it threatens the loss of apex predators and influential species, but also the well-being of tens of millions of fishers who rely on this resource for income and food.

Climate change undoubtedly will have important consequences for aquatic ecosystems, having proximate effects due to changes in temperatures and flow regimes and more subtle effects due to changes in riparian vegetation, disturbance intensity and frequency, water chemistry, and species interactions. Whether species will be able to shift to locations within their physiological tolerances depends on chance and terrain, as dispersal routes and suitable habitat may not always be available. Because precipitation and runoff are expected to become more extreme under future climates, the role of disturbance in structuring biological assemblages may increase in importance.

Despite the seriousness of these threats, rivers have great restorative powers, advances in science are beginning to point the way toward holistic, ecosystem-based management, and public awareness and concern are growing rapidly. Advances in bioassessment provide the tools to monitor freshwater biota and ecosystems in order to quantify human impacts and evaluate the effectiveness of management actions. The practice of river restoration is growing rapidly, and although inadequately assessed and documented at present, this field holds great promise for the future. It is also important to identify areas that are relatively unaltered or harbor a distinctive biota and thus are most worthy of protection, and devise appropriate strategies tailored to the distinctive challenges of freshwater conservation. Most importantly, water development and conservation planning need to be integrated so that sustaining ecosystem function and providing for human livelihoods and well-being are pursued as linked goals.

Chapter fourteen

The foundations of stream ecology

Ecologists engaged in the study of running waters have developed a number of conceptual models whose purpose is to synthesize empirical information that describes structure, function, and processes of lotic ecosystems over their enormous range of natural variations. Such models are of great value in organizing what might otherwise be a collection of seemingly unique case studies into a broader understanding based on unifying principles. They gain power and acceptance from their ability to predict outcomes in new settings and explain differences observed among, for example, streams of differing discharge or occurring in different landscape and climatic settings. Models occasionally are proven inadequate, but exceptions also can strengthen models by revealing needed extensions.

Students wishing to explore the full range of models that currently influence our thinking about streams and rivers will benefit from the papers by Minshall et al. (1983), Statzner and Higler (1985), Junk et al. (1989), Petts (1984) Townsend et al. (1994), Poff et al. (1997), Lorenz et al. 1997, Lake (2000), Galat and Zweimüller (2001), Poole (2002), Ward et al. (2002), Weins (2002), Benda et al. (2004), and Thorp et al. (2006). Two models in particular, the river continuum concept (Vannote et al. 1980) and nutrient spiraling (Newbold et al. 1982a), have been especially influential to this generation of stream ecologists. More recently, the long-standing recognition that fluvial networks are both heterogeneous and hierarchical has been freshly infused by collaborations between ecologists and geomorphologists, leading to more explicit formulations of the episodic connectivity of spatially distinct units, and hence more appreciation of discontinuities along the continuum (Poole 2002, Ward et al. 2002, Thorp et al. 2006). An expanded view of scale, both temporal and spatial, enhanced through the contributions of hydrologic and geomorphological studies and with concepts from landscape ecology (Weins 2002), has greatly benefited stream ecology. At smaller scales extending down to cellular and molecular processes, new methods using isotopes and tools of microbial ecology promise rapid advances in our understanding of underlying mechanisms (Zak et al. 2006). Perhaps inadequately captured at present in the conceptual models discussed by the authors cited above, advances in our ability to understand functional relationships at the microbial and molecular scales may drive many of the advances in lotic ecology in coming decades.

Today's students have the enviable opportunity to observe future developments in stream ecology, and we have little doubt that the next several decades will be as exciting as recent decades. In closing, we provide our short list of foundational principles on which the future will build. Students can gain a diversity of viewpoints by consulting the papers cited within.

14.1 The Spatial Framework

The dendritic structure of stream channels reflected in network position and stream order (Figure 1.2), the hierarchical nesting of smaller habitat units within larger units (Figure 1.3), and the longitudinal gradient imposed by the unidirectional flow of water from sources to sea establish the large-scale spatial stage for river systems. As the fluvial system transitions along its length from its erosional upper reaches through its middle reaches of episodic erosion and deposition, and then to its depositional lower reaches (Schumm 1977), changes in the size and supply of sediments and the river's power (Figure 3.13) cause channel structure to change predictably. As important as the longitudinal axis is, rivers are of course three-dimensional systems (Figure 1.1), in which exchanges along lateral and vertical axes play vital roles (Ward 1989).

A river is often conceptualized as a continuum of flowing water, but in many regions, rivers are periodically interrupted by lentic waters. The effects of dams and impoundments are well documented (Section 13.2.1.1) and include habitat fragmentation, changes to flow and thermal regimes, and altered transport of sediments, nutrients, and organic matter. The effects of a dam eventually dissipate, although often not for many tens of kilometers. Because many rivers have multiple dams, they experience repeated breaks in the river continuum, described as the serial discontinuity concept (Ward and Stanford 1983). Recovery of the river downstream of each dam depends on dam size, its position along the river network, tributary inputs, and other factors. In the case of rivers that historically were connected to extensive floodplains, dams and levees may permanently sever lateral connectivity (Ward and Stanford 1995), resulting in the loss of critical ecosystem functions.

Less attention has been paid in river ecology to the natural interruptions that result when chains of lakes occur along a river's course. Lakes may have modest effects on dispersal, flow, and temperature relative to dams, but considerable influence on suspended and dissolved material in transport. A study of a chain of small lakes interspersed among river segments in Alaska's North Slope found that streams exported most ions and dissolved nutrients to lakes, whereas lakes exported dissolved organic carbon (C) to streams (Kling et al. 2000, Larson et al. 2007). In general, lakes are expected to retain particulates due to settling, and nutrients because of biological utilization, but results to date reveal considerable variation in patterns among lake chains (Soranno et al. 1999). The position of lakes along the river continuum also influences lake chemistry; lakes high in the catchment tend to be precipitation dominated whereas lakes lower in the landscape receive more groundwater inputs (Soranno et al. 1999). Although the river is indeed a continuum, lakes and impoundments along with tributary inputs and abrupt changes in topography may all result in discontinuous change of critical variables along a river's length.

Lateral connectivity at the aquatic–terrestrial boundary is an important and somewhat neglected dimension of river systems, due partly to an emphasis on small streams rather than large rivers and partly to the fact that lowland rivers in developed regions have been extensively modified. Although river–floodplain interactions are not limited to rivers of any size or region, large tropical rivers that have an annual flood cycle, flow through low-lying topography and remain largely unregulated, such as the Orinoco and Amazon Rivers of South America, provide excellent case studies. The period of flooding, which includes distinct phases of lateral inundation, throughflow of intermingled river and floodplain water, and drainage, can last several months and be highly predictable in timing and duration (Figure 14.1). In other river systems including those not in the tropics, the timing of flooding may be less predictable and rivers may not overflow their banks, and so the effect is more of a "flow pulse" (Puckridge et al. 1988). Tockner et al. (2000) argue that floodplains may be more common in the upper and middle reaches of temperate rivers, where floods are shorter and less predictable than in lowland tropical rivers but the expansion and contraction in discharge nonetheless still plays an important ecological role.

Vertical connectivity is the third important spatial dimension of rivers. Groundwater enters stream channels along multiple flow paths, both deep and shallow, which vary with rainfall, soil moisture, and season, and result in distinctive signatures in their chemical constituents, including nutrients and DOC. Especially in gravel-bed rivers with substantial subsurface connectivity, the hyporheic zone is a third habitat dimension which harbors a diverse meiofauna and provides relative safety to eggs of fish and invertebrates. Conditions within the sediments can be particularly important to nutrient cycling because of their role in abiotic uptake and especially because patches that differ in the availability of oxygen and organic matter determine the opportunities for nitrogen (N) transformations that influence how N is used within and possibly lost from the stream.

Integrating across dimensions and spatial scale, it is apparent that lotic ecosystems are spatially complex, hierarchical networks dominated by their longitudinal gradient but at the same time interrupted by lakes, dams, stepped changes due to tributary inputs, and discrete habitat types (Poole 2002). Key processes operate at different spatial and temporal scales and

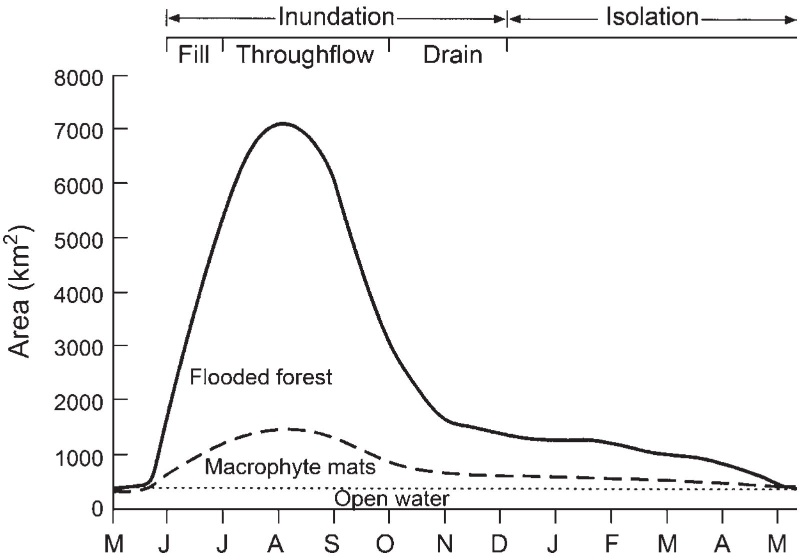

FIGURE 14.1 Contributions of flooded forest, macrophyte mat, and open water to the Orinoco floodplain area throughout the hydrological cycle. (Reproduced from Lewis et al. 2001.)

are the subject of different academic disciplines; however, the integration of these elements is critical to a full understanding of lotic ecosystem structure and function (Figure 14.2). In addition, landscape constraints on the physical structure of a stream ecosystem will determine which processes have local preeminence. For example, when lateral connectivity is high, the stream system will be strongly influenced by floodplain interactions, when vertical connectivity is high the stream system will be strongly influenced by interactions with the hyporheos, and when both lateral and vertical connectivity are constrained the stream will be most strongly influenced by upstream processes and by interruptions due to lakes and dams.

14.2 Community Assembly is Determined by the Species Pool, Habitat Sorting, and Species Interactions

The literature of community ecology is rich with concepts and models that address the central questions of this field, namely, what determines the compositional and relative abundance of species at a locale. Among many debated issues, the importance of regional versus local processes and of chance establishment versus mechanistically driven community assembly continue to be of great interest. On the one hand is the view that the biological assemblages of streams are made up simply of those species able to reach a

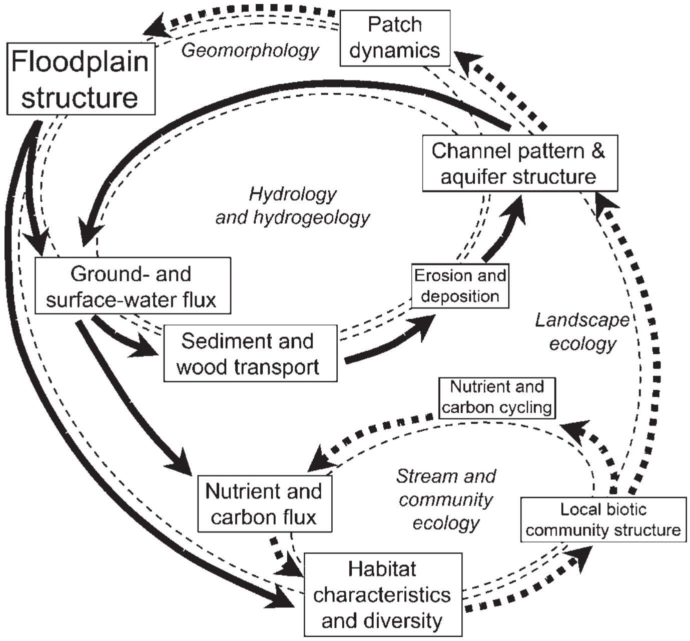

FIGURE 14.2 A conceptualization of the dynamic processes taking place within the riverine landscape of a floodplain river. Large text represents large spatial and long temporal scales, small text connotes fine spatial and short temporal scales. *Solid arrows* represent linkages driven predominantly by physical processes and *dashed arrows* represent biogeochemical interactions. Thin dashed ovals represent feedback mechanisms studied primarily by specific academic disciplines shown in italic text within each oval. (Reproduced from Poole 2002.)

particular location and survive in the habitats that it affords (Section 10.3.2). Many species play ecologically similar roles, and chance determines which hold sway at any particular moment. On the other hand is the view that biological communities have repeatable structure that results not only from environmental factors, but also from the interactions among species, including certain key species. For many years, researchers emphasized local-scale processes centered on niche relationships and species interactions operating within closed systems, but interest has increasingly shifted toward consideration of the regional species pool, and the importance of dispersal and colonization in linking local to regional processes. The metacommunity viewpoint is one in which spatially segregated assemblages of species develop in distinct patches that may or may not be similar in their environmental conditions (Leibold et al. 2004). Metacommunities are connected by dispersal, just as is the case for their individual populations. Although similar in many ways to the older patch dynamics perspective (Townsend 1989), the metacommunity perspective incorporates trade-offs between species not only in the typical dimensions such as resource use, but also, for example, between local resource utilization and colonization success.

The stream environment is heterogeneous across all spatial and temporal scales. Individual habitat patches typically are distinctive in their environmental conditions including current, substrate, temperature, organic matter accumulations, biofilms, and so forth. Many species will differ in how well they are suited to particular conditions along an environmental gradient (Figure 5.5), and because multiple environmental gradients exist, species sorting along environmental gradients is likely to play a significant role in determining local abundances. Fluvial environments also are subject to a considerable degree of temporal instability, particularly from hydrologic disturbance, and so patch residency by populations and assemblages must often be short. In some situations there may be a reasonably well-defined series of stages in patch development, as seems true of desert streams subject to episodic flash flooding. In other cases, the image of a shifting mosaic of patch types, perhaps more typical of gravel-bed streams, may be more appropriate. Regardless, it is evident that dispersal and colonization are important to the long-term presence of species and assemblages.

Species that succeed in a given environment and particularly those that become very abundant must possess traits that enable them to excel at utilizing resources, avoiding enemies, and resisting stresses (Tilman 1982). This also is evident in the differential success of invasive species, where most have limited influence on receiving communities and a relatively few have wide impact (Section 13.2.2). At the other extreme there may be species that persist primarily because they are adept at colonizing short-lived environments. When two outdoor experimental channels in southern England were flooded and allowed to become colonized, they accumulated 35 taxa in 1 month (Ladle et al. 1985, Pinder 1985). On day 16 the midge *Orthocladius calvus* completely dominated the channels, and by day 37 it had virtually disappeared. Remarkably, this was an undescribed species, in a region where the Chironomidae are relatively well known. Between the extremes of the few species that dominate across many locations and inferior competitors that are quickly displaced, there may be many species that exhibit trade-offs between their abilities to reach new environments and their success once they are established. One consequence may be a decline in assemblage similarity with increasing distance between sites, as reported in a study of New Zealand streams and attributed to distance limitations of dispersal (Thompson and Townsend 2006).

An emphasis on the importance of the regional species pool on local community assembly (Figure 1.5) obviously is in accord with the hierarchical view of physical habitat within the stream network (Figure 1.3). However, although it is attractive to visualize a hierarchical series of filters, this concept is largely untested in fluvial systems, and the best evidence to date is that filters at the microhabitat scale are most influential (Lamouroux et al. 2004). Furthermore, as a counterpoint to concepts that emphasize the roles of the regional species pool and colonization dynamics, species interactions within lotic assemblages unquestionably can be strong (Figures 9.11 and 9.15). A complete understanding of what forces determine local assemblages will need to invoke species interactions as well as species sorting according to the match between traits and environment. This will be subject to the constraints imposed by a modest number of species that, due to their abundance or their interaction strength, modify the opportunities for other species to persist. But environmental conditions often are short-lived in running waters, and so the ability to colonize and reestablish populations will almost invariably be an important dimension for lotic assemblages.

14.3 Streams are Transporting Systems

Rivers transport great quantities of water and dissolved and particulate material to the world's oceans. Truly, "rivers are the gutters down which run the ruins of continents" (Leopold et al. 1964). Water runoff from the world's land masses balances the excess of precipitation over evapotranspiration (Figure 2.2), but is very unevenly distributed by region (Table 2.1) and through time (Figure 2.3). Rivers transport about 15 billion tons of suspended materials annually to the oceans, and about 4 billion tons of dissolved material (Schlesinger 1997). Many aspects of climate, geology, and terrain contribute to regional variation in the solid and dissolved loads of rivers, and fluctuations in discharge are the primary cause of temporal variation (Figure 3.10). As discharge varies across all timescales including interannual, decadal, and longer, channels are shaped and reshaped in endless cycles in which the river seeks an equilibrium between channel shape and the forces of erosion and deposition, subject to the physical constraints set by water and sediment supply, and by elevational extent.

From an ecological perspective, unidirectional current and transport are uniquely riverine characteristics. Current influences the growth and survival of individuals and populations through multiple pathways (Figure 5.2), and scouring floods can decimate periphyton and animal populations, resulting in system dynamics that are governed by episodic cycles of renewal and loss (Figure 10.8). Disturbance frequency is a key process influencing assemblage structure, acting like a switch to favor one group of organisms over another, and contributing to overall diversity by preventing the displacement of vulnerable species by dominant species (Section 10.3.3). Accidentally or deliberately, young fish and perhaps some invertebrates use current as an aid in their downstream travel.

The dynamics of organic matter and nutrients within lotic ecosystems are profoundly influenced by the transport capacity of streams and rivers. On an annual basis, rivers carry to the oceans an estimated 0.4 billion tons of organic C, composed of roughly equal quantities of particulate and dissolved organic carbon (Meybeck 1981). Forested headwater streams process coarse particulate organic matter (CPOM) in place, but are inefficient at processing the majority of dissolved organic matter (DOM) and fine particulate organic matter (FPOM), and so more is exported to downstream ecosystems than is metabolized (Webster and Meyer 1997). Lakes, impoundments, and floodplains can store substantial quantities of transported organic matter, and microbial processing within the lower reaches of large rivers (Cole and Caraco 2001) also may be significant.

Nutrients are bioavailable primarily in dissolved inorganic form, and their downstream passage is most likely to be influenced by the stream ecosystem when biological demand is high relative to nutrient supply and when hydrologic conditions facilitate uptake. In most years more than half of the annual nitrate export from a reference stream in the Hubbard Brook Experimental Forest, New Hampshire, occurs during spring snowmelt, from March to May, when both stream flow and nitrate concentrations are high (Figure 14.3). Similarly, a phosphorus (P) budget of a New Hampshire stream found that half of the annual inputs and two thirds of the exports occurred in just 10 days of the year (Meyer and Likens 1979). However, when bioavailable N or P is added to a stream reach it is rapidly immobilized by the biota of the streambed, and can quickly finds its way into all trophic levels (Section 11.3.3.3). Thus, streams can occupy two ends of a continuum in terms of nutrient processing: a throughput mode at high discharge and a processing-retention mode at low flows. A full understanding of nutrient retentiveness at the stream reach and its scaling up to the network is an area of much current interest. If instream nutrient retention has contributed significantly to the nitrate decline described by Bernhardt et al. (2005a) that took place over several decades (Figure 14.3), then studies of nutrient cycling in forests and streams will need to be better integrated than has been true to date. Reach-scale studies have convincingly demonstrated the attenuation of dissolved inorganic N in transport by processes of uptake and transformation (Peterson et al. 2001, Webster et al. 2003), and this complements basin-scale estimates of nitrate removal, presumably due to denitrification (Alexander et al. 2000) and the cumulative effect of N removal along the entire flow path (Seitzinger et al. 2002). However, until we obtain a fuller understanding of the eventual fate of inorganic N retained in small streams, and whether it is permanently removed by denitrification or exported in particulate organic forms, the importance of processes within the stream network to downstream export remains unsettled.

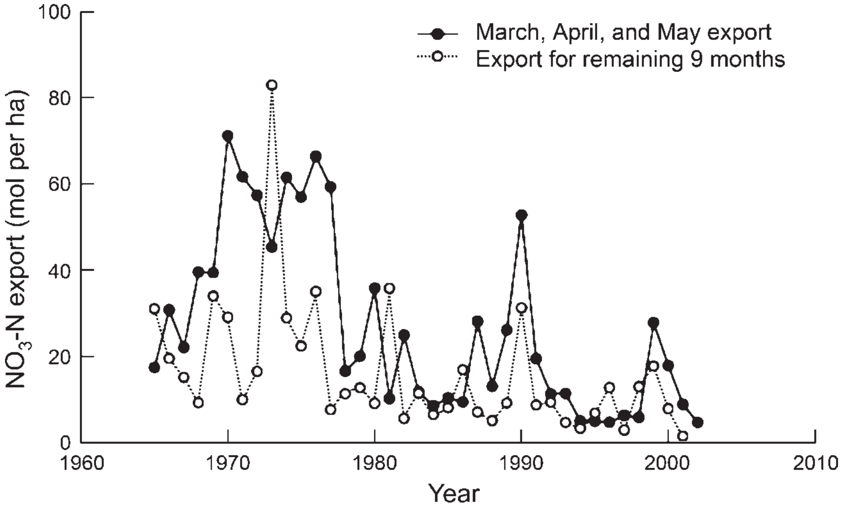

FIGURE 14.3 Spring nitrate export (grams of nitrogen as nitrate [NO_3-N] per hectare) compared with export from the rest of the year for a reference stream in Hubbard Brook Experimental Forest. Note also the long-term decline in nitrate export. Possible explanations include greater retention within the forest ecosystem, reduced forest disturbance, and greater instream processing. (Reproduced from Bernhardt et al. 2005.)

14.4 Primary Production and Allochthonous Detritus are Basal Resources in Lotic Ecosystems

The basal resources of stream food webs are primary producers and detritus, which together comprise a diverse mix of energy sources, the importance of which varies with environmental conditions. Algae in surface films are prevalent in small streams through mid-order rivers that receive adequate light (Figure 7.13), and planktonic algae are a possible energy source in large lowland rivers. Detrital energy sources are ubiquitous, although the processing of CPOM (Figure 7.3) is primarily a feature of low-order streams within forested regions. Clearly, the relative importance of these basal resources varies with position along the river continuum (Figure 1.7), as Vannote et al. (1980) articulated for a river network originating within a forested landscape. Under those circumstances, the basal resources of headwater streams are dominated by inputs of leaf litter, mid-order streams receive sufficient light to support greater productivity of benthic algae, and large lowland rivers are dominated by FPOM and DOM, although some phytoplankton also are present. Functional feeding groups of macroinvertebrates are presumed to track these longitudinal patterns in resource supply.

The river continuum concept has proven to be a resilient encapsulation of the relative roles played by different basal resources along an idealized river system. Furthermore, the longitudinal distribution of functional feeding groups often, although not invariably, can be shown to be at least approximately in accord with expectations (Figure 14.4). Nonetheless, the applicability of this model to running waters worldwide has been questioned (Winterbourn et al. 1981, Lake et al. 1986, Statzner and Higler 1985) and it is apparent that the hypothesized pattern of changing energy pathways from headwaters to river mouth is only a first approximation of a more complete understanding of how energy is utilized within lotic ecosystems. In particular, energy supplied via microbial pathways and from lateral inputs both deserve much more attention, and there is growing evidence that the quantitatively largest energy sources are not necessarily those of greatest importance to consumer production.

Although DOM and FPOM are unquestionably the largest C pools in lotic ecosystems, budget analyses (Section 12.4.1) reveal that their utilization is modest relative to export. However, as we learn more about the functional linkage between primary production and microbial utilization of DOM and FPOM within biofilms, especially in low-order stream networks, and of the longitudinal decline in DOM concentrations evident in large lowland rivers (Figure 12.9), it is apparent that substantial quantities of organic matter are mineralized by microbial activity along the river continuum. Whether this microbial production is a link to macroconsumers or is mostly dissipated by the respiration of microbes and the meiofauna remains uncertain. Biofilms may also serve to blur the boundaries between primary producer and detrital energy pathways, and so contribute to instances where functional groups correspond less well to expectations under the river continuum concept.

For many lowland rivers, energy inputs may derive primarily from upstream sources, including tributaries and whatever production occurs within the main channel, but lateral inputs can be of great importance in rivers that inundate their floodplains (Junk et al. 1989). During the annual flood pulse (Figure 14.5), organic matter from the floodplain as well as algae and organic matter from fringing channels and floodplain lakes make substantial contributions to the secondary production of the river–floodplain biota. Indeed, the most productive freshwater fisheries are located in large rivers with extensive floodplains, where the recruitment of young fishes correlates with interannual variation in the strength of flooding and thus determines the size of the catch when those juveniles mature into

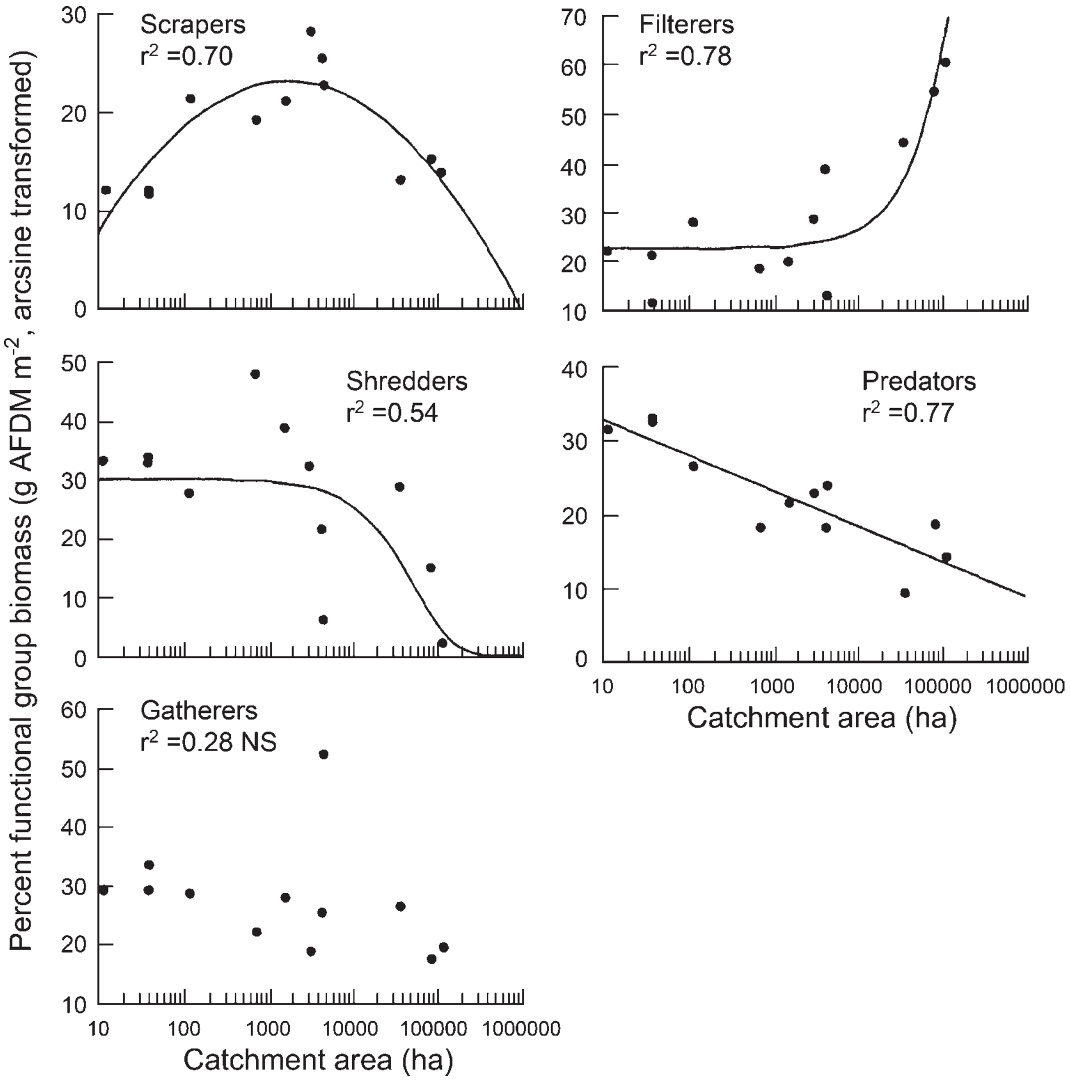

FIGURE 14.4 Relationships between relative dominance of feeding groups and catchment area in the Ball Creek–Coweeta Creek–Little Tennessee River continuum. Dominance is expressed as percentages of total habitat-weighted biomass at each sampling station. (Reproduced from Grubaugh et al. 1996.)

harvested size classes (Welcomme 1979). In the Rio Solimoes, the growth of omnivore fishes was clearly linked to hydrological seasonality (Bayley 1988), as was also true in the lower Mississippi river provided that flooding coincided with temperatures above 15°C (Schramm and Eggleton 2006). However, as important as the floodplain may be to secondary production in large rivers, at least one fourth of the fish species from a number of large temperate rivers can complete their life cycle in the main channel (Galat and Zweimuller 2001). Fishes including larvae and juveniles were abundant in the main channel of the Illinois and Mississippi Rivers and appeared to be supported by in-channel production based on the presence of zooplankton and invertebrates in their diet

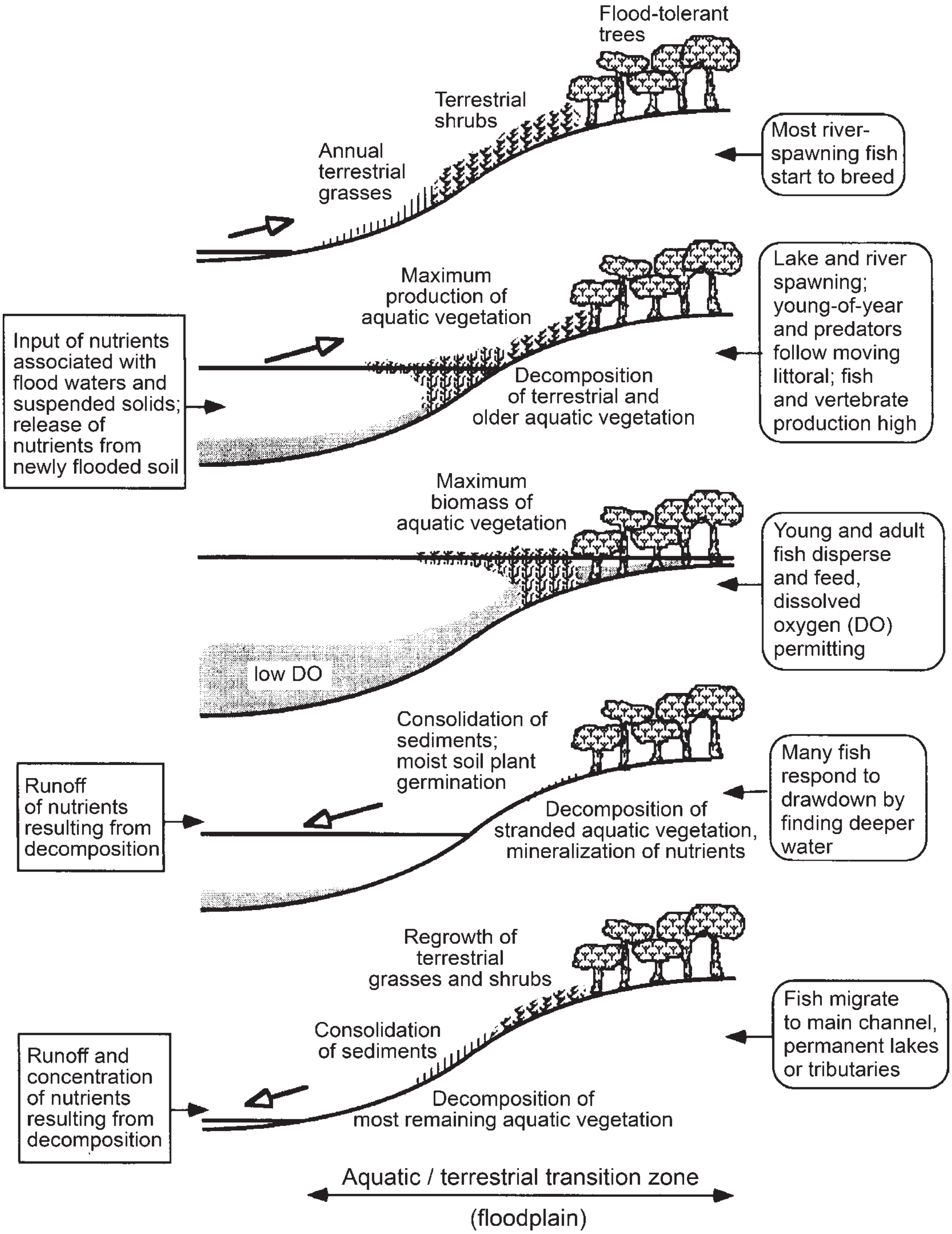

FIGURE 14.5 During the annual flood pulse in a floodplain river, the littoral boundary of the river moves laterally with the rise and fall of the flood pulse, influencing fish recruitment and exchanges of nutrients and organic matter. (Reproduced from Bayley 1995, after Junk et al. 1989.)

(Dettmers et al. 2001). These apparently contrasting findings may reflect differences in the role of floodplain inundation in tropical versus temperate settings, or between more pristine versus more constrained rivers with more developed floodplains. In rivers that have high primary production, are regulated, or where the floodplain is not as productive as the main channel due the timing of the flood, fish production may be more dependent on in-channel production (Junk and Wantzen 2004). In rivers with extensive flooding driven by an annual flood pulse, the original model may apply.

There is no question that detrital energy sources are important inputs of organic C in virtually all lotic ecosystems, but budgetary accounts of inputs and exports may fail to provide an accurate view of the energy supplies that fuel higher trophic levels. However, by analyzing the signature of certain isotopes in animal consumers it is possible to identify their primary food supplies, and in a number of instances where the energy sources were assumed to be allochthonous, a surprising dependency on autochthonous production was revealed. Isotopic signatures of fishes and invertebrates indicated that transported organic matter, including living and detrital algal components, was the main source of C for primary consumers in both constricted and floodplain reaches of the Ohio River (Thorp et al. 1998). In the Orinoco floodplain, macrophytes and leaf litter from the flooded forest represented 98% of the total C available, but isotope analysis showed that phytoplankton and periphyton were the major C source for fish and macroinvertebrates (Lewis et al. 2001). In addition, isotope data did not indicate that vascular plant C reached invertebrates through the microbial loop, suggesting instead that virtually all detrital C entered a "microbial dead end" and thus did not contribute to animal secondary production in the Orinoco floodplain. From the perspective of ecosystem metabolism, large lowland rivers do indeed have a low P/R ratio and are highly heterotrophic, reflections of the high microbial respiration supported by DOM and POM. Secondary production by macroconsumers, however, may be based to a much greater extent on autochthonous production that occurs within the channel or inside channels and floodplain lakes (Figure 14.6). According to the riverine productivity model (Thorp and Delong 1994, 2002), autochthonous C fuels secondary production in rivers with constricted channels and can be an important but not the main source of C for macroconsumers in rivers with floodplains.

14.5 Rivers are the Product of their Landscapes

In a prescient essay published in 1975, Noel Hynes wrote that "in every respect the valley rules the stream." Geology determines the availability of ions and the supply of sediments, topography determines slope and degree of containment, climate and soils determine vegetation and hence the availability of organic matter and extent of shade, and so on. Decades of research support this view. The river continuum concept describes how basal resources and thus consumer assemblages and stream metabolism change along a river's length owing to changes in river size and terrestrial influences. The flood pulse model reminds us that rivers can interact extensively with surrounding land during regular cycles of inundation. In addition, our perspective on rivers within landscapes has expanded to encompass more explicit consideration of the physical template and spatial hierarchy provided by the river network (Section 14.1), and been enriched by concepts borrowed from the emerging field of landscape ecology. Intriguingly, Hynes (1975) also opined that every stream "is likely to be individual and thus not really very easily classifiable." The many efforts to classify streams and their limitations discussed in Section 3.4.3 do not make a convincing rebuttal to Hynes' statement. But three decades of effort to place the individuality of streams within the frameworks of scale and landscape has significantly

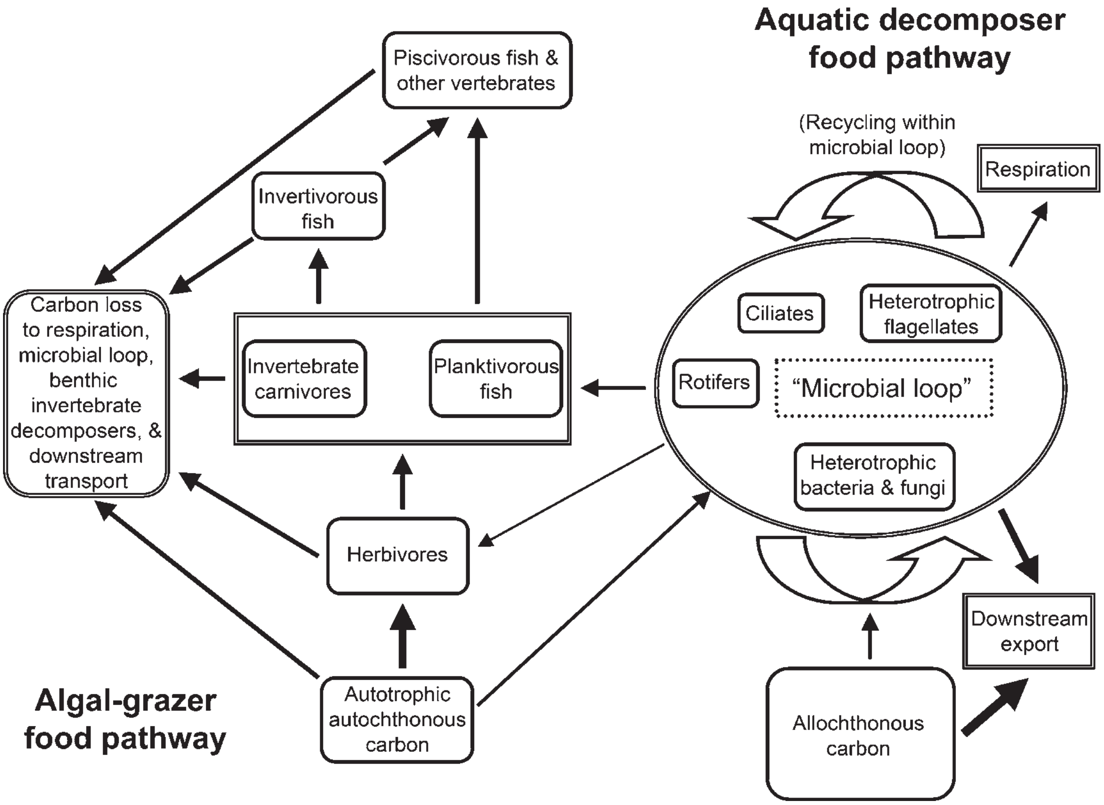

FIGURE 14.6 The riverine productivity model for large rivers (≥fourth order) proposes that secondary production by macroinvertebrates and fishes depends on autochthonous organic matter produced in the river channel and in the riparian zone, which are more labile but less abundant than organic matter of allochthonous origin transported from upstream reaches. The latter dominates the total amount of organic matter transported by rivers and contributes to high rates of microbial respiration but contributes little to the higher food web. (Reproduced from Thorp and Delong 2002.)

advanced our understanding of the causes of that individuality.

Rivers are shaped by environmental factors that control essentially all aspects of the river's physical appearance, vary from place to place, and can be organized hierarchically according to spatial scale (Snelder and Biggs 2002). Climate, topography, geology, and vegetation cover are fixed environmental variables that the river cannot influence, and because climate tends to be expressed at a larger spatial scale than topography, followed by geology and vegetation, their influence is approximately hierarchical (Figure 14.7). These four controlling factors operate at the macroscale and mesoscale of the river basin and catchment. At smaller scales of network position and valley landform, local processes are of greater importance.

The emerging view of rivers within a landscape perspective builds from recent ideas concerning the dynamical nature of local patches of the environment, the hierarchical nature of environmental controls, and the interconnections (or lack thereof) of spatial elements of lotic ecosystems in longitudinal, lateral, and vertical dimensions. The study of patch

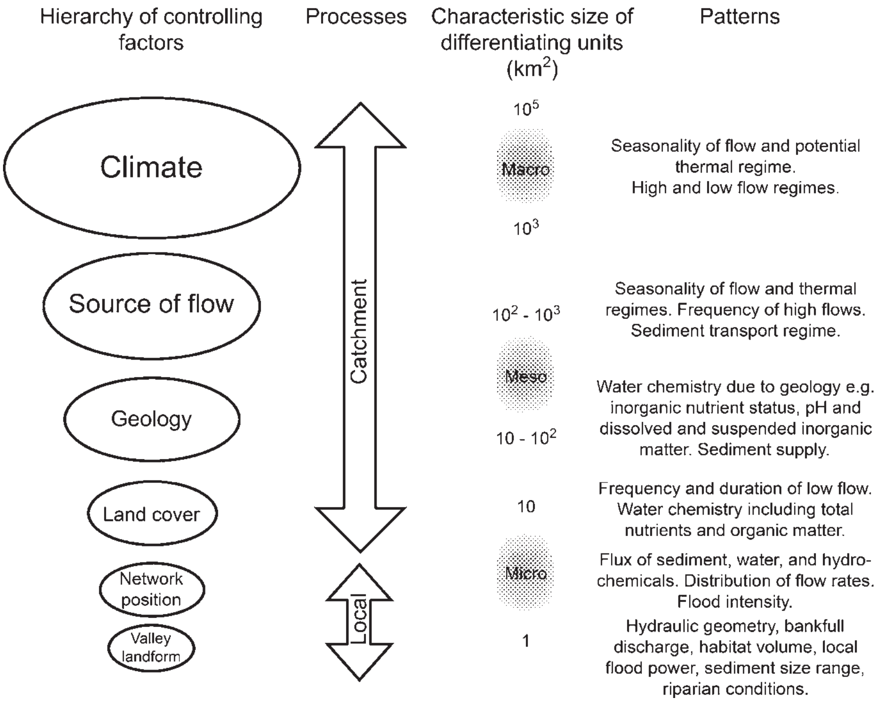

FIGURE 14.7 The hierarchy of controlling environmental factors and the spatial scales at which various physical characteristics of the riverine environment are expressed. (Reproduced from Snelder and Biggs 2002.)

dynamics in streams (Pringle et al. 1988, Townsend 1989) initially emphasized how episodic disturbance could create patches within the environment, the biological assemblages of which were in varying stages of successional recovery, interconnected at larger spatial and longer temporal scales by dispersal and recolonization. Although the language is somewhat different, nutrient dynamics similarly depend on processes that occur in spatially distinct locations associated with the availability of organic matter and the supply or lack of oxygen. For complete N cycling to occur, processes that occur in different areas have to be linked by the waterborne movement of different forms of dissolved N from one location to another.

Landscape ecology studies the interactions between spatial pattern and ecological processes in heterogeneous systems across a range of scales, emphasizing the importance of discrete patches, ecotones (the boundaries between patches), and the connectivity among patches (Ward et al. 2002, Weins 2002). In general, ecological processes are scale dependent so that factors operating at larger scales influence smaller scale systems but not the converse, in accord with the hierarchical directionality of influence described by Frissell et al (1986), Snelder and Biggs (2002), and others. Borrowing some central themes from landscape ecology (Weins 2002), one can assert that patches vary in their physical, chemical, and biological conditions (habitat quality, nutrient processing, and productivity); patches can be relatively persistent and discrete; patch context has an important influence on patch processes (local flowpaths, supplies of nutrients, and organic matter); connectivity is important (e.g., to overall assemblage dynamics and nutrient cycling); and events at the patch scale integrate to produce patterns observed at large scales while simultaneously being influenced by larger-scale patterns and processes.

The landscape perspective is much like the view of a river as seen from the window of an airplane, or perhaps from several airplanes flying at different altitudes. There is a patchiness of physical environments, formed by the interaction of hydrologic and geomorphological processes, which gives rise to repeatable patterns within a region but different patterns in different regions because of the hierarchical arrangement of controlling environmental variables described in Figure 14.7. Because river systems are both heterogeneous and hierarchical in structure, it follows that species assemblages, inputs of nutrients and organic matter, ecosystem processes, and hydrologic exchanges differ among patches but are linked at larger scales (Wu and Louck 1995, Poole 2002) (Figure 14.2). The location and arrangement of these patches is due in part to the arrangement of tributaries in a river network and in part to local and chance processes (Benda et al. 2004). Assemblages of species, ecosystem processes, and the relative magnitude of longitudinal, lateral, and vertical interactions differ among patches, but are interconnected at the larger scale of the river segment (Thorp et al. 2006).

Although it may be most intuitive to think of patches as small-scale elements, in the nested hierarchy of lotic ecosystems, patchiness is expressed at multiple scales, and dynamics within a patch are governed by both internal dynamics and by supplies of materials or organisms that are the outcome of processes in other patches and possibly at other scales. Patch structure and function is highly subject to the temporal pulsing of fluctuating hydrologic conditions, so that their state is highly dynamic and possibly ephemeral. This underlies the perspective that the river itself is a complex, shifting mosaic of channel features, habitat units, surface and subsurface zones, floodplains, and riparian corridors in which the diversity of the physical template provides the setting in which biologically diverse communities flourish and ecological processes interact across a range of scales (Poole 2002, Ward et al. 2002).

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