Marine larval ecology

Marine larval ecology is the study of the factors influencing the dispersing larval stage exhibited by many marine invertebrates and fishes. Marine organisms with a larval stage usually release large numbers of larvae into the water column, where these larvae develop and grow for a certain period of time before metamorphosing into adults. Most marine larvae are capable of dispersing long distances from their release site, although determining their actual dispersal distance is a significant challenge due to their microscopic size and the lack of an appropriate larval tracking method. Understanding dispersal distance, however, is important for a variety of reasons, including fisheries management, effective marine reserve design, and control of invasive species.

Theories on the evolution of a biphasic life history

Marine larval dispersal is one of the most important topics in marine ecology today. Most marine invertebrates and many fishes have evolved a life cycle involving a demersal adult and a pelagic larval stage or pelagic eggs that have the capacity to be transported long distances.[1] There are several theories behind why these organisms have evolved this biphasic life history:[2]

- Larvae use a different food source than adults, which may decrease competition between life stages.
- Pelagic larvae have the potential to disperse long distances, colonize new territory, and move away from habitat that has become overcrowded or otherwise unsuitable.
- A long pelagic larval duration can help a species break its parasite cycles.
- Pelagic larvae avoid benthic predators.

Pelagic larval dispersal, however, is not without its risks. For example, while larvae do avoid benthic predators, they are exposed to a whole new suite of predators in the water column.

Larval development

Marine larval development can be broadly classified into three categories: direct development, lecithotrophic, and planktotrophic. Direct developers are characterized by a larval stage that has very low dispersal potential and usually looks like the adult form of the animal. These larvae are also known as “crawl-away larvae,” since numerous marine snails exhibit this type of development, and their larvae crawl away from the egg mass. Lecithotrophic larvae generally have greater dispersal potential than direct developers. Many fish species and some benthic invertebrates have lecithotrophic larvae, which are provided with a source of nutrition to use during their dispersal, usually a yolk sac. Though some lecithotrophic species are capable of feeding in the water column, many, such as tunicates, are not, and must settle before depleting their food source. Consequently, these species have short pelagic larval durations and do not disperse long distances. Planktotrophic species, on the other hand, generally have fairly long pelagic larval durations and feed while in the water column. Consequentially, they have the potential to disperse long distances. This ability to disperse is one of the key adaptations of benthic marine invertebrates.[3] During their time in the water column, planktotrophic larvae feed on phytoplankton and small zooplankton, including other larvae. Planktotrophic development is the most common type of larval development, especially among benthic invertebrates. The relatively long time most planktotrophic larvae spend in the water column and their apparently low probability of successful recruitment led some early researchers to develop a “lottery hypothesis” that states animals release huge numbers of larvae to increase the chances that at least one will survive, and that larvae cannot influence their probability of success.[4] [5] [6] This hypothesis, though, views larval survival and successful recruitment as chance events, and numerous studies on larval behavior and ecology have shown this to be false.[7] Though it has been generally disproved, the larval lottery hypothesis does represent an important understanding of the difficulties faced by larvae during their time in the water column, particularly because it recognizes the low probability of larval survival.

All three types of marine larvae face two major problems: avoiding predation and finding an appropriate site to settle.

Predator avoidance

One of the major difficulties faced by larvae is the threat of predation. Larvae are small and plentiful, so many animals take advantage of this food source. The situation is particularly dangerous for invertebrate larvae in estuaries; estuaries are nursery grounds for planktivorous fishes. Estuarine species' larvae have evolved strategies to cope with this threat, including methods such as direct defense and avoidance. Direct defense is usually only evident in species in which larval development takes place entirely within the estuary. Studies have shown that larvae that do not leave estuaries are larger than larvae that develop in the open ocean. Additionally, many estuarine larvae have large spines and other protective structures. These defenses work because most planktivorous fishes are gape-limited predators—what they eat is determined by how wide they can open their mouths—so larger larvae are harder for them to ingest. Morgan showed that spines do indeed serve a protective function by cutting off spines of some estuarine crab larvae and monitoring differences in predation rates between despined and intact larvae.[8] Despined larvae suffered significantly higher predation rates than intact larvae, and were preferentially chosen during feeding trials with both types of larvae present. Additionally, Morgan showed that large-spined estuarine larvae usually keep their lateral spines relaxed, but raise them when approached by a predator. Therefore, predator deterrence in estuarine larvae is not only morphological but also behavioral.

A second strategy to deal with estuarine predators is to avoid them on small or large spatial scales. Some larvae do this at a small scale by simply sinking when approached by a predator. However, a more common avoidance strategy is to become active at night and remain hidden during the day, since most fishes are visual predators and need light to hunt. This strategy is not only evident in estuaries, but is also the main predator-avoidance strategy in the open ocean, since the water column lacks topography and thus hiding places. Most pelagic larvae and other planktonic species undertake diel vertical migrations between deeper waters with less light and fewer predators during the day and shallow waters in the photic zone at night, where their microalgal food source lives. By retreating to areas of low light during the day, marine larvae (and other zooplankton) can significantly decrease their risk of predation.[9] On a larger scale, most estuarine invertebrate larvae avoid predators by leaving the estuary and developing in the open ocean, which has fewer planktivorous fishes. The most common strategy for leaving an estuary is reverse tidal vertical migrations. In this strategy, larvae use the tidal cycle and estuarine flow regimes to aid their departure to the ocean, a process that is well-studied in many estuarine crab species.[10] [11] [12] [13]

The process of reverse tidal vertical migrations begins when female crabs release larvae on a nocturnal spring high tide in an attempt to limit predation by planktivorous fishes. As the tide begins to ebb, larvae swim to the surface waters and are carried away from their site of hatching towards the ocean. When the tide reaches its low and begins to flood, larvae swim towards the bottom of the estuary, where water moves more slowly due to the boundary layer. This prevents them from being sloshed back and forth within the estuary in the surface waters. When the tide again changes back to ebb, the larvae swim to the surface waters and resume their journey to the ocean. Depending on the length of the estuary and the speed of the currents, this process can take anywhere from one tidal cycle to several days.[14]

Dispersal and settlement

Probably the most widely accepted theory explaining the evolution of a larval stage is the need for long-distance dispersal ability. Sessile organisms such as barnacles and tunicates, as well as sedentary species like mussels and crabs, need some mechanism to move their young into new territory, since they cannot move long distances as adults. Many species have relatively long pelagic larval durations—the amount of time a larva is in the water column before it is competent to settle—on the order of weeks or months.[15] [16] During this time in the water, larvae feed and grow, and many species move through several stages of development. For example, most barnacles molt through six naupliar stages before molting to a cyprid, the stage at which they seek an appropriate settlement substrate. This allows the larvae to use different food resources than the adults and gives them time to disperse. This strategy, however, involves a certain degree of risk. While some larvae have been shown to be able to delay their final metamorphosis for a few days or weeks, few if any species are able to delay metamorphosis indefinitely, and most species cannot delay it at all.[17] [18] If these larvae metamorphose too far from a suitable settlement site, they perish. Due to the imperative of finding a suitable settlement site within a certain timeframe, many invertebrate larvae have evolved complex behaviors and endogenous rhythms to ensure their successful and timely settlement, which will be explained below. While many estuarine species exhibit swimming rhythms of reverse tidal vertical migration to aid in their transport away from their hatching site, the same species can exhibit tidal vertical migrations to reenter the estuary when they metamorphose and are competent to settle.[19] This process is similar to the reverse tidal vertical migrations described in the section discussing predator avoidance above, but instead of swimming down on flood tide, settlers remain in the surface waters, allowing themselves to be transported into the estuary. Another change that many larvae undergo after they reach their final pelagic stage is to become much more tactile, clinging to anything larger than themselves. For example, Shanks observed crab postlarvae in the lab and found that they would swim vigorously until they encountered a floating object.[20] Postlarvae would then cling to the object for the duration of the experiment. Shanks hypothesized that by clinging to floating debris, crabs can be transported towards shore due to the oceanographic forces of internal waves, which carry floating debris shoreward regardless of the prevailing currents. If they are able to successfully return to shore, settlers encounter a new suite of problems concerning their actual settlement and successful recruitment into the population. Space is a limiting factor for sessile invertebrates on rocky shores, and larvae might not find any open habitat. Additionally, settlers must be wary of adult filter feeders, which usually cover the rocks at settlement sites and eat particles the size of larvae. Settlers must also avoid becoming stranded out of water by waves, and must select a settlement site at the proper tidal height to prevent desiccation and avoid competition and predation. To overcome many of these difficulties, some species rely on chemical cues to assist them in selecting an appropriate settlement site. These cues are usually emitted by adult conspecifics, but some species cue on specific bacterial mats or other qualities of the substrate.[21] [22] [23]

Self-recruitment

One of the most important unanswered questions in larval ecology concerns the degree of self-recruitment in populations. For most of the short history of the field of larval ecology, larvae were considered to be passive particles that were carried by ocean currents to locations far from their site of hatching. This led to the belief that all marine populations were demographically open, connected by long distance larval transport. Recent work, however, is starting to show that many populations may be self-recruiting, and that larvae and juveniles are capable of purposefully returning to their natal sites.

Researchers take a variety of approaches to estimating population connectivity and self-recruitment, and several studies have demonstrated their feasibility. Jones et al.[24] and Swearer et al.[25] , for example, both investigated the proportion of [reef fish] larvae returning to their natal reef after their time in the water column. Each study found higher than expected (possibly as high as 60%) self-recruitment in these populations, using variations of a typical mark, release, recapture sampling design. These studies were the first to provide conclusive evidence of self-recruitment in a species with the potential to disperse far from its natal site, and laid the groundwork for numerous future studies.[26]

Implications

The principles of marine larval ecology can be applied to a number of fields both inside and outside the marine realm. Successful fisheries management relies heavily on understanding population connectivity and dispersal distances, and these processes are driven by larvae. Dispersal and connectivity must also be considered when designing natural reserves, both on land and in the water; if populations are not self-recruiting, then solitary reserves may lose their species assemblages. Additionally, many invasive species are able to disperse long distances during an early life stage, such as seeds in land plants or larvae in marine invasives. Understanding the factors influencing their dispersal is key to controlling their spread and managing already established populations. Through the continued study of the ecology of these microscopic creatures, scientists can better understand and more effectively manage myriad populations of both land and sea.

See also

- Crustacean larvae

References

[1] Grosberg, R.K. and D.R. Levitan. 1992. For adults only? Supply-side ecology and the history of larval biology. Trends Ecol. Evol. 7: 130-133.

[2] Swearer, S. E., J. S. Shima, M. E. Hellberg, S. R. Thorrold, G. P. Jones, D. R. Robertson, S. G. Morgan, K. A. Selkoe, G. M. Ruiz, and R. R. Warner. 2002. Evidence of self-recruitment in demersal marine populations. Bull. Mar. Sci. 70(1) Suppl.: 251-271.

[3] Strathmann, R. R., T. P. Hughes, A. M. Kuris, K. C. Lindeman, S. G. Morgan, J. M. Pandolfi, and R. R. Warner. 2002. Evolution of local recruitment and its consequences for marine populations. Bull. Mar. Sci. 70(1) Suppl.: 377-396.

[4] Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. Cambridge Philos. Soc. 25: 1-45.

[5] Roughgarden, J., Y. Iwasa, and C. Blaxter. 1985. Demographic theory for an open population with space-limited recruitment. Ecology 66: 54-67.

[6] Caley, M.J., M.H. Carr, M.A. Hixon, T.P. Hughes, G.P. Jones, and B. Menge. 1996. Recruitment and the local dynamics of open marine populations. Evolution 35: 1192-1205.

[7] Kingsford, M. J., J. M. Leis, A. Shanks, K. C. Lindeman, S. G. Morgan, and J. Pineda. 2002. Sensory environments, larval abilities, and local self-recruitment. Bull. Mar. Sci. 70(1) Suppl.: 309-340.

[8] Morgan, S. G. 1989. Adaptive significance of spination in estuarine crab zoeae. Ecology 70: 462-482.

[9] Zaret, T.M. and J.S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance. Limnol. Oceanogr. 21: 804-813.

[10] Cronin, T.W. and R.B. Forward, Jr. 1979. Tidal vertical migration: An endogenous rhythm in estuarine crab larvae. Science 205: 1020-1022.

[11] Tankersley, R.A. and R.B. Forward, Jr. 1994. Endogenous swimming rhythms in estuarine crab megalopae: implications for flood-tide transport. Mar. Biol. 118: 415-423.

[12] Zeng, C. and E. Naylor. 1996. Endogenous tidal rhythms of vertical migration in field collected zoea-1 larvae of the shore crab Carcinus maenas: implications for ebb-tide offshore dispersal. Mar. Ecol. Prog. Ser. 132: 71-82.

[13] DiBacco, C., D. Sutton, and L. McConnico. 2001. Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange. Mar. Ecol. Prog. Ser. 217: 191-206.

[14] Forward, R.B. Jr, and R.A. Tankersley. 2001. Selective tidal-stream transport of marine animals. Oceanogr. Mar. Biol. Annu. Rev. 39: 305-353.

[15] Brothers, E.B., D.M. Williams, and P.F. Sale. 1983. Length of larval life in twelve families of fishes at "One Tree Lagoon," Great Barrier Reef, Australia. Mar. Biol. 76: 319-324.

[16] Scheltema, R.S. 1986. On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. Bull. Mar. Sci. 39: 290-322.

[17] Gebauer, P., K. Paschke, and K. Anger. 2004. Stimulation of metamorphosis in an estuarine crab, Chasmagnathus granulata (Dana, 1851): temporal window of cue receptivity. J. Exp. Mar. Biol. Ecol. 311: 25-36.

[18] Goldstein, J.S., M.J. Butler IV, and H. Matsuda. 2006. Investigations into some early-life history strategies for Caribbean spiny lobster and implications for pan-carib connectivity. J. Shellfish Res. 25: 731.

[19] Christy, J.H. and S.G. Morgan. 1998. Estuarine immigration by crab postlarvae: mechanisms, reliability and adaptive significance. Mar. Ecol. Prog. Ser. 174: 51-65.

[20] Shanks, Alan L. 1985. Behavioral basis of internal-wave-induced shoreward transport of megalopae of the crab Pachygrapsus crassipes. Marine Ecol. Prog. Series 24: 289-295.

[21] Crisp, D.J. and P.S. Meadows. 1962. The chemical basis of gregariousness in cirripedes. Proc. Roy. Soc. Lond. B158: 364-387.

[22] Pawlik, J.R. 1986. Chemical induction of larval settlement and metamorphosis in the reef building tube worm; Phragmatopoma californica (Sabellidae: Polychaeta). Mar. Biol. 91: 51-68.

[23] Elliott, J.K., J.M. Elliott, and R.N. Mariscal. 1995. Host selection, location, and association behaviors of anemonefishes in field settlement experiments. Mar. Biol. 122: 377-390.

[24] Jones, G. P., M. J. Milicich, M. J. Emslie and C. Lunow. 1999. Self-recruitment in a coral reef fish population. Nature 402: 802-804.

[25] Swearer, S. E., J. E. Caselle, D. W. Lea, and R. R. Warner. 1999. Larval rentention and recruitment in an island population of a coral-reef fish. Nature 402: 799-802.

[26] Levin, L. 2006. Recent progress in understanding larval dispersal: new directions and digressions. Int. Comp. Biol. 46: 282-297.

Article Sources and Contributors

Marine larval ecology *Source*: http://en.wikipedia.org/w/index.php?oldid=374277641 *Contributors*: Art10, Chris the speller, Epipelagic, Glaucothoe, IceCreamAntisocial, Lumos3, Neelix, Pmetzger, Sandstein, Stemonitis, Twirligig, WereSpielChequers, 10 anonymous edits

License