# Larval dispersal in the marine environment

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## Key vocabulary

**Benthic**: Living on the seafloor
**Pelagic**: Living in the water column
**Invertebrate**: An animal without a backbone. In the marine environment, this includes everything except fish, birds, and mammals. There are 37 phyla (major groups) in Kingdom Animalia that are classified as invertebrates, while vertebrates all belong to a single sub-phylum. Some phyla of invertebrates include:

- Phylum Porifera: sponges
- Phylum Cnidaria: corals, anemones, jellyfish, and hydroids
- Phylum Mollusca: clams, mussels, snails, octopi, and squid
- Phylum Arthropoda: shrimps, crabs, lobsters, and other crustaceans
- Phylum Echinodermata: sea stars, sea urchins, sea cucumbers, and sand dollars
- Phylum Chordata: sea squirts

**Sessile**: An animal that lives in one place as an adult, usually attached to a surface
**Mobile**: An animal that moves throughout its lifetime
**Plankton**: Organisms that are too small or weak to swim against ocean currents
**Nekton**: Organism that are large enough or strong enough to swim against ocean currents
**Larva**: The first life-stage of an organism, which usually looks very different from the adult and may have a different habitat (i.e. pelagic vs. benthic)
**Dispersal**: The process by which a larva is carried by ocean currents away from its parents
**Competent**: A larva that has developed enough to be capable of settlement and metamorphosis
**Settlement**: The process by which a larva selects a benthic habitat and (if sessile) attaches to it
**Metamorphosis**: A series of physical changes that occur as a larva becomes a juvenile
**Post-settlement mortality**: Death of a juvenile soon after metamorphosis, usually the result of predation or environmental stress
**Recruitment**: Survival of a juvenile beyond the first 24 hours or until observed by a researcher
**Recruit**: A newly-settled juvenile observed by a researcher

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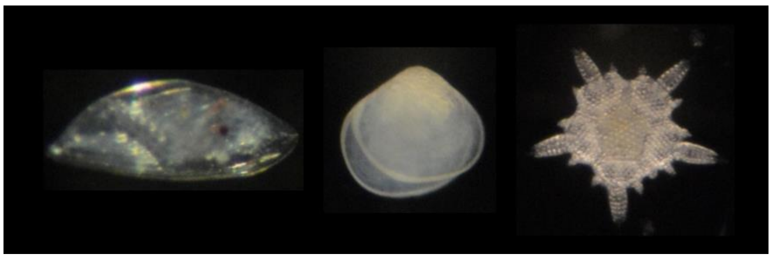
## Introduction

Many marine organisms reproduce via a larval phase, which often looks different from the adult and has a different habitat. Benthic invertebrates reproduce almost exclusively via larvae, and in most cases, these larvae are pelagic, meaning they develop to competency in the water column. Many marine fishes also reproduce via larvae, but in these cases, both the adults and the larvae are pelagic. Evolutionary theory suggests that reproduction via a larval phase is adaptive for benthic organisms because it reduces competition between adults and young. It also promotes gene flow between populations as larvae disperse to new habitats. For sessile organisms, the larval phase is the only time in the life-cycle when individuals can disperse and colonize new habitats.



Examples of larvae and young juveniles. Left, a cyprid larva (grows up to be a barnacle); middle, a veliger larva (grows up to be a clam); right, a newly-metamorphosed ophiuroid (grows up to be a brittle star).

Larvae are planktonic, so they are carried by ocean currents. Individuals can only control how fast or far they disperse by controlling their vertical position in the water column. Generally speaking, ocean currents are fastest at the surface and slowest near the seafloor, so a larva that swims up will be carried away from its parents, while a larva that swims down will stay close to home. Water is actually a thick, viscous medium in comparison to other fluids like air. Because water is always moving, it is actually pretty difficult for a larva *not* to disperse[1]. Some larvae change their vertical position throughout development, and this is known as "ontogenetic vertical migration." One well-known example is estuarine crabs, which swim up when they are young to ride the river outflow current out of the estuary to sea and swim down when they are competent to ride the incoming tidal current back into the estuary.

## Research topic 1: Settlement cues

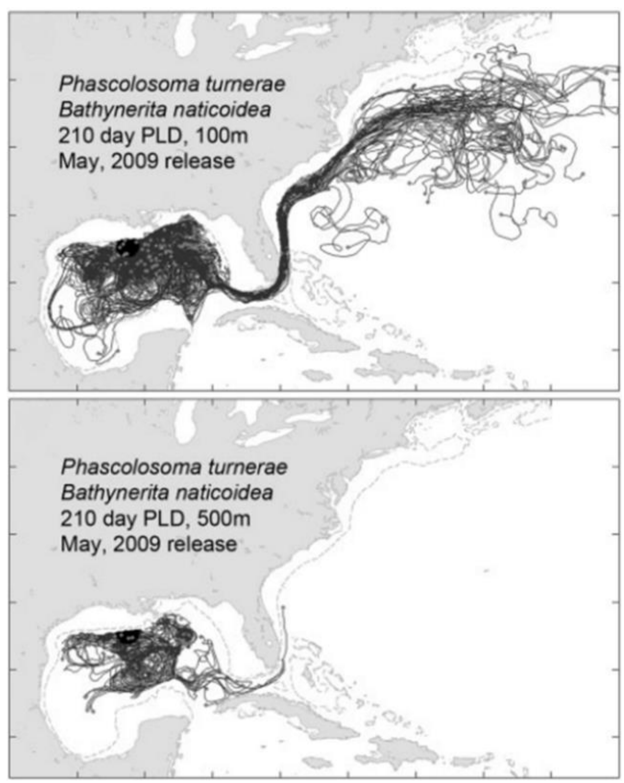
One of the earliest lines of research involving marine larvae – one which is still under investigation today – is how larvae select the sites where they will settle and metamorphose. Larvae are exposed to a number of environmental cues in the pelagic environment, which they can use to orient themselves to suitable habitats. For example, some larvae prefer to settle under rocks or overhangs, so they swim away from light when they are competent. We call this "negative phototaxis." Many larvae use chemical cues from adults of their same species to locate suitable settlement habitats. We call this "gregarious settlement," and it's a common behavior in tube worms and barnacles that settle in the intertidal zone[2,3]. Most larvae use a combination of physical and chemical cues to choose where they will settle, and some even crawl around on a surface to choose just the right spot. Species that are susceptible to predators often settle in small pits or depressions where they will be protected[4], and species that need to filter particles out of the water column to feed will choose areas with optimal current flow[5].

Larvae also respond to chemical cues from bacteria on surfaces where they might settle. Bacteria live in what's called a biofilm – a matrix of live and dead bacterial cells, proteins, and extracellular molecules that covers the surface in a thin layer. Some of the classic experiments conducted by scientists decades ago involved baking or scraping biofilms off of rocks, then seeing how larvae responded to them. Based on these experiments, we know that biofilms are absolutely essential to settlement, they vary by location, and the settlement cue contained within them is likely a protein that sticks up from the biofilm's surface. One research group in Hawaii working on a tube worm called *Hydroides elegans* has even isolated the protein that cues *H. elegans* to settle, the bacterium that makes the protein, and the genes that encodes the protein[6].

## Research topic 2: Larval tracking

At its very core, the field of larval biology seeks to answer two fundamental questions: (1) Where do the larvae come from? and (2) Where do the larvae go? It is extremely difficult to study larval dispersal in the marine environment because of the sheer size difference between the ocean (very, very big) and larvae (very, very small). Scientists can collect larvae directly by filtering large volumes of water, but we also use indirect methods to answer to those two fundamental questions.

One powerful tool is called "biophysical modelling." Scientists work together to create a model of current flows in the ocean and simulate larval dispersal. They choose where the "larvae" are released, how long they remain in the water column, and what depth they disperse at. Model results can be used to predict where larvae might disperse. A major lesson that scientists have learned from biophysical modelling is that dispersal depth matters a lot. For example, the figure at right here shows results for simulated "larvae" of two species, a peanut worm (*P. turnerae*) and a snail (*B. naticoidea*), released in the Gulf of Mexico[7]. In the top panel, the "larvae" disperse at 100 m depth, and in the bottom panel, they disperse at 500 m depth. You can see the 100 m "larvae: disperse much farther!




Biophysical modelling results for *P. turnerae* and *B. naticoidea*. After Young et al. (2012).

Scientists also use biochemical analyses to track where larvae came from. For many species with shells, such as clams and snails, the juvenile shell grows along the edge of the larval shell after settlement. Therefore, scientists can collect newly-settled juveniles and compare the trace element composition of the larval and juvenile shells to see if the individual was spawned near its settlement location or far away. By analyzing the isotopes in a larva's tissues, scientists can also sometimes tell where a larva has been while it was dispersing in the water column. Such stable isotope analyses revealed that larvae of the deep-sea hydrothermal vent crab *Bythograea thermydon* actually swim to the surface and feed on plankton there before returning to the deep sea to settle[8].

## Research topic 3: Delayed metamorphosis

Larvae usually develop in the water column for a period of time before they are competent to settle. This amount of time depends on the species and can vary from just 24 hours[9] to over a year[10]. Some larvae can prolong their larval period and avoid settlement if they are unhappy with the conditions. Various scientists use different terms to describe this phenomenon, including "prolonged competence" or "delayed metamorphosis." As an example, coral larvae usually only take 4-5 days to develop to competence and settle soon after, but if they are kept in the lab and not offered suitable settlement conditions (i.e. kept in clean glass jars with no biofilm), some individuals can remain in the water column > 200 days[11].

A newly-settled juvenile coral

Delaying metamorphosis can be adaptive for a larva when suitable settlement habitats are not available, but it also comes with a cost. Larvae that delay metamorphosis have higher post-settlement mortality, slower growth as juveniles, and reduced fecundity as adults[12–14]. They contribute fewer offspring to the next generation, so populations of their species are not as well-connected as they may seem[15]. Larvae that delay metamorphosis can also become "desperate" to settle. The older a larva is, the more likely they are to settle in a sub-optimal habitat[16], which can affect the rest of their juvenile and adult life, especially for sessile species.

## Outstanding questions in larval biology

A lot of questions still remain in the field of marine larval biology. Because larvae are so small and have such low densities in the ocean, it is difficult for scientists to measure basic parameters. For example, we know that invertebrates and fish alike have high post-settlement mortality, but it is difficult to measure what proportion of larvae survive to actually become recruits. Larvae in remote environments such as the deep sea are especially hard to study, so for many species, we do not know when the larvae are spawned, what depth they disperse at, or what they even look like.

My research focuses on the colonization of isolated, island-like habitats such as shipwrecks. I want to figure out how larvae reach these habitats that are far away from any source population. Do only a few larvae reach the wreck? If so, what is different about these larvae compared to other individuals? Marine larval biology is an exciting field!

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