Induction of settlement in merozooplankton

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INDUCTION OF SETTLEMENT IN MEROZOOPLANKTON

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Contents

Summary

The merozooplankton consists mostly of embryos and larvae that drift in the water column for a limited time period before settling on the seafloor to become benthic organisms. The time at which settlement occurs and the selection of settlement sites are

key events in the life cycles of most species and have important consequences for population demography, community structure, speciation and extinction. For these reasons, manipulation of merozooplankton settlement is viewed as a promising tool for enhanced sustainable exploitation and restoration of marine populations.

It is now known that the time of settling and the site at which settlement occurs can be influenced by a variety of exogenous environmental factors, some of which are referred to as settlement cues. Comprehensive understanding of the nature of cues and their action mechanisms is crucial for achieving reliable manipulation of merozooplankton settlement. This article summarizes the main biological and environmental forces that influence merozooplankton life and particularly the cues that influence settlement, pointing to major gaps in the current understanding.

1. Introduction

1.1. Scope of the approach

An enormous diversity of organisms belonging to several kingdoms live suspended and drifting in the oceanic water column because they have little or no ability to resist the large-scale or small-scale motions of water masses. The animals amongst these, which often have small body size, are known collectively as marine zooplankton. Some plankters reside in the water column for their entire life cycles, but others, known as meroplankton, are temporary residents in the plankton, often living there only during the early (embryonic and/or larval) life-history stages. This article will deal with animal meroplankton (i.e. merozooplankton). Because these organisms, unlike phytoplankton, are not photoautotrophic, they are not confined to the upper layers of the sea. Indeed, meroplanktonic animals are known to occupy the water column from the surface to at least abyssal depths.

Most of the merozooplankton consists of developmental stages (embryos, larvae and post-larvae) of organisms, including both invertebrates and fishes, that live on or near the bottom as adults. It is estimated that about 70 to 80% of all benthic marine invertebrates produce planktonic larvae. The quantitative contribution of merozooplankton to the total zooplankton is highly variable in both space and time. For example, in samples from a single area, the meroplankton may vary seasonally from 8 to 80% of the total zooplankton. On the basis of body size, most meroplankters are classified as microplankton (50 to 500 µm) or mesoplankton (0.5 to 5 mm).

However, in jellyfish with metagenetic life cycles, the large sexually reproducing adult is often the meroplanktonic stage, the benthic stage consisting of an asexually reproducing polyp stage in the benthos. Thus, meroplankton may fall into the category of macroplankton (5-50 mm) or megaplankton (5 cm to 50 cm). Nanoplanktonic (5-50 µm) and ultraplanktonic (< 5 µm) meroplankton are rare, unless ephemeral sperm clouds are considered as part of the merozooplankton.

The meroplankter, whether a developing embryo or larva or an adult stage, represents the dispersing phase of the life cycle and therefore plays an important role in the maintenance and expansion of populations and in facilitating genetic flux between metapopulations. In

the sea, the probabilities of extinction and speciation events are strongly influenced by meroplanktonic stages.

Henceforth in this article, the term "meroplankter" will refer not to metagenetic adult jellyfish but to meroplanktonic larvae capable of selecting an adult habitat on the sea floor. Following the usage of previous workers (e.g. Pawlik 1992), settlement is defined as the process by which larvae leave the plankton and enter the juvenile or adult habitat. This chapter attempts to offer a multidisciplinary overview of the settlement process by summarizing and discussing the newest ideas and findings on larval anatomy, physiology, behavior, settlement cues, and transduction.

1.2. Importance of settlement in merozooplankton.

Because settlement of meroplanktonic larvae is important for a variety of ecological and economic reasons, from fisheries to fouling, humans have been very interested in understanding and manipulating the settlement process. Larval settlement plays a significant role in establishing spatial and temporal patterns of abundance, thereby influencing the structure of benthic communities.

Many larvae select habitats behaviorally, on the basis of physical and biological attributes of the bottom. For example, recent studies on the surf clam *Spisula soliddissima*, which is a common species in sandy, but not muddy, areas of the east coast of North America, showed that larvae consistently choose sand over mud at settlement and that larval habitat selection contributes significantly to the adult field distribution, despite differences in larval supply over scales of kilometers. Major pulses in larval release and larval settlement also affect the short-term structure of planktonic communities; larvae may function as planktonic predators, as food for other predators, or both.

Restoration and management of natural communities may sometimes be enhanced by manipulation of settlement and recruitment in key structuring species. For instance, Morse and Morse (1996) suggested the use of artificial substrata with specific settlement inducers to enhance recruitment of coral planulae in reef restoration projects. The use of settlement cues has also been suggested as a way of assuring sustainable exploitation of some invertebrate fisheries, including edible bivalves and of drug-producing sponges and ascidians.

Although there have been few actual attempts to manipulate settlement cues on large scales in the field, preliminary results appear promising In oyster hatcheries, neurotransmitter precursors and culture supernatants of some film-forming bacteria, which are cues inducing settlement in many invertebrates, are used successfully for improving spat settlement.

Important research effort is currently being directed at inhibiting settlement of fouling organisms (e.g. Fusetani 1997). Benthic animals foul hulls, ballast tanks, industrial intake and outfall pipes, oil-platforms, aquaculture installations, and a wide variety other immersed structures and costly equipment. The estimated annual cost that biofouling causes to just the shipping industry worldwide is about US$3.5 billions. Current antifouling paints incorporate a variety of environmentally toxic substances that yield

relatively poor results at the expenses of high environmental cost. Therefore, the interest of searching for natural, non-toxic substance that inhibit settlement of fouling organisms is obvious.

Larval settlement may potentially be used in population control of invading species. For instance, it is well known that the predatory European crab *Carcinus maenas* has invaded at least five regions on three continents, with potentially important ecological and economic impact. One potential mechanism for controlling crab populations is to artificially enhance settlement of the rhizocephalan barnacle *Sacculina carcini,* a parasitic castrator of green crabs.

Settling larvae are often used in environmental bioassays and marine pollution tests because they are often good indicators of sublethal effects.

2. Biological and environmental challenges faced by merozooplankters

As relatively small animals that live in the plankton only temporarily, meroplankters interact with the aquatic environment in ways that are radically different from those of fish and other large organisms that reside in the water column for their entire lives. Some of the major peculiarities of larvae are those processes that take place at settlement.

2.1. Life-span constraints

Marine fish and mammals may occupy the water column for periods ranging from a year to a century, but meroplankters must complete their planktonic periods in days, weeks or in some cases a little more than a year. As early life history stages, they are constrained by a progressive developmental program of morphogenetic change. Nevertheless, many larvae exert some control over the duration of their planktonic lives. Indeed, we now know that the duration of meroplanktonic life is dependent not only on the timing of the developmental program, but also on a variety of exogenous factors, not the least of which is the presence of a suitable settlement substratum.

In general, the longer a larva remains in the plankton, the greater its opportunities for dispersal and for finding an appropriate juvenile habitat. However a longer planktonic life also increases the time that larvae are exposed to a multiplicity of environmental and physiological mortality factors, including the possibility of running out of energy (see section 2.3.).

Selective forces operating over millions of years have probably balanced acceptable dispersal distances against tolerable risks of mortality to yield larval lives that are appropriate for each species. This trade-off involves complex interactions of many factors. Despite much discussion of larval mortality and the optimal levels of dispersal, the relationship remains poorly understood. For example, the realized dispersal of an ascidian, *Lissoclinum patella,* is about one order of magnitude less than its potential dispersal. Long-distance dispersal—in the range of hundreds of kilometers—is sometimes achieved by larvae that feed on smaller plankton and stay in the water column for many months. Such far-wandering larvae are known as teleplanic. Larvae that remain in the water for weeks to months may either feed or rely on endogenous yolk supplies and can

potentially disperse for kilometers to hundreds of kilometers. Some larvae, notably those of sessile colonial invertebrates, occupy the plankton for only minutes to days. These so-called anchiplanic larvae are virtually all non-feeding The selective advantages of different dispersal strategies remain unclear in most cases.

Dispersal is followed by settlement (see Figure 1), but settlement can only occur after larvae have attained a threshold level of physiological and morphological maturity that renders them "competent" for settlement.
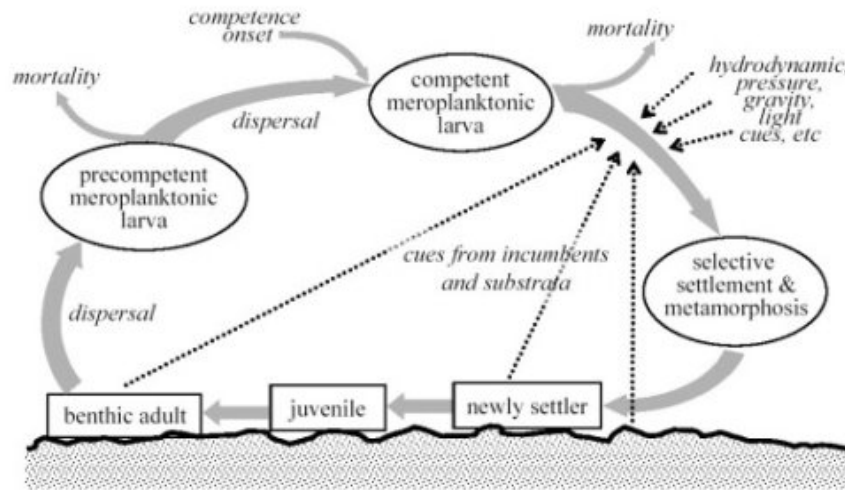

Figure 1. Diagram of a generalized life cycle of a benthic invertebrate with a meroplanktonic larval stage.

Attainment of competence may occur within minutes in short-lived larvae such as some ascidian tadpoles, but in most species, competence is only attained after days or months of dispersal. Larvae remain competent for variable, but limited, periods of time during which some can delay settlement until an appropriate substratum is found. Any natural or experimental induction or inhibition of settlement is most likely to be successful during the competent period.

In many larvae, settlement is accompanied by a series of rapid morphological and physiological changes known as metamorphosis. During metamorphosis, larval organs are lost and tissues are transformed into structures that will be useful in the benthic environment. Thus, settlement involves a change from the planktonic to benthic habitat whereas metamorphosis involves changes in structure and function that prepare organisms to cope with their new benthic environments.

2.2. Constraints of locomotion and substratum exploration

The relatively small body sizes and the poor motion abilities of most meroplankters have profound effects on the survival and settlement of larvae. Seawater is continuously in motion because of forcing by wind, tides, density differences, the Coriolis force, etc. Molecules of seawater stick to each other and to solid surfaces they contact, a property known as viscosity. The relative importance of viscous and inertial forces in animal

locomotion is given by the Reynolds number (Re), which depends on the animal size, the animal swimming speed (or fluid velocity with respect to the animal), and the kinematic viscosity of the fluid (see Glossary).

For instance, the Reynolds number calculated for a large whale swimming at 10 m s^{-1} is about 3 x 10^8, for a tuna swimming at the same speed is about 3 x 10^7, and for a 300 µm-long invertebrate larva moving at 1mm s^{-1} is about 3 x 10^{-1}. In general, Reynolds numbers of marine invertebrate larvae (meroplankton) range between 0.1 and 10, with most larvae having Re numbers around 1. This means that larval locomotion is, in most cases, dominated by viscous forces and that the effects of inertial forces are negligible.

Predominance of viscous over inertial forces makes a major difference in the life of an organism. A small meroplankter swimming slowly through seawater would be equivalent to a human swimming in a pool of honey. Larvae generate such small inertial forces that they stop instantaneously when swimming ceases. Swimming mechanisms used by larger organisms that rely upon streamlining and gliding do not work at these small scales. The most effective and common swimming mechanisms for meroplankters are cilia.

Cilia function like hinged oars, generating thrust on a power stroke by extending the cilium out from the body and minimizing drag on the recovery stroke by holding the cilium in close. Although cilia operate efficiently as a locomotory mechanism, the velocities they generate, which range from 0.1 to 10 mm s^{-1}, are generally much lower than current speeds in the environment. Thus, on a large scale, larvae should be transported wherever the water currents carry them. One might predict that this situation would prevent any sort of selective settlement and that larvae would be deposited virtually at random with respect to substratum. However, there is overwhelming evidence that substratum exploration and selective settlement occur in nature.

It is generally agreed that passive transport and random deposition of larvae operate at a different spatial scale than active substratum selection. As expressed by Pawlik (1992), "larvae passively accumulate and are deposited under the influence of hydrodynamic processes operating at large spatial scales (tens of meters to kilometers), while active substratum selection occurs only at much smaller scales (centimeters to meters)".For example, cyprid larvae of the barnacle *Balanus amphitrite* are transported passively until they initially contact the substratum, but they explore actively thereafter, responding behaviorally to flow direction, shear stress and various biological and physical cues associated with the surface at the time of settlement. Whereas early barnacle larvae are at the mercy of the currents, settling cyprids are dislodged only under particularly severe conditions of shear stress.

Water viscosity plays an important role in permitting behavioral exploration of substrata. Because water molecules stick to each other and to solid surfaces, water velocity becomes progressively slower with decreasing distance to the substratum. This region of slower flow is known as the benthic boundary layer. In the lowermost portion of this layer, termed the viscous sublayer, both water movement and turbulence are minimal (see Figure 2). The thicknesses of both the boundary layer and the viscous sublayer are dependent on the water velocity in mid-water and the roughness of the substratum.

Merozooplankters entering the boundary layer should have some chance to maneuver, explore the substratum for cues, and perform selective settlement at a microhabitat scale. From laboratory experiments, Butman (1986) predicted that a variety of polychaete larvae attempting to settle on a soft bottom dominated by tidal currents would be unable to explore the substratum for about 60% of the tidal cycle because of their sizes and swimming speeds. Larvae would only be able to explore the sea floor during about 40% of the tidal cycle, when their size would allow them to maneuver within a 100µm-thick boundary layer.
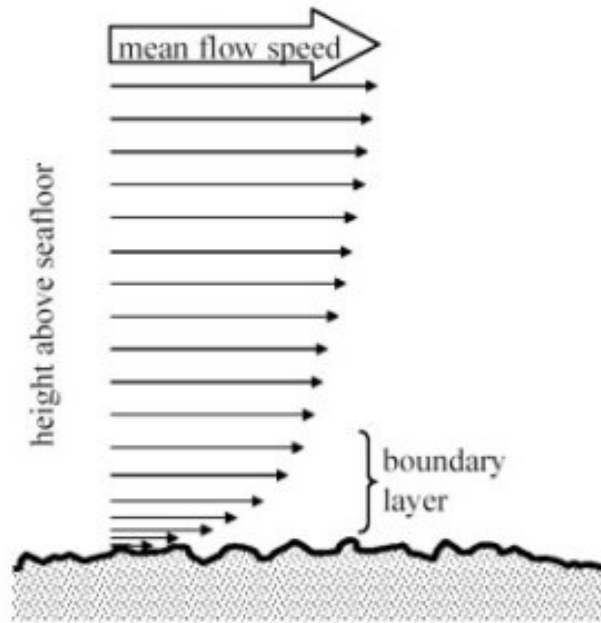

Figure 2. Idealized diagram of a vertical profile of flow velocity, in which a typical decrease in mean flow velocity as result of water viscosity and friction with the seafloor is shown. The boundary layer is recognized as the deepest part of the water column, in which flow velocity decreases until a level in which viscosity smoothes out all turbulence.

Because turbulent energy is low within the boundary layer, mass transfer occurs mostly by molecular diffusion rather than by eddy diffusion. Therefore, chemical cues for selective settlement released within the deepest sublayer of the boundary layer are likely to remain at a high concentration for a longer period of time than if they were released higher in the water column.

In general, invertebrate larvae spend most of their planktonic life drifting in the water column; they approach the sea floor and initiate an exploratory phase only after attaining metamorphic competence (see Figure 1). To reach the seafloor, larvae either swim vertically downward or sink passively (by increasing skeletal mass, decreasing drag, losing floatation structures, depleting buoyant yolk, etc). During the phase of substratum exploration prior to settlement, larvae may leave and re-enter the boundary layer repeatedly, until they select a site for settlement. The exploratory phase can be quite complex, depending on the species. For instance, three behavioral sub-phases has been described during settlement of the barnacle *Semibalanus balanoides*, each operating at a different spatial scale: 1) "broad exploration", at an estimated spatial scale of about 1m; 2)

"close exploration", at a scale of about 1 mm, and 3) "inspection", at a scale below 300 µm. When appropriate cues are present, cyprid larvae may shorten or even skip some of these phases.

2.3. Constraints of feeding and energy resources

The viscous forces operating at low Reynolds numbers influence not only locomotion; they also have enormous implications for the way these organisms feed. Larvae cannot capture particles with porous filters because viscosity causes the filters to push the particles away. Consequently, those merozooplankters that feed on smaller plankton (planktotrophic larvae) have developed complex systems of cilia or appendages that create asymmetrical flows that concentrate particles and facilitate ingestion. Other merozooplankters (lecithotrophic larvae) do not feed; they rely entirely on the yolk provisions provided in the egg by the mother. A majority of invertebrate larvae are planktotrophic. It has traditionally been assumed that planktotrophy is the ancestral condition and that lecithotrophy is derived. However, there is intense, on-going debate about this issue. Some meroplankters are able to absorb dissolved organic matter from seawater as a supplementary energy source.

The source of nutrition is important not only for the survival of a larva, but also has important implications for dispersal, settlement and recruitment success. For instance, the duration of the competent phase of pelagic life in *Semibalanus balanoides* depends on the levels of critical neutral lipids. In general, planktotrophic larvae reside in the plankton longer than lecithotrophic forms, as the energy provisions of the latter are limited. Settlement and metamorphosis often require a substantial expenditure of energy, so successful recruitment requires that larvae build or maintain a certain threshold level of energy reserves. Evidence from several different invertebrate groups indicates that larvae delaying settlement and overspending their energy reserves face higher levels of mortality at either the settlement or early post-settlement stages.

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Biographical Sketches

Manuel Maldonado is a Senior Scientist at the Centro de Estudios Avanzados of Blanes (Spanish Council for Scientific Research). For the past ten years, he has studied sublittoral and deep-sea habitats worldwide, investigating diverse aspects of reproduction, ecology and evolution of marine benthic invertebrates, with a particular focus on sponge biology. Dr. Maldonado has co-authored more than 40 publications, including peer-reviewed journal articles, book chapters and books.

Craig M. Young, Professor of Biology at the University of Oregon and Director of the Oregon Institute of Marine Biology, is a marine biologist who specializes in ecological aspects of embryological and larval development in marine invertebrates. For the past twenty years, he has worked in deep-sea habitats worldwide, using manned submersibles and remotely operated vehicles to study aspects of reproduction, ecology and development on continental slopes and at hydrothermal vents and cold methane seeps. He is particularly interested in early life-history stages of ascidians, sponges and echinoderms. Professor Young's publications, which number more than 150, include several edited books*, Atlas of Marine Invertebrate Larvae* being the most recent. He currently serves as an editor of *Advances in Marine Biology*, as a member of the editorial board of *Invertebrate Biology*, and as a member of the Ridge 2000 Steering Committee for the U.S. National Science Foundation.