

Settlement and Recruitment of Pelagic Larvae to Benthic Habitats

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1 Introduction

For aquatic species living in benthic (or bottom) habitats including bivalves, barnacles, corals, crabs, sea stars, urchins, and worms, complex biphasic life-cycles often separate dispersing larval stages from their source population of reproductive adults (see [1] for review of bivalves; echinoderms in Figure 1). Adults typically broadcast eggs and sperm into the water where fertilization occurs via water currents, which also facilitate the dispersal of planktonic larvae (see Table 1 for examples of organisms with biphasic life histories). Indeed, most larvae spend a significant amount of time (minutes to months), dispersing via the pelagic (or open water) environment. Consequently, their benthic populations may be considered open systems [2–4], where recruitment processes, rather than their own reproductive output shape population structure [5]. In contrast, there is also growing evidence that some larvae self-recruit back into their source populations, highlighting the importance of local recruitment processes [6–9]. Practically speaking, most populations likely exist on a continuum between these contrasting models and it is, therefore, important to understand both the spatiotemporal patterns of recruitment and the processes that shape them.

Recruitment is the addition of early age classes to a population [10]. From an ecological perspective, successful recruitment has profound effects on population dynamics, community structure, and ecosystem function [2, 11, 12]. In an applied context, accurate recruitment prediction is fundamental for sustainable resource management [13]. Recruitment is comprised of three stages [14–16]: (i) larval supply, (ii) larval settlement, and (iii) post-settlement (Figure 1). Larval supply refers to the density or concentration of competent larvae ready to settle in a given area [17]. Larval settlement includes processes that affect the transition from larvae

in the water column to metamorphosis (loss of larval features and development of features used in the benthos) on bottom substrate [18]. Finally, post-settlement involves factors that influence the survival of benthic juveniles after metamorphosis [19]. For any benthic species, recruitment into the adult population requires successful navigation of all three of these stages.

From larval supply through the post-settlement period, recruitment success is intimately tied to water movement (i.e. hydrodynamics). For instance, the fluid environment serves the medium that facilitates the dispersal of larvae (e.g. advection, swimming). In addition, the physical and chemical characteristics of water (e.g. temperature, pH, salinity) are important for larval development and survival. Processes such as the transport of settlement chemical cues, the successful attachment of larvae to benthic substrates, and the post-settlement survival/migration of juveniles are also linked to water.

1.1 Patterns of Recruitment

Recruitment processes operate at multiple spatial scales. At the largest spatial scales, recruitment is shaped by ocean basin-wide circulations such as the Pacific Decadal Oscillation, North Atlantic Oscillation, and El Niño-Southern Oscillation [20–22]. At continental-scales, latitudinal gradients have been detected with higher recruitment at northern versus southern sites along the California Current [23, 24] in the Pacific Ocean. At regional scales, nearshore circulation patterns represent fluid-mediated barriers to recruitment [25, 26]. At local scales, there are many examples of recruitment patterns, including height onshore (e.g. zonation), substrate type, and strong juvenile–adult associations [27–29], to predictable variation at the microscale with higher recruitment into small pits/depressions (<1 cm) versus flat surfaces [30, 31].

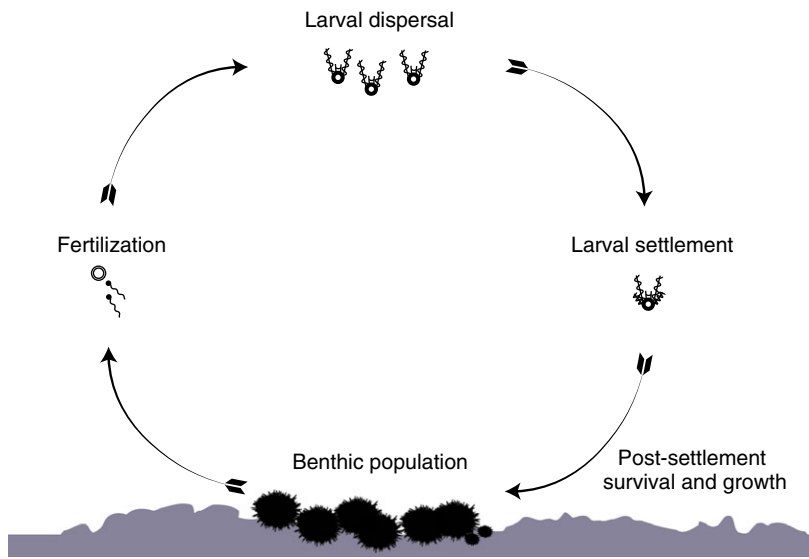


Figure 1 Schematic of biphasic life-history and benthic marine recruitment involving a sea urchin. Male and female urchins broadcast sperm and eggs into the water column where fertilization occurs, followed by larval development. Larvae disperse in the water column as planktonic organisms that cannot swim against water currents but can swim up or down in the water column. Larvae settle to the bottom where they attach and metamorphose into juveniles that typically remain in the benthos where post-settlement processes affect their survival and growth. If they recruit into the population they may reach sexual maturity as adults.

Table 1 Examples of organisms with biphasic life-history.

Phylum	Organism	Larval type	Larval characteristics	Predominant adult habitat
Porifera	Sponges	Calciblastula, parenchymella	Ciliated, flagellated	Hard and soft substrates
Cnidaria	Corals	Planula	Ciliated	Coral reef
Platyhelminthes	Polyclad flatworms	Müller's larva (Mulleria)	Ciliated	Hard substrates
Annelida	Polychaete worms	Trochophore	Ciliated	Hard and soft substrates
Mollusca	Bivalves, snails	Veliger	Ciliated	Hard and soft substrates
Brachiopoda	Brachiopods	Lingula	Ciliated	Hard surfaces
Arthropoda	Crabs, lobsters	Nauplius, zoea	Setae	Hard and soft substrates
	Barnacles	Nauplius, cyprid	Setae	Hard substrates
Echinodermata	Sea urchins	Pluteus	Ciliated	Hard substrates
	Ses stars	Bipinnaria	Ciliated	Hard substrates
	Sea Cucumbers	Auricularia	Ciliated	Soft substrates
Ectoprocta	Bryozoans	Cyphonaute	Ciliated	Hard substrates
Hemichordata	Acorn worms	Tornaria	Ciliated	Soft substrates

In addition to the spatial variation described earlier, recruitment also varies predictably over temporal scales. For example, the timing of recruitment for many benthic invertebrates occurs consistently during the spring months [23, 24]. The exact timing of recruitment, however, may be site-specific with little to no synchrony among sites [32]. Recruitment also varies reliably with lunar/tidal cycles, as recruitment is higher during new moons and neap tides (i.e. first and third quarter moon) [33]. On a daily timescale, changing sea breezes (onshore in the afternoon) induce diurnal changes in upwelling circulation and temperature, leading to changes in recruitment intensity [34, 35]. It is clear that recruitment varies across several spatial and temporal scales, and

several theories have been postulated to explain the processes that drive this variation.

1.2 Processes Explaining Patterns of Recruitment

A number of theories have been forwarded to help explain variation in benthic recruitment (Table 2). Several of these theories highlight factors that affect the pool or reservoir of larvae available for settlement. This includes processes that impose limitations on successful fertilization, thus limiting larval supply [36]. The "*fertilization limitation hypothesis*" suggests that factors such as benthic flow conditions, degree of aggregation/group size, and position within group can affect fertilization rates [36, 57]. This also leads to

Table 2 Theories regarding marine benthic recruitment.

Stage	Theory	Model	Prediction	Source
<i>Larval Supply</i>	Fertilization limitation	Gamete dilution limits fertilization success	Allee effect for small populations	[36, 37]
	Transport hypothesis	Transport of larvae determines if competent larvae are distributed to favorable habitats	Distributions will correlate to hydrographic events and geographic features	[38, 39]
	Intermittent upwelling hypothesis	Coastal upwelling affects the delivery of larvae to shore	Higher larval supply correlates with weakened upwelling	[40, 41]
<i>Larval Settlement</i>	Lottery hypothesis	Larvae abundant, but recruitment limited by available space to settle	Recruitment largely stochastic as larvae recruit only as space becomes available	[42]
	Match–mismatch hypothesis, sweepstakes reproductive success	Larval pelagic period must coincide with resource availability	If larvae disperse at times when resources are limited, recruitment fails	[43–45]
	Differential settlement	Larval settlement in response to environmental cues	Recruitment affected by adults, food, predators	[14, 46]
	Desperate larvae hypothesis	Larvae unable to prolong their planktonic lives settle in uninhabited areas	Gregarious populations founded by “desperate larvae”	[47]
	Differential larval behavior	Fundamental differences in larval behavioral “types”	Gregarious populations started by “founder” larvae	[47]
	Larval predation hypothesis	Consumption of larvae by predators	Recruitment diminished near predators	[48]
<i>Post-Settlement</i>	post-settlement mortality	Variation in survival of post-settlement juveniles	Recruitment will be enhanced in areas of refuge where mortality is reduced	[15, 49, 50]
	Recruitment window hypothesis	Finite period of time where settled larvae survive to recruitment age	If larvae settle outside of the window, survival and recruitment are impaired	[51]
	Phenotype–environment mismatch hypothesis	Some juvenile phenotypes selected against when mismatched with microenvironment conditions	Subsets of juvenile population will be limited to different habitats	[52]
	Juvenile migration	Behavior rather than recruitment or mortality maintains distribution pattern	Distribution will concentrate near favorable habitats	[53, 54]
	Spatial heterogeneity/refugia hypothesis	Refuge use reduces loss to predation, competition, and physical disturbance	Recruitment elevated in areas that provide refuge for post-settlement juveniles	[27, 55, 56]

the prediction that the per capita fertilization rate is low at low adult densities. The “*transport hypothesis*,” states that differences in the transport of larvae (i.e. availability) may account for variation in recruitment patterns [38, 39]. Therefore, it is expected that recruitment should correlate with hydrographic events and geographic features that concentrate larvae. As a variant of the transport hypothesis, the “*intermittent upwelling hypothesis*” predicts that recruitment at the regional scale will correlate with periods of upwelling relaxation, which result in elevated larval retention near shore [40].

A second set of hypotheses have been forwarded to explain the spatial and temporal variation in the recruitment by focusing on processes involved in larval settlement. Early work centered around the “*lottery hypothesis*” that considered larvae as passive vectors with little control over their dispersal and settlement [2, 58, 59]. For sessile species like barnacles or mussels, space can be a limiting resource and consequently, larval settlement is largely dictated by available substratum suitable for settlement [2]. As illustrated in Figure 2, barnacle recruitment in Narragansett Bay, RI occurs on almost all exposed hard surfaces, including the shells of living mussels, because space is a limiting resource for settling larvae. The “*match-mismatch hypothesis*” centers upon the degree of synchronization between the timing of larval food resources (e.g. phytoplankton blooms) and larval supply [43]. For instance, mussel larval supply rises, and settlement is high during periods of high phytoplankton abundance in eastern Canada. In contrast, when phytoplankton densities fall or the blooms occur earlier or later than when larvae appear, there is a “mismatch” and recruitment fails [60]. Similarly, “*sweepstakes recruitment*” may occur for species with high variation in reproductive success, in which only a small number of individuals contribute to the next generation [44]. Most individuals fail to match the timing of their reproductive activities (e.g. fertilization, larval transport, and settlement) with favorable environmental conditions. Observed genetic differentiation among cohorts of bivalves suggests that different adults may be contributing to different recruitment event [61–63].

“*Preferential settlement*” of larvae occurs in response to cues such as the presence/absence of food, resident adults, or predators [64, 65]. Conversely, the “*desperate larvae hypothesis*” [47, 66] was presented to explain the gregariousness aggregations of polychaete worms. This theory postulates that larvae that are unable to locate conspecifics cannot continue their planktonic existence and are forced to settle into uninhabited areas. Toonen and Pawlik [47] also presented an alternate explanation for the observed pattern, as the “*larval behavior hypothesis*,” which suggests that there may be two distinct behavioral types of larvae produced by the same species.

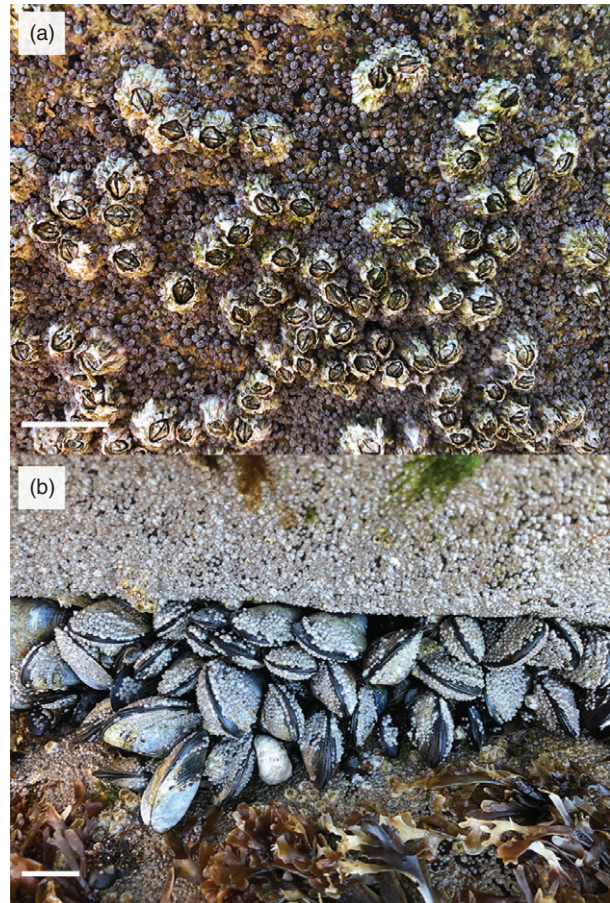


Figure 2 Early post-settlement barnacle (*Semibalanus balanoides*) recruitment in Narragansett Bay, RI, USA. (a) Early post-settlement juveniles settled amongst last year's adult cohort. (b) Space-living settlement by juvenile barnacles on shells of mussels (*Mytilus edulis*). Scale bars equal 2.5 cm. Images taken on 23 March 2019.

One type colonizes uninhabited areas whereas a second type settles in response to conspecifics. Lastly The “*larval predation hypothesis*” emphasizes that ecological factors, including predation, reduces recruitment in habitats with predators [48].

Once larvae settle to the benthos, mortality rates can be dramatic [49] and variations in recruitment may result from differences in “*post-settlement mortality*” rather than settlement processes [50]. In a similar manner, the “*recruitment window hypothesis*” suggests that the number of larvae that survive to reproductive age settle during a narrow period of time (e.g. just 21 days in barnacles *Semibalanus balanoides*) [51]. The “*phenotype–environment mismatch hypothesis*” suggests that high levels of post-settlement mortality can result when larvae settle in sites with microenvironmental conditions that select strongly against their phenotype [52]. Given the high rates of post-settlement mortality,

recruitment should be higher in areas where mortality is reduced including spatially heterogeneous habitats in which there may be refuges for new recruits (“*spatial heterogeneity/refugia hypothesis*”) [27, 55, 56]. Finally, migration is a possible mechanism that could explain observed patterns of recruitment in species that are relatively motile. Indeed, migration to more favorable habitats, as opposed to recruitment or mortality, affect population distributions in Australian gastropods (*Bembicium auratum*) [53].

Clearly, there are many factors that affect recruitment of pelagic larvae into benthic populations. These factors generally fall into three main categories including (i) larval supply, (ii) larval settlement and metamorphosis, and (iii) post-settlement survival in the benthic environment [19].

2 Larval Supply

2.1 Fertilization

As indicated earlier, many benthic species are broadcast spawners, releasing their gametes into the water column. This results in “*external fertilization*,” whereby gametes make physical contact with each other outside of the body in the water column. Fertilization rates are affected by the physical flow environment, as some level of water motion helps increase sperm–egg contact rates. For example, bed roughness caused by the presence of bivalves generates turbulence and recirculation zones, which retained sperm packets and stretches them, thus enhancing sperm–egg encounter and reducing sperm dilution [67]. High-energy surf zones may, however, limit fertilization by promoting increased sperm dilution [68]. The consequence of these challenges to fertilization is that benthic organisms may experience some degree of sperm limitation, which lowers fertilization success. Not surprisingly, organisms have developed strategies to counter the effects of sperm limitation including adults that live in or form aggregation during spawning events, synchronous spawning and releasing gametes in viscous forms that do not disperse quickly [37, 69, 70]. In sea urchins, fertilization rates correlate with both larger adult body size and higher density of reproductive adults [57, 71–74]. Gamete characteristics such as egg size and sperm swimming speed/longevity/potency also influence fertilization rates [75–77]. For example, sperm may use chemoattractants to locate eggs, which promotes increased fertilization success [78]. Lastly, sea cucumbers have been observed synchronously spawning, resulting in very high mean fertilization rates of 97.5% [79].

Synchronous mass spawning among multiple different species has also been observed in the field and is

assumed to be a strategy to overwhelm predators [80, 81]. In corals, the timing of mass spawning events are synchronized by an endogenous clock set by zeitgebers (e.g. rhythmically occurring environmental factors), such as moonlight, solar insolation, rainfall, and rapid rises in sea surface temperature [82–86]. Although inter-specific mass spawning may increase fertilization rates, it also raises questions concerning how gametes from different species are prevented from cross-fertilizing. Not surprisingly, many species prevent cross-species fertilization through physical, electrical, cortical, and/or molecular blocks to the binding and fusion of egg and sperm [87–89]. Once gametes meet, an egg may be fertilized by multiple sperm, a phenomenon known as polyspermy, which can lead to reproductive failure. To prevent multiple fertilizations, many species prevent the entry of more than one sperm into the egg [90]. In the ctenophore *Beroe ovata*, however, multiple sperm enter the egg and the egg pronucleus binds with one sperm pronucleus to form a zygote [91].

Environmental conditions can also affect fertilization in broadcast spawners. Fertilization rates in some species (e.g. sea urchins) have been found to be robust to changes in pH [92], whereas other organisms like corals are sensitive to acidification [93]. Moreover, fertilization in organisms from sites that with low pH variability exhibit higher sensitivity to changes in pH [94]. Fertilization is also sensitive to temperature change in some sea urchins, corals, and bivalves [95–97]. Moreover, the combined effects of multiple environmental stressors (e.g. temperature, pH, salinity, suspended sediments) can further reduce fertilization rates [98, 99].

2.2 Hydrodynamics and Larval Transport

For successful recruitment, there must be an adequate pool of larvae available to settle, known as “*larval supply*.” The transport of larvae is affected by fluid motion at multiple scales. For instance, currents moving parallel with the shore can produce a region of slow-moving water near the coast known as the “*coastal boundary layer*” (CBL) [26, 100]. Although larval supply appears to be higher within the CBL than at locations farther offshore, it is depressed in the waters immediately adjacent to shore [101, 102]. Whether this reduction in larval density is due to transport, predation, and/or settlement remains unclear.

At a regional scale, larval supply is also affected by a phenomenon called coastal upwelling. Winds can deflect water currents up to 90° to the right (or left) of the direction of the wind in the northern (or southern) hemisphere due to the Coriolis effect. The net movement of surface waters is 90° perpendicular to the direction of the wind, a phenomenon called

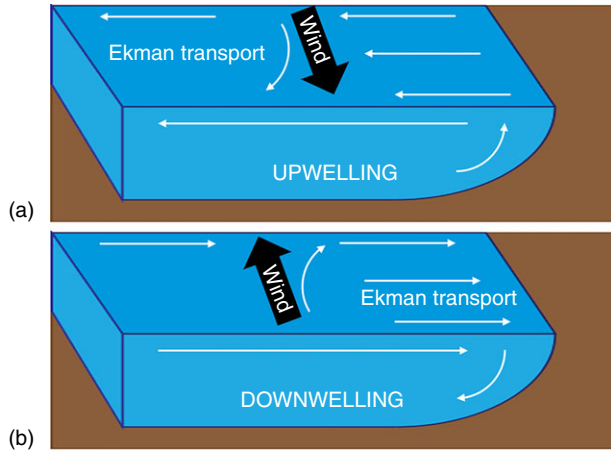


Figure 3 Wind-driven coastal upwelling currents in the northern hemisphere. (a) Coastal upwelling moves surface waters offshore and, (b) coastal downwelling moves water towards shore.

“*Ekman transport*” [103]. When currents flow parallel to coastal margins, as in the case of eastern boundary currents that move equatorward alongshore in ocean basins, they can be deflected (to the right) offshore by winds blowing in the equatorward direction and onshore by winds blowing poleward (Figure 3). Offshore currents effectively pull water away from the coast, which is replaced by deeper water that upwells to the surface (Figure 3). Conversely, onshore currents transport water including suspended larvae toward shore and can lead to downwelling of coastal waters. The intensity of offshore transport in upwelling ecosystems can vary on temporal scales ranging from days to decades.

Larval supply and recruitment have been linked to onshore transport during periods of upwelling relaxation [38]. This relationship was confirmed in mussels and barnacles on the California, Oregon, and New Zealand coasts and has been termed the “*intermittent upwelling hypothesis*” [40, 104]. It has been demonstrated that low recruitment of red and purple sea urchins, *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*, occurs in areas of predictable upwellings and offshore transport [105–108]. Moreover, larval settlement of red and purple urchins has been linked to onshore advection of water [23, 104]. It is relevant to note, however, that there are contrasting results that do not show the same relationships between mussel and barnacle settlement and upwelling strength [109]. Moreover, surveys indicate that 45 species of nearshore crustaceans are not transported offshore, but rather remain within 6 km of shore during peak upwelling season [110]. In the Gulf of Maine, green urchins showed a positive correlation between water motion and larval supply, yet no correlation with either parameter to recruitment [111]. A subsequent study,

however, suggested that recruitment was influenced by onshore wind-driven currents [112].

Local hydrographic conditions may also influence larval dispersal. For coral, crab, and sea urchin larvae, near-field circulation can dramatically influence larval retention and recruitment [113, 114]. In Monterey Bay, CA, sea breezes blow onshore during the day and land breezes blow offshore at night. This results in currents changing direction and can lead to alternating periods of local up- and downwelling [35]. Depending on onshore topography (e.g. slope), larval supply in the surf zone can be either higher or lower compared to sites farther from shore [115]. From a mechanistic perspective, wave-induced drift (e.g. Stoke’s drift) toward shore can indeed promote the retention of larvae close to shore [116].

It is important to note that larval supply should be determined in an appropriate manner that accounts both for the concentration of larvae in the water and also for its delivery in the water column [117]. In this case, the larval flux is used because it represents the product of the larval concentration and the water velocity. Difference in larval flux can be informative [67] unlike simple measurement of velocity or concentration.

2.3 Larval Behavior

In many invertebrates, larval supply and recruitment differ with vertical position in the water column relative to the shore [118–120]. For most benthic organisms, larvae are small (μm to mm scale) and swim slowly (mm s^{-1} to cm s^{-1}) relative to environmental flows [121, 122]. Horizontal water velocities, however, often vary with water depth and thus, larvae that undergo vertical migrations (i.e. swim upward or downward) can affect their likelihood of recruitment by placing themselves within currents that disperse them or transport them to suitable locations for recruitment. Indeed, vertical positioning behavior by larvae in the water column suggests that vertical, rather than horizontal migration is more likely for slow swimming larvae [123, 124]. Some larvae (e.g. oysters, *Crassostrea virginica*) can sense hydrodynamic cues (e.g. high-energy dissipation rates and accelerations) to spur upward swimming behavior [125].

Lower temperatures reduce larval swimming speeds, potentially reducing their ability to maintain vertical position [126]. However, improved diet quality may serve to counteract this thermal effect, thus preserving a larva’s swimming capacity and vertical positioning [127]. There is also evidence that echinoid larvae orientation may be associated with pycnoclines (density), haloclines (salinity), turbidity fronts, and tidal bores [128, 129].

While in the water column, dispersing larvae are exposed to pelagic predators such as planktivorous

fish, medusa, and ctenophores [130–132]. Possible defensive mechanisms in larvae include nematocysts, spicules, spines, shells, mucous, transparency, chemical defense, and diel vertical migration to avoid visual predators. Echinoid larvae may also undergo cloning, effectively replicating themselves, in the presence of predators [133].

Larval development and survival are also affected by various chemical and physical attributes of the fluid environment. Lower growth and survival of larvae maintained at cooler temperatures suggest that low water temperatures may set the northern range limit of some mussels [134]. Water temperatures also affect development time, potentially affecting larval supply [135]. Not surprisingly, the developmental rate of some larvae (e.g. polychaetes, echinoids) has been shown to be affected by multiple environmental factors such as temperature, pH, salinity, and nutrition [136–138]. Variable time to competence for larvae of the opisthobranch, *Haminaea callidegenita* affects recruitment by allowing for both short-distance and long-distance dispersal [139]. Patterns of gene expression in larval sea urchins also vary with water conditions such as pH, temperature and salinity [140–142].

3 Larval Settlement

Larval settlement from the water column onto the substratum is the second important stage in the recruitment process. In some cases, larval settlement rather than larval supply or post-settlement mortality can be more important with regards to recruitment [143]. On intertidal shores, for example, vertical gradients of larval settlement shape patterns of recruitment [144, 145]. For instance, oyster larval settlement and recruitment rates are higher at lower intertidal elevations. Conversely, barnacle larvae maintain higher vertical position in the water column, which correlates with settlement patterns on adjacent shores [144].

3.1 Near-Bottom Processes

Larval settlement is closely linked to the physical characteristics of both the substratum and the fluid flowing above the substratum (Figure 4). In the water column, sea urchin larvae use turbulent shear associated with wave-swept habitats as a trigger for accelerated development. This broad-scale hydrodynamic cue prepares larvae to be receptive to the presence of chemical settlement cues [147]. As larvae leave the water column, boundary-layer flow also becomes an important factor affecting settlement [148, 149]. For instance, contact rates between larvae and benthic substrates are

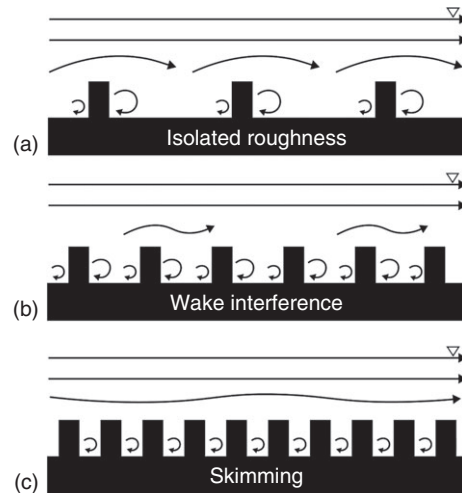


Figure 4 Hydrodynamic regimes for benthic flows including: (a) isolated roughness flow; (b) wake interference flow and; (c) skimming flow. For further details regarding flow-roughness interactions, see [67].

limited at lower water velocities [150]. Some larvae (e.g. *C. virginica*) have developed swimming strategies to accelerate their approach to the substrate through the boundary layer [151]. In some cases, shear stresses associated with faster flows may limit larval settlement and attachment to the substrate [152, 153]. Moreover, it is not surprising that for some larvae, hydrodynamic conditions also act as important cues for settlement [154].

For settling larvae, substrate characteristics can influence recruitment by several means. For instance, early models recognized that larval settlement rates would scale with bottom roughness [146]. Such models did not account for the complex three-dimensional flows in environmental boundary layers [155], yet empirical relationships between benthic topography and larval settlement have been confirmed for a wide array of benthic taxa. Many species from gastropods to cirripedes to scleractinian corals use local topography such as cracks, pits, and grooves in rock substratum for settlement [31, 156, 157]. For oyster (*C. virginica*), larval settlement occurred most often between benthic roughness elements where shear stresses were up to 20× lower [158]. Moreover, solitary species with limited attachment to the substrate (e.g. barnacles) settled in crevices near the base of roughness elements, whereas clonal organisms with stolon-mat forms (e.g. bryozoans) were not as restricted in where they settled [159]. Not surprisingly, the spacing and height of physical model replicates of adult clams (*Potamocorbula amurensis*) affect the instantaneous turbulent structure above their beds, thus dictating the potential anchoring ability of juvenile recruits [160]. Measurements of near-bed turbulence indicate that the spatial configuration of mussel roughness in the field

influence the creation and magnitude of skimming versus wake-interference flow, which can inhibit or enhance larval settlement in mussels, respectively [67]. For weak-swimming coral larvae, the structural complexity associated with reefs helps promote settlement [161].

3.2 Biological Associations

Beyond topographic features of the substratum, larval settlement can also be affected by the presence of macrophyte (aquatic plant and macroalgae) canopies. Seagrasses undulating under unidirectional flow induce canopy-scale eddies (synchronous water oscillations) called “monami” [162, 163]. Enhanced mixing associated with this type of water motion can promote increased rates of larval settlement within seagrass canopies [164, 165]. Macroalgal canopies may also reduce flow, leading to increased sedimentation within the understory [166]. Larval settlement under a kelp canopy may be higher for some taxa (e.g. sea stars) and lower for others (e.g. brittle stars and sea urchins), suggesting that post-settlement processes may play an additional role [167]. This is consistent with Pacific and Atlantic sea urchins, where larval settlement was similar inside and outside of a kelp forest yet adult densities were higher outside the forest likely due to post-settlement processes [167, 168].

Some larvae settle preferentially on other species, a phenomenon called “*associative settlement*” [64], whereas other larvae settle near conspecifics via “*gregarious settlement*” [50, 66, 169]. For gregarious corals, there are distinct subpopulations of “founder” larvae that settle in new areas without conspecifics, and the remaining “follower” larvae only settle in the presence of conspecifics [47].

Barnacle larvae (*Balanus glandula*, *B. crenatus*) may avoid settling near competitors [144], and some barnacles (*B. glandula*) avoid areas associated with benthic predators [170, 171]. Benthic predators may directly reduce settlement by removing larvae from the water column [50, 172]. Predation pressure at this stage may be dramatic with up to 77% of potential settling mussel larvae being ingested by adult mussels [173]. However, for other taxa (e.g. barnacles and oysters), predation is not a major factor affecting recruitment [48, 169].

3.3 Settlement Cues

Settling larvae use a range of proximate cues to locate appropriate habitat for recruitment [65]. For instance, a wide variety of benthic organisms use coralline red algae as a settlement cue [14, 112, 174–177]. In many taxa, settlement is temperature dependent [178–180]. Indeed, bottom roughness/hydrodynamics [160, 181–183], pH [184–186], dissolved O₂ concentration [187], salinity

[188], sound [189–191], biofilms [192, 193], light/color [194–196], and food availability [197, 198] have all been demonstrated to influence larval settlement [50, 181, 183, 192, 193, 199]. Furthermore, larval settlement patterns are affected by the interaction among multiple environmental factors such as temperature, salinity, nutrition, pH, oxygen, and biofilm [188, 200–202].

Water pollution can affect settlement in several ways. Pollutants such as oil and especially the dispersant Corexit[®] 9500 reduce larval settlement in several species of coral [203]. Similarly, larval settlement in polychaetes and bryozoans is inhibited in polluted waters, with cyanide, ammonia, and phenolic compounds suspected as possible agents [204].

Most chemical cues associated with larval settlement are tactile in nature, requiring direct contact between larvae and the substratum [50]. Most are molecules of high-molecular-weight. Larvae of many species settle in response to chemical cues associated with conspecifics [205], bacterial biofilms [206], and crustose coralline algae (e.g. glycolipids and polysaccharides) [177]. Isolated compounds that induce larval settlement may be bioactive (e.g. amino acids, neurotransmitters) or inorganic (e.g. H₂S, NH₃, H₂O₂, and cations such as K⁺) in nature, for review see Refs [207–209].

For chemical cues in the water column, turbulent mixing is generally thought to lead to rapid dilution. However, it has been suggested that slow-moving boundary layer flows (i.e., within eddies) and intermittent pulsing of high concentrations in turbulent flows may make chemical cues for settlement available as a signal [210]. Indeed, some waterborne settlement cues have been shown to promote settlement under a range of hydrodynamic conditions [211]. Moreover, chemical cues used by invertebrates have been demonstrated to travel on the order of 1 m [212, 213], although fish larvae have detected a chemical cue from corals 1 km away [214].

A number of candidate genes for oyster settlement have been identified [215]. Coral larvae exposed to crustose algae upregulated genes related to settlement behavior (SH3PXD2A and Dmrta2; [216]). An mRNA transcript related to gamete quality (e.g. sperm motility) has also been identified in oysters [217].

4 Post-Settlement

4.1 Post-Settlement Mortality

Once larvae have settled, there are many processes that affect their abundance and distribution in the benthos. For example, larval condition can affect post-settlement growth and survival [218–220]. Importantly, the area available to settling larvae does not necessarily predict adult distributions [27, 221], and post-settlement

constraints are assumed to play an important role in limiting recruitment (for review see [15]). Indeed, barnacle larvae will settle preferentially at sites with favorable hydrodynamic conditions for post-settlement growth and survival [154]. Early post-settlement juveniles are frequently subject to fluid forces (e.g. drag, lift) that can lead to dislodgement [222]. Adaptations to prevent dislodgement include byssal threads, cements, and antennular attachment organs [223, 224]. Indeed, there is evidence in a number of bivalve taxa that they undergo a secondary settlement process involving young juveniles, which translocate in the water column to adult habitat [1, 54, 225]. Besides water motion, important post-settlement processes include predation [226–228], parasitism [229], disease [230], and intra-specific and inter-specific competition [231, 232], which can reduce recruitment and/or lead to post-settlement migration [233]. Interestingly, inter-cohort predation by juveniles on postlarvae (i.e. megalopae) for blue crabs (*Callinectes sapidus*) was found to significantly reduce recruitment [234]. Blue mussels (*Mytilus edulis*) increase aggregating behavior in the presence of a predator (European lobster, *Homarus gammarus*) [235]. Other species such as the mytilid, *Choromytilus chorus* are limited in dispersal to areas under macroalgae (*Gymnogongrus furcellatus*), which serve as refuges from predators like dogwhelks, *Nucella crassilabrum* [236].

Given the high rates of mortality in post-settlement juveniles (>90%) [49], it is not surprising that there are myriad of examples of refuge use by post-settlement juveniles in benthic ecosystems. Many benthic invertebrates show a size refuge, where larger individuals experience lower predation pressure compared to smaller individuals [237]. Juvenile sea urchins on the west coast of North America take advantage of this type of size refuge by hiding under the spine canopy provided by larger adults [28]. These spatial refuges provide juveniles with protection from predation and extreme water motion [55, 213], but limit juvenile growth by preventing access to kelp [238, 239]. Juvenile invertebrates such as Iceland scallops (*Chlamys islandica*) and Dungeness crabs (*Cancer magister*) hide under shells and rocks [240, 241] and juvenile barnacles often occupy physical refuges such as crevices or empty tests [242, 243]. Kelp holdfasts also provide refuge habitat for juvenile recruitment of many benthic taxa [244]. Juvenile brittle stars (ophiuroids) cling to conspecific adults and in some cases, this behavior is interspecific [245]. Whereas eelgrass blades facilitate post-settlement survival by providing juvenile mussels refuge from predation [165], macroalgal canopies may have a negative effect on recruitment. For juvenile barnacles (*Semibalanus balanoides*), the sweeping of algal fronds (*Fucus spiralis*) can inhibit successful recruitment [246]. In fact, the negative effect on barnacle

recruitment by mechanical abrasion from macroalgae (*Ascophyllum nodosum*) may outweigh the positive effect of reducing predation under the algae [247].

4.2 Post-Settlement Migrations

After settling on a benthic site, some larvae can reenter the water column and undergo a “secondary settlement” [183, 248, 249]. Barnacles may reject unsuitable substrate based on physical and chemical characteristics [250]. In some juveniles, secondary settlement can occur via thread drifting, bubble formation, or rafting on macroalgae [1, 251–254]. Mussels such as *M. edulis* settle first on filamentous algae, hydroids, or byssal threads of adults and after metamorphosis, cut their byssal threads freeing them to re-enter the water column. Analogous phenomena are found in corals, which have larvae that re-enter the water column by reversible metamorphosis [255].

In a similar manner, post-settlement juveniles may undergo significant benthic movement. Recruitment of juvenile mussels (*Perna perna*) varied consistently among different of rock surfaces aspects, suggesting a significant role for post-settlement migration and/or mortality [256]. Post-settlement blue crabs (*C. sapidus*) can re-enter the water column and disperse planktonically, especially during periods of high water flow (e.g. $>20 \text{ cm s}^{-1}$) [257]. For many bivalves (e.g. migrations observed in 25 bivalve taxa), this form of secondary migration occurs in response to changes in phytoplankton community structure [258]. Once settled, some mobile species (e.g. sea urchin, *S. droebachiensis*) undergo minimal migration due to crowding by adults [259]. In contrast, many mobile crabs (decapods) undertake significant post-settlement migration as an important mechanism for habitat selection [260, 261]. Post-settlement juvenile sea urchins use waterborne chemical cues to locate the protection of larger adults (Figure 5) [213]. In this case, the juveniles respond to a secondary chemical cue released from adults after the adults detect predators, which would provide a mechanism for juveniles to avoid unnecessary competition with adults except in the case of imminent danger.

4.3 Environmental Conditions and Anthropogenic Change

Although the use of refugia and migration to other areas can ameliorate the effects of post-settlement threats on a local scale, they cannot protect recruits from larger-scale changes in environmental conditions. Changes in water temperature, for instance, affect post-settlement behavior, stress, growth, and mortality of early post-settlement

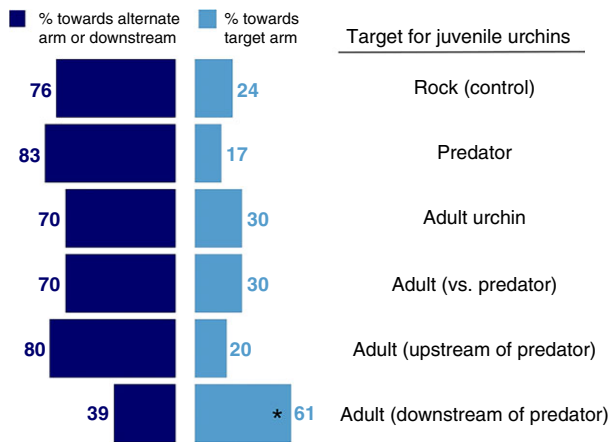


Figure 5 Movement of juvenile sea urchins in a Y-maze with respect to various upstream targets. Dark blue bars represent the percentage of juveniles that moved away from the target that was placed upstream in one of the arms of the Y-maze (e.g. to the opposite arm or in the downstream direction). Light blue bars represent the percentage of juveniles that moved towards the target arm. Targets were alternated between right versus left arms of the Y-maze between trials. Asterisk represents significant juvenile movement towards target arm. Trials were run for 12 hours and $N = 21, 24, 27, 27, 30, 30$. For detailed description of methods and analyses, see [212].

juveniles in many benthic taxa [104, 262–264]. For intertidal organisms like mussels, juvenile mortality can also increase due to rising air temperatures and associated desiccation [265]. Water temperatures can also impart nonlethal effects on post-settlement growth [266, 267] and short-term upregulation of heat shock proteins [216]. Thermal stress in air may impart nonlethal effects such as a reduction in developmental stability for juvenile mussels [268]. Moreover, field surveys of juvenile coral recruitment show that rising temperatures correlate with both slower growth and higher mortality [269]. Post-settlement growth in juvenile barnacles (*B. glandula*) is affected by the interactive effects of multiple environmental stressors such as temperature and flow [267].

In many regions, ocean acidification potentially impacts the recruitment of post-settlement juveniles, especially in those species with calcareous skeletons. Low pH increases juvenile mortality in bivalves [270].

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Nonlethal effects of lower pH, include reduced post-settlement growth in juvenile corals [93] and barnacles [271]. Whole-transcriptome analysis for juvenile corals (*Acropora millepora*) showed differential expression of metabolism- and calcification-related genes after three days of exposure to low pH conditions, but the levels of expression returned to normal after nine days [272]. Scleractinian corals regulate their internal pH at the site of calcification independent of local conditions, making them more resistant to acidification [273]. Moreover, dramatic pH fluctuation in intertidal tidepools suggests that some organisms may potentially be able to cope with increasingly acidified water conditions [274].

5 Conclusion

The biphasic life history of many benthic organism involves a free-swimming planktonic larval stage that disperses from adult population. As larvae mature, they use various mechanisms to seek out suitable benthic (bottom) habitat to colonize in a process known as larval settlement. Once in the benthos, they undergo metamorphosis during which they lose larval structures and develop those structures more characteristic of the benthic habitat. During this period and the time that follows, they are vulnerable to post-settlement processes that lead to high mortality rates, yet some individuals survive and enter the population as recruits. Successful recruitment is thought to be related to several major factors including (i) larval supply, (ii) larval settlement, and (iii) post-settlement. We identified a rather large number of hypothesis associated with each of these major factors; three for larval supply, six for larval settlement and five for post-settlement. Whereas the rather large number of hypotheses may be intimidating, it likely reflects the diversity of evolutionary and ecological trajectories that have been experienced by a wide variety of organisms. It is, therefore, doubtful that any single hypothesis will be sufficient to explain the variation in recruitment exhibited by benthic organisms with biphasic life histories.

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