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SPECIAL FEATURE: REVIEW Spatial Connectivity and Scaling

Complexity and simplification in understanding recruitment in benthic populations

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Abstract Research of complex systems and problems, entities with many dependencies, is often reductionist. The reductionist approach splits systems or problems into different components, and then addresses these components one by one. This approach has been used in the study of recruitment and population dynamics of marine benthic (bottom-dwelling) species. Another approach examines benthic population dynamics by looking at a small set of processes. This approach is statistical or model-oriented. Simplified approaches identify "macroecological" patterns or attempt to identify and model the essential, "first-order" elements of the system. The complexity of the recruitment and population dynamics problems stems from the number of processes that can potentially influence benthic populations, including (1) larval pool dynamics, (2) larval transport, (3) settlement, and (4) post-settlement biotic and abiotic processes, and larval production. Moreover, these processes are non-linear, some interact, and they may operate on disparate scales. This contribution discusses reductionist and simplified approaches to study benthic recruitment and population dynamics of bottom-dwelling marine invertebrates. We first address complexity in two processes known to influence recruitment, larval transport, and post-settlement survival to reproduction, and discuss the difficulty in understanding recruitment by looking at relevant processes individually and in isolation. We then address the simplified approach, which reduces the number of processes and makes the problem manageable. We discuss how simplifications and "broad-brush first-order approaches" may muddle our understanding of recruitment. Lack of empirical determination of the fundamental processes often results in mistaken inferences, and processes and parameters used in some models can bias our view of processes influencing recruitment. We conclude with a discussion on how to reconcile complex and simplified approaches. Although it appears impossible to achieve a full mechanistic understanding of recruitment by studying all components of the problem in isolation, we suggest that knowledge of these components is essential for simplifying and understanding the system beyond probabilistic description and modeling.

Keywords Larval dispersal · Larval transport · Models · Population dynamics · Reductionism · Sampling interval

Introduction: the problem

Benthic populations

Ecologists study how ecosystems function, how communities are structured, and the role individuals play in their environment. A fundamental issue that concerns ecology is the change of population size in time, which is partially dependent on survival and reproduction. Survival and reproduction are fundamental processes ecologically and evolutionarily, as individuals contribute genes to the next generation only if they survive to reproduce. The study of

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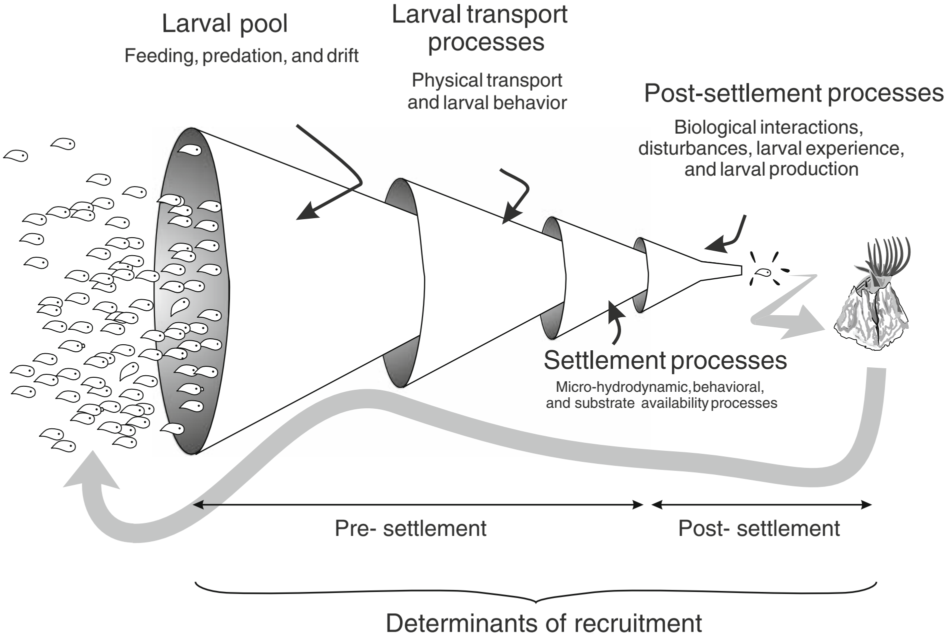

Fig. 1 Processes influencing recruitment in bottom-dwelling species. Modified from Pineda (2000)

ecosystems, communities, and populations makes most sense when these fundamental processes are taken into account. Thus, much research in ecology is devoted to understanding and resolving the different components influencing survival to reproduction, from zygote to adulthood, and their consequences for population change through time.

The population dynamics of marine species is strongly influenced by interactions with their physical environment. Marine species rely on the movement of water to deliver their food, to fertilize their eggs, and to disperse and transport their offspring. All species are influenced by biotic interactions, including competition and predation, yet the coupling between the physical and biological environments is particularly complex in nearshore benthic animal species inhabiting hard substrates. The life cycle of these animals spans two very different habitats. Their minuscule larvae inhabit a three-dimensional habitat, and can be transported by oceanic currents over an enormous range of spatial and temporal scales (Scheltema 1986). Currents help larvae disperse and larvae must then return to shore to settle—an uncertain journey because shoreward flows can be unpredictable in time, and variable along the shore and with depth. After settlement, i.e., attachment to the bottom, the sedentary post-larval stages interact on a hard, 2D substrate where predation, competition for space, disturbance by biotic and abiotic events, and positive interactions combine to produce a characteristic spatial mosaic in which individuals grow and reproduce. The pelagic environment, which modulates food delivery and larval supply to bottom environments, then links benthic systems on even larger spatial scales (e.g., Noda 2004; Navarrete et al. 2005; Broitman et al. 2008). Thus, dynamics of nearshore benthic populations reflect at least four types of processes:

1. larval pool dynamics, including larval feeding environment and dispersal away from adults;
2. larval transport;
3. settlement; and
4. post-settlement abiotic and biotic processes, including larval production (Fig. 1).

These processes are non-linear and operate at disparate scales. Understanding each separately is a formidable task; linking them together in an effort to understand how marine benthic systems operate as a whole is very challenging, and has not yet been done successfully. Nevertheless, making this link is key to solving crucial problems in contemporary marine population dynamics, including management and conservation.

Knowledge of the determinants of recruitment is one of the most important goals in the study of marine benthic population dynamics, but recruitment is a difficult problem that has vexed ecologists for a long time (Coe 1956; Planque and Buffaz 2008). Recruitment is offspring survival after an arbitrary period of time, for benthic invertebrates, a few days or weeks after settlement. In many benthic populations, local recruitment is effectively uncoupled from local fecundity (Hatton 1938; Coe 1956; Yoshioka 1982; Connell 1985; Roughgarden et al. 1985; Eckman 1996). In these populations, recruitment is key for the demography and population dynamics of marine species (Hughes 1990; Nakaoka 1993; Caley et al. 1996; David et al. 1997). Many variables determine recruitment of shallow-water animals with a two-phase life cycle (Fig. 1), including pelagic pre-settlement factors and benthic post-settlement processes. Thus, recruitment is a complex process in the sense that it is determined by many factors operating and interacting on multiple time and spatial scales in numerous environments (Connell 1985; Nakaoka 1993; Eckman 1996; Letcher et al. 1996; Sponaugle et al. 2006).

Complexity and reductionism in the study of benthic recruitment

Marine ecologists have traditionally studied the factors that affect the spatial and temporal dynamics of recruitment and benthic populations one by one. However, understanding recruitment and the population dynamics of these species requires an approach that considers the pelagic and benthic factors simultaneously (Lewis 1977; Eckman 1996). Furthermore, our attempts to elucidate the dynamics of nearshore populations have been limited by a failure to identify relevant empirical phenomena and scales because of the dimensionality of this complex problem.

Research of complex systems[1] is often reductionist, whereby the system under study is broken into components smaller than the whole, and components are resolved separately with hope that individual resolution will result in understanding of the system. Reductionism has various definitions, and epistemologists have studied this problem for a long time (e.g., Popper 1982), including reductionism in ecological problems (Saarinen 1980). Here we use reductionism in its basic connotation, meaning separating multiple components of the system or problem with the goal of understanding the whole (Wimsatt 1980). We highlight issues in studying the recruitment and population dynamics of benthic marine invertebrates, that is, the changes in population size through time of bottom-living organisms.

The apparent advantages of the reductionist approach in general, and its use for addressing benthic recruitment in particular, are many. Benefits include a belief that the whole can be explained by its parts ("i.e., mechanistic understanding of the various processes in Fig. 1 will result in a mechanistic understanding of recruitment"), and a tacit understanding that resolving the individual components of the problem is simpler and more tractable than resolving the entire problem. Indeed, while resolving separate components may be done within a few years, and optimistically within the duration of a grant or of a doctorate thesis, resolving whole systems may take an entire lifetime, and some complex systems have never been entirely resolved. Alternatively, the futility of the reductionist approach can be argued. First, resolving each component separately may not explain how the entire system works if the components interact in a way that is unpredictable from their separate properties, that is, the interactions among the components produce "emergent properties", whether these exist or not. Second, a complex system can be affected by a multitude of factors at different times, and these factors may have different scales. In this case, understanding each factor separately may yield little resolution on how the entire system works because the relative contribution of each component is not clear; misunderstanding grows geometrically with the consideration of more than one temporal and spatial scale. Thus, even if a system shows no "emergent" properties, the sheer complexity resulting from multiple processes and scales makes the whole system difficult to understand and model using the components alone. In this contribution, we consider this second case, the complexity arising from multiple processes operating at disparate spatial and temporal scales.

Early on, ecologists framed the problem of benthic recruitment as a question of pre-settlement versus post-settlement factors (Hatton 1938; Lewis 1977), including the processes in Fig. 1. The problem is complex in the sense that each process includes many mechanisms, interactions, and scales. Below we discuss examples of pre-settlement and post-settlement processes: larval transport, and the post-settlement factors influencing recruitment. We highlight their complexity, the significance of this complexity for overall understanding of recruitment, and then speculate on ways in which this complexity can be approached.

Larval transport by internal bores: variety of scales and processes

Onshore transport of larvae by internal tidal bores highlights the complexity of larval transport, including the variety of mechanisms and scales involved. Larval transport is the translocation of a larva from point *a* to *b* (Pineda et al. 2007). Here we discuss onshore larval transport from a location offshore *a* to location nearshore *b* by internal tidal bores.

Internal waves and internal tides (i.e., internal waves of tidal period) generate at tidal periodicity by interaction of tidal currents with bottom topographic features such as shallow banks and the continental shelf edge. An initial disturbance attached to the topographic feature is released at some point and evolves into an undular bore, a train of rank ordered non-linear internal waves (e.g., Scotti et al. 2007). The internal bores can reach shallow waters only when the water column is density-layered (stratified) by temperature and salinity, and when the thermocline (the zone in the ocean where temperature rapidly changes with depth) is shallow. If there is no density layering, or if the

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[1] In ecology and other empirical sciences, complexity is used with several connotations. Here we use in the sense of a problem consisting of many parts, and processes with many interactions, and scales.

thermocline is deep (say, 100 m) there would be no waveguide for internal motions to propagate into shallow nearshore waters. In Southern California, as in most other temperate coastal oceans, density layering is seasonal, with the waters thermally stratified in spring and summer. The local shallowing of the thermocline, which allows the internal bores to propagate into shallow waters, is related to coastally trapped waves. These waves generate south of California, in Baja California, due to changes in the wind field, and they drop and raise the sea level a few centimeters as they propagate, and in response to this change in sea level the thermocline shallows and deepens (Brink 1982). When the thermocline shallows for a few days in response to the passage of the coastally trapped waves, internal bores manifest in the nearshore, and it is then that larvae can be transported onshore (Pineda and López 2002). However, during El Niño, an interannual phenomenon, the thermocline deepens and moves away from the shore, and internal bores are not apparent in shallow waters during these events (e.g., Zimmerman and Robertson 1985). Temporally, fortnightly variability of temperature during the spring and summer in the nearshore may also be related to internal tidal bores (Pineda 1991). Spatially, variability in stratification along the shore leads to differences in internal motions, presumably causing variation in larval transport which results in consistent differences in invertebrate settlement (Pineda and López 2002).

The seasonality of internal motions is revealed by a water temperature record in Panama (see also Jimenez 2001 for evidence of internal bores in Costa Rica). Figure 2 shows increased high-frequency temperature variability from February to May, with decreased variability during the rest of the year; this seasonal pattern in high-frequency variability must be related to the presence of internal motions. That is, internal motions cause the high-frequency variability (Fig. 3). What causes the seasonal pattern? It does not appear to be in phase with seasonal warming, and may be somehow related to a seasonal shallowing of the thermocline that is likely to be related to meso-scale and large-scale processes. In the Pacific coast of Panama (at about 8°N) it rains about 3 m of water, mostly in the rainy season (“invierno”), from May to December (D’Croz and O’Dea 2007), and this seasonality in freshwater input may have an effect on the density layering and the occurrence of internal waves.

Internal bores often occur at the leading edge of the internal tide in deep (Holloway 1987) and shallow waters (Cairns 1967; Winant 1974), and in the shallow near shore they evolve into gravity currents (Pineda 1994) where mass transport occurs (Simpson and Britter 1979). In Southern California, and in other temperate and tropical settings such as Massachusetts Bay and Panama, the process occurs in two phases. In phase 1 (“cold phase”) the internal tidal bores produce onshore advection of subsurface water shallowing and outcropping of the thermocline (Cairns 1967; Winant 1974). As subsurface cold water is advected shoreward, warm nearshore surface water is displaced offshore. During phase 2 (“warm phase”), a few hours later, the surface and bottom flows reverse, the dense cold water sinks and is displaced offshore, and warm water flows shoreward, all the way to the shore, often led by a surface internal tidal bore warm front (Pineda 1994, 1999). The cold and the warm phases have been implicated in the onshore transport of larvae, but clear evidence of transport only exists for phase 2 (Pineda 1999). For example, Fig. 3 shows internal bores in about 16 m, in Panama. The upper panel shows that the cold water occurs in sporadic groups of events, that is, on days 91–93, but not on days 94–95. Figure 3 lower panel shows the warm and cold water phases of the internal tidal bore, each one lasting several hours, and the high-frequency, few minutes internal motions that accompany these internal tidal bores. During onshore transport in the warm phase, which lasts a few hours, larvae accumulate in the propagating front, and the small-scale circulation at the front implies that only plankton that swim up against the downwelling currents at the front are transported effectively by the internal bore warm front. Modeling larval transport during phase 2 (e.g., starting at about day 91.38 plus 25 min), as a gravity current, underscores the importance of behavior, and demonstrates that this physically simple process can be very intricate to model (Helfrich and Pineda 2003; Scotti and Pineda 2007). Finally, in addition to the shallow internal tidal bores, deep undular bores (Lamb 1997) and internal waves of elevation (Klymak and Moum 2003; Scotti and Pineda 2004) may also transport material and particles.

In summary, processes influencing larval transport by internal tidal bores can include tides (i.e., generation), remote winds (i.e., coastally trapped wave modulation of thermocline depth), and even large-scale interannual forcing such as El Niño (modulation of thermocline depth). On the Pacific coast of Panama, for example, processes may also include meso-scale circulation and the length of the rainy season. Relevant scales include seconds (behavior), hours (accumulation in fronts), semidiurnal, fortnightly, a few weeks, annual, and interannual, with spatial scales ranging from millimeters to hundreds of kilometers.

Post-settlement factors influencing recruitment

After larvae transport and settle, they still must survive to adulthood if they are to contribute to population growth. The problem of how many settlers join the adult population is a key component of the recruitment problem. In a similar way that larval transport is complex, with many processes, dependencies, interactions, and scales, the problem of how many settlers join the adult population is also intricate and

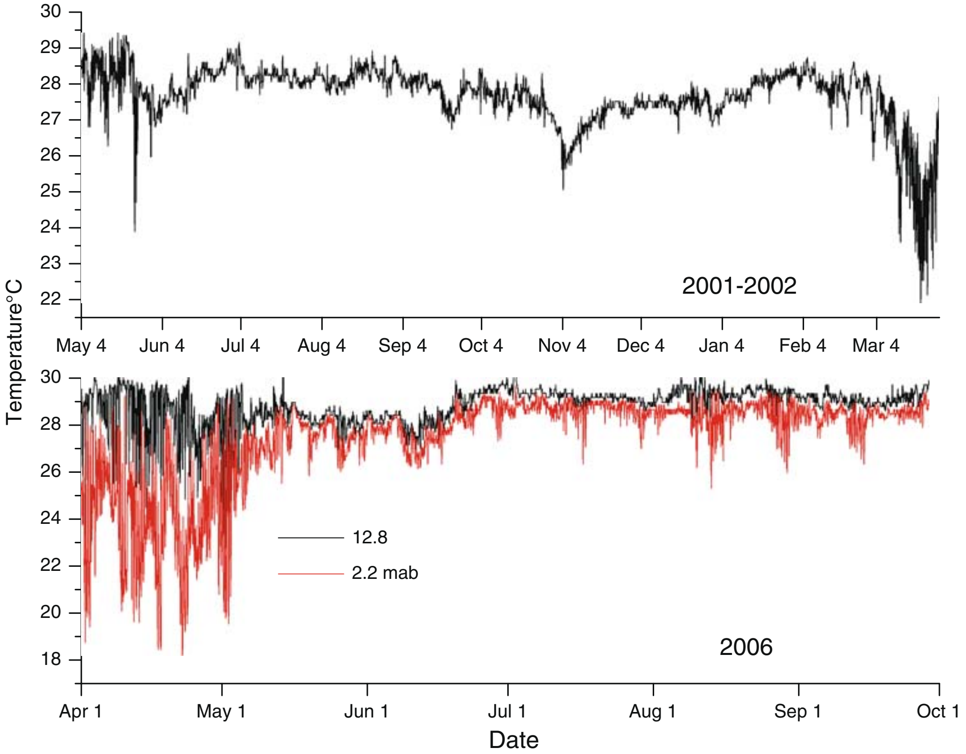

Fig. 2 Temperature variability in the Pacific nearshore of Panama. *Top* May 2001 to late March 2002, recorded in a small cove at the Pacific nearshore of Panama (7°44.611′N, 81°34.545′W). Onset Tidbit temperature logger recorded temperature every hour at the bottom, in about 7 m water depth, and a three-point running average is plotted. *Bottom* April to late October 2006. Nearshore open coast of Panama (7°44.093′N, 81°35.032′W). Loggers 2.2 and 12.8 m above the bottom (mab) sampled every 8 min and a five-point running mean is plotted. Mean water depth is about 16 m

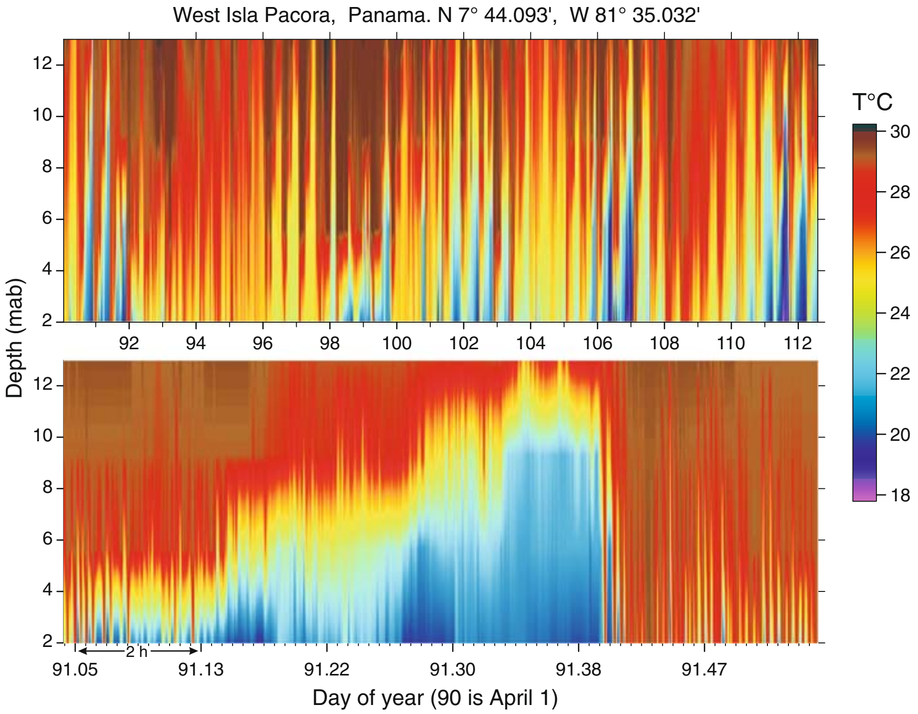

Fig. 3 Contoured temperature variability. Same location as in Fig. 2, bottom (16 m water depth). Onset Stowaways XT with external probe were placed 2, 6, 10, and 13 m above the bottom (mab), and recorded temperature every minute

multifaceted. For example, consider the challenge of studying the regional and temporal variability of the post-settlement processes influencing recruitment of the acorn barnacle, *Semibalanus balanoides.* Researchers have identified experimentally many factors that influence early survival (Table 1). (Factors that influence survival to reproduction are less well studied.) Thus, experiments or models designed to examine recruitment of this species should incorporate predators, inter-specific and intra-specific competitors for space and food, habitat suitability, disturbances, physiological factors such as temperature stress, and hydrodynamic conditions.

Table 1 Potential factors influencing recruitment of barnacles *Semibalanus balanoides* in New England

Factor	Effect	Reference
Larval supply	Affects numbers of settlers and recruits	(Minchinton and Scheibling 1991; Pineda et al. 2002)
Predation (i.e., predatory snails and crabs, etc.)	Increases mortality, frees space for growth, alleviates interspecific competition	(Connell 1961a; Menge 1976; Minchinton and Scheibling 1993a; Leonard et al. 1998, 1999; Bertness et al. 1999)
Juvenile performance	Affects feeding efficiency and growth, survival, and reproduction	(Jarrett and Pechenik 1997; Leonard et al. 1998; Jarrett 2003)
Density dependence/ competition	Mortality. Also limits food and space availability and causes changes in body formation (i.e., hummocks). Positive density dependence creates buffers from physical stressors	(Connell 1961b, 1985; Menge 1976; Bertness 1989; Minchinton and Scheibling 1993a; Jenkins et al. 2008)
Suitable substrate/ substrate patchiness	Influences recruitment strength and causes shifts in settlement patterns	(Bertness et al. 1992; Petratis et al. 2003)
Disturbances (biological and physical)	Influences hydrodynamics and suspension feeding. Dislodges and damages barnacles	(Connell 1961a, 1985)
Temperature and thermal stress	Influences juvenile growth, abundance, and community composition; causes physiological stress and stresses on metabolic and reproductive processes	(Bertness et al. 1999; Leonard et al. 1999; Leonard 2000)
Hydrodynamics/ flow rates	Food delivery	(Bertness et al. 1991; Leonard et al. 1998)

For example, an experiment designed to test how many of these factors affect recruitment of barnacles in the rocky intertidal zone could have the following treatments: location (along a coastline), tidal height, cages to exclude predators (quadrats with and without cages and cage controls), density (high and low adult density to examine intraspecific competition), surface (quadrats on horizontal and vertical areas), exposure (quadrats in high and low energy locations), temperature stress (shaded and not shaded quadrats), algae (quadrats with and without algae), and year to determine interannual variation. For a completely randomized design at a given location, tidal height, and surface type, quadrats would have to be established with and without cages and with cage controls, in areas with and without algae, in shaded and not shaded areas, and with different densities of adults. The investigator could choose to remove or not remove adults or algae to achieve the desired factor level to test the effects of algae or adults. These factors would likely be nested within locations of different wave exposure along a coast.

Underwood (2000) discusses the difficulty of piecing together information gleaned from multiple studies to create better predictive models and understanding of the variation in the abundance of species. He argues that experiments should be conducted at broader spatial scales and should include more habitat types. Temporal scales should be increased so that the turnover of individuals is documented. This would allow sufficient temporal data to look for trends and evaluate the effect of disturbance. Experiments should be repeated in space and time for results to be generalizable. Given that conducting an experiment that involves just a few factors from Table 1 is a daunting task, superimposing the above recommendations with adequate replication would render an experiment even more formidable. While multi-way ANOVA models have been used in barnacle recruitment studies (e.g., 4 or 5 factors in Jeffery 2000; Bulleri 2005; Lee et al. 2006), including spatial and temporal components can add several crossed and nested terms and higher-order interactions that become difficult to interpret. To test a range of similar factors in soft bottom habitats becomes even more difficult in that sampling the bottom habitat is necessarily destructive because cores must be taken to census animals living in these habitats. Furthermore, many organisms that live in soft sediments are mobile so they may survive a set of conditions by migrating from an area or test location—an option not available to many hard substrate settlers that tend to be sessile. An experiment involving all the factors, repeated, and performed over a wide range of environments and years, would be of such prohibitively huge magnitude and cost that a small version of the US NASA program would be needed to fund it.

Simplification by first-order approaches

The complexity in larval transport, dispersal, and post-settlement processes influencing recruitment can be reduced by using first-order approximations. Simplification

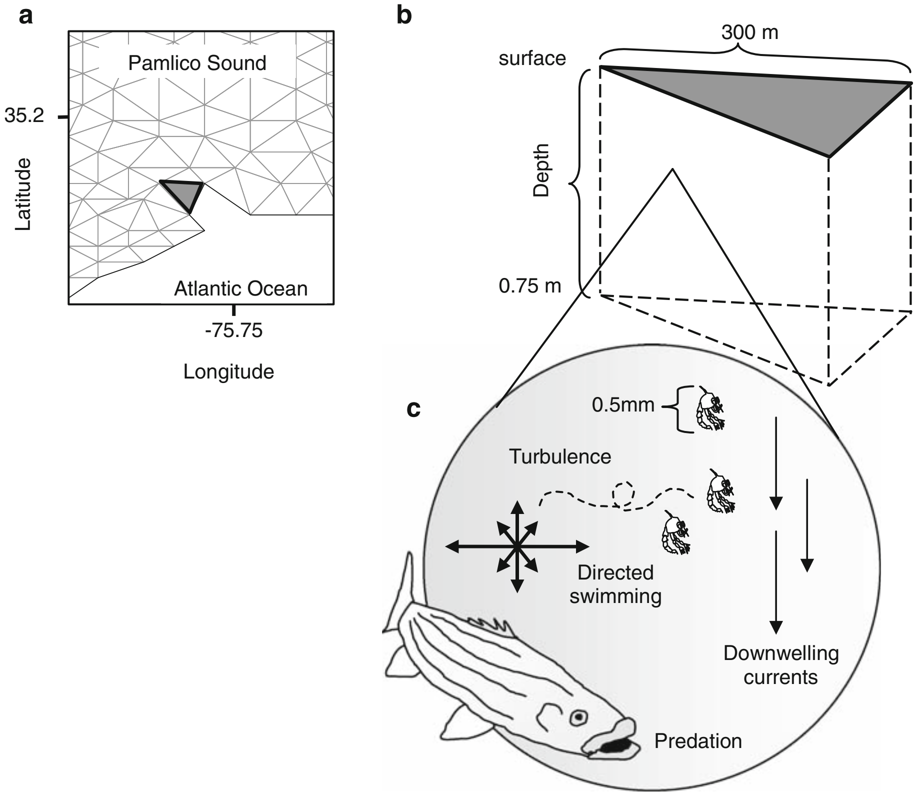

Fig. 4 Example of a biophysical dispersal model grid. Flow fields are only calculated at points (nodes) where the triangles that comprise the grid meet. **a** Close-up (plan) view of grid size generated by a finite element model used to simulate dispersal near Hatteras Inlet in the Pamlico Sound estuary off the East Coast of the United States (see Reyns et al. 2007 for more detail). *Shaded* cell in (**a**) is depicted in 3D in (**b**) (not drawn to scale). **c** Demonstrates examples of the biophysical mechanisms that can operate on sub-grid scales (on smaller spatial scales that can be resolved by the model grid) to influence the dispersal of crab larvae

by first-order approaches includes process reduction and data synthesis by modeling and statistical techniques, and also by description of supposedly primary processes by broad-brush observation of natural systems, both spatially and temporally. We address examples of simplification by modeling and broad-brush sampling. For an example of a recent statistical approach for addressing recruitment see Planque and Buffaz (2008).

Simple models of larval transport and dispersal for understanding recruitment: small-scale physical processes, mortality estimates, and larval behaviors

First-order approaches include biophysical numerical circulation models that feature simplified or no larval behavior. They address only hydrodynamic processes that are well understood and dominate the flows on certain scales, for example tidal and meso-scale wind driven flows, and spatial settings with idealized linear coasts. Additionally, such models use rough estimates of larval mortality for generic species and remote locations because larval mortality rates for almost all species in the ocean are poorly characterized (see below).

Resolution of small-scale processes Most biophysical dispersal models utilize relatively large grid sizes (meters to kilometers) to compute flow fields, but:

1. larvae interact with biophysical conditions in their surrounding environment on scales approaching their body size; and
2. complex flows, particularly those found nearshore where many larvae originate from and must return to for the completion of their life cycle, are not captured in these model grids.

Examples of small-scale oceanographic processes excluded from models include microscale turbulence, surface waves, internal bores, and propagating convergences. Thus, the mismatch between the scales used in models and the scales over which biophysical mechanisms and larval behaviors operate (i.e., “sub-grid scales”; Fig. 4) is likely to hinder our ability to accurately predict dispersal patterns using simulation models (but see a recent example of a model quantifying the relative importance of biological and physical factors on spatial scales relevant to larvae; Paris et al. 2007). Leis (2007) provides a comprehensive discussion on how to integrate sub-grid scale processes, particularly larval behaviors, into numerical models of dispersal. Although his review focuses on reef fishes, his advice should be considered when developing dispersal models for benthic marine invertebrates. Nonetheless, the exclusion of small-scale hydrodynamic processes that transport larvae excludes processes that would often result in reduced dispersal (see discussion in Pineda et al. 2007).

Issues with larval behavior and mortality estimates Marine invertebrate larvae, typically on the order of micrometer to millimeters in size and with relatively slow horizontal swimming speed capabilities (reviewed by Chia et al. 1984), have been historically considered passive particles whose dispersal outcomes are dictated by the speed and direction of ocean currents (Thorson 1950; Scheltema 1986; Gaylord and Gaines 2000). Within the last decade, however, it has become increasingly recognized that larvae have well-developed sensory systems (e.g., see review of larval crustacean sensory systems in Jeffs et al. 2005) that allow them to behaviorally respond to environmental conditions in ways that may impact their dispersal (Forward and Tankersley 2001; Metaxas 2001; Queiroga and Blanton 2005; Montgomery et al. 2006). Despite the growing consensus that larval behavior plays an important role in driving dispersal patterns, for most species behaviors are poorly characterized or have been examined in laboratory settings that may not accurately reflect conditions experienced by larvae in the field. For example, many laboratory studies have examined larval swimming speeds in relatively small containers where drag along the sides creates "wall effects" that may produce unrealistic swimming speed measurements (reviewed by Chia et al. 1984). Moreover, experimental studies rarely consider the multitude of environmental conditions that larvae may encounter in the field (i.e., changes in salinity, temperature, food availability, turbulence, current velocities, etc.), suggesting that larval behaviors documented in the laboratory may be a subset of what larvae are capable of in the field. Further, most larval dispersal studies examine population-level responses of larvae to environmental conditions, without considering how individual larval behavioral variability might influence dispersal patterns. Consequently, as researchers increasingly utilize numerical ocean circulation models coupled with Lagrangian particle-tracking algorithms to simulate larval dispersal, we need better documentation of the suite of behaviors employed by larvae in the ocean for model predictions to be robust. Model development must also be improved to incorporate multiple behaviors. For example, most models only incorporate vertical positioning behaviors, and rarely consider horizontal swimming behaviors, ontogenetic behavioral changes, predator–prey interactions, or mortality (e.g., Reyns et al. 2006, 2007).

Mortality rates of larvae are notoriously difficult to obtain given that individuals cannot be easily tracked in the ocean, because of their small size, and that mortality is likely to change ontogenetically. It is generally accepted that larval mortality rates must be great in the plankton, but estimates are highly variable (from 23% daily, reviewed by Morgan 1995, to <3% daily, Johnson and Shanks 2003). Moreover, mortality estimates are often generated from laboratory data, but larvae reared under field conditions may have substantially different growth and mortality rates than those reared in the laboratory (Pechenick and Levine 2007). Given these uncertainties, incorporating mortality into dispersal models becomes tenuous. Recently, mortality rates calculated from field distributions of two barnacle species in California indicated that mortality is substantially greater (20–40% daily, Tapia and Pineda 2007) than previously assumed (~5% daily, Gaylord and Gaines 2000). Thus, dispersal predictions generated from models with inaccurately low mortality estimates (or in some cases no mortality) have a tendency to over-predict dispersal (Roberts 1997) when compared to models that use higher mortality (Cowen et al. 2000).

Coarse interval in settlement and recruitment measurements

Coarse sampling intervals for tracking settlement and recruitment are first-order approximations used to identify the number of individuals that settle and join the adult population. First-order estimates include weekly, fortnightly, or monthly field sampling, and carry the implicit assumptions that settlement correlates with larval supply (but see Porri et al. 2006), and that the sampling interval is adequate for identifying the onshore physical transport mechanisms and for estimating individuals that recruit to the population. The latter assumption is reasonable if the number of individuals settling and post-settlement mortality are uniform over time; estimates of mean settlement of recruits will be unbiased and have relatively low variance. Uniform settlement and mortality are not the norm for most organisms (e.g., Wethey 1986), however, and if the goal of the research is to correlate settlement with physical processes which vary on short time scales, sampling must be more frequent than the process of interest. Studies have examined the effects of sample frequency on abundance estimates of larvae, settlers, and recruits of species that have high daily variability in abundance (Booth 1991; Michener and Kenny 1991; Minchinton and Scheibling 1993b; Hettler et al. 1997; Moksnes and Wennhage 2001). To understand how sampling frequency biases our interpretation of the mechanisms that affect settlement, consider that processes that vary at high frequency (say on scales of one day) will be missed with weekly sampling because sampling interval determines which frequencies in a time series can be identified. The shortest time-scale that can be identified from a time series is twice the sampling interval (the Nyquist frequency, Chatfield 1989). Hence, sampling settlement every week may be correlated with processes that vary fortnightly and at longer intervals (Fig. 5) such as relaxation from Ekman upwelling. Weekly sampling, however, will not detect settlement related transport by

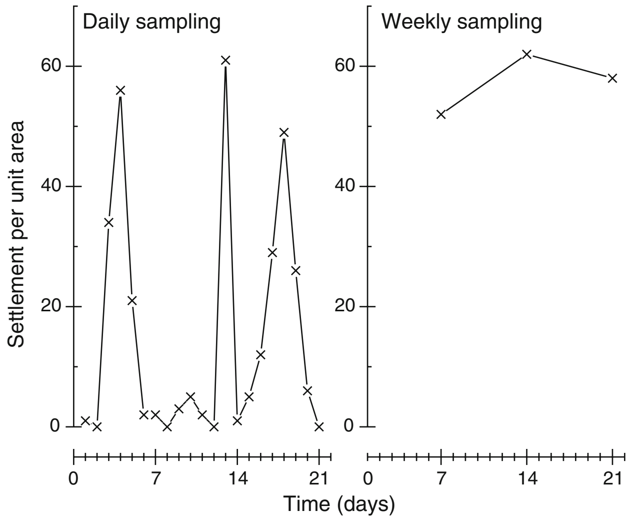

Fig. 5 Simulated settlement time-series obtained at different sampling intervals. Redrawn from Pineda (2000). See also Michener and Kenny (1991)

internal tidal motions, which have shorter time scales (for more discussion see Pineda 2000). Therefore, sampling coarsely biases our view of the physical processes that transport larvae towards meso-scale mechanisms that have correspondingly long time scales (Stommel 1963), such as Ekman upwelling relaxation. Finally, researchers have paid little attention to small-temporal scales after settlement, yet for some systems processes on very fine temporal scales are most important in influencing recruitment (Gosselin and Qian 1996; Pineda et al. 2006).

Issues with first-order approximations

Use of first-order approximation may have biased our view of the dominant scales of dispersal, the openness of benthic populations, and the processes influencing larval transport and survival to adulthood. The use of hydrodynamic models featuring only well known processes, simplified topographies, no larval behavior, and low mortality estimates, have led to broad estimates of dispersal and population openness. These estimates must be inaccurate compared with those from models that include small-scale processes, realistically complex shore configurations, vertical positioning larval behaviors, and high mortality rates, all of which tend to reduce larval dispersal (Table 2, see also discussion in Pineda et al. 2007). Likewise, sampling individuals every few weeks does not really resolve the putative hydrodynamic processes responsible for the influx of recruits, and whether these processes are important for population growth. Coarse intervals may not capture the fundamental processes that influence survival to adulthood.

The view that dispersal is broad is changing to a paradigm implying that dispersal is more restricted (e.g., Cowen et al. 2000; Sponaugle et al. 2002). Another emergent view is that small-scale spatial and temporal processes have a much greater importance than previously thought (Pineda 2000; Pineda et al. 2007). Several lines of evidence support these new paradigms, including:

1. unexpected high levels of self-recruitment;
2. higher mortality rates than those traditionally assumed; and
3. constrained scales of larval transport (see discussion in Pineda et al. 2007).

Revealingly, all these lines of evidence originated in empirical studies, and none come from first-order approaches.

The reason first-order approaches have not been more successful in resolving the recruitment problem and its components may be fundamentally a simple lack of empirical understanding of the first-order processes. That is, the processes responsible for transporting the larvae that successfully disperse and settle and the processes accounting for the individuals that survive to reproduce are not well determined (e.g., Cowen 2002; Pineda et al. 2007). A first-order approach would be powerful when the primary factors influencing recruitment are well understood and determined. Hypothetically, assuming that factors influence recruitment additively, one could say that factor A determines $x\%$ of recruitment, factor B $y\%$, and so on, and thus base the selection of the primary processes and mechanisms on those relative contributions and interactions. Yet, in larval transport, dispersal, and recruitment studies, those factors are rarely known, and at best are only suspected. Assessing relative contribution is, so far, out of the question. In hurrying to adopt synthetic approaches without first having determined rigorously the empirical system, ecologists may have followed a contorted path to understanding recruitment. Beyond generating hypotheses to be tested in the field, the utility of first-order approximations for resolving and predicting the problem of recruitment is so far unclear. This will change, we hope, when the empirical systems are better determined (see below).

Discussion: reconciling complexity and simplification in recruitment studies

The natural ecological world is complex, yet mechanistic understanding of some ecological systems beyond probabilistic modeling and description requires much simplification and abstraction. How, then, can we reconcile natural complexity with the goal of mechanistically understanding recruitment? This difficult question is of enormous importance for understanding natural populations, and for

Table 2 Potential simplifications by focusing on "first-order processes" and how this influences estimations of larval transport and dispersal

Simplification	Examples of how simplification influences the magnitude of larval transport and dispersal	Simplification over-estimates total larval transport and dispersal?
Simplified topography	Linear topography reduces along-shore flow reversals, regions of slack flow, and residual flows	Yes
Passive larval behavior	Passive behavior eliminates the possibility of larvae positioning themselves in layers with reversed flows Passive behavior reduces the efficiency of transporting mechanisms such as gravity currents and internal motions	Yes, in most open coastline cases (but see North et al. 2008 for an estuarine counter-case)
Cross-shore homogeneity in physical processes. Surfzone and nearshore small-scale processes are not modeled	Many small-scale flows are non-linear, produce mass transport, and can result in reduced offshore diffusion yet they are not well understood and are not included in numerical models of dispersal. Processes include the sea breeze, advection by surface gravity waves, internal motions, and microscale turbulence	Yes
Mortality estimates	Very low larval mortalities used in models for the US West coast were calculated from data from a barnacle in the UK	Yes

management and conservation applications. We argue that the solution includes a mix of:

1. empirical resolution;
2. process reduction; and
3. simplification (i.e., syllogistic and mathematical abstraction; see for example Eckman 1996).

Below we offer examples of how to reduce the number of empirical processes when studying recruitment, and where to stress empirical determination. From a reduced set of empirically tested and well determined processes, syllogistic and mathematical simplifications will more aptly help understand and resolve the problem of recruitment.

Process reduction: focus on common processes

Invertebrate and vertebrate marine larvae possess an enormous range of behaviors that may enhance or suppress larval transport and dispersal influencing recruitment (Metaxas 2001; Kingsford et al. 2002). Multiplying the number of potentially relevant behaviors by the number of hydrodynamic processes that may transport larvae, results in a vast number of possibilities that may be impossible to resolve in a reasonable way. Swimming up against downwelling currents is a behavioral response that may work in multiple situations when examining larval transport and dispersal and their importance to recruitment. Many oceanographic phenomena involving gravity currents, including internal bores, upwelling relaxation, and estuarine flows, produce fronts, or surface and bottom features where two bodies of water collide (Simpson 1997). Fronts feature convergent vertical currents, and it has long been known that for plankton to remain in fronts they have to swim against the downwelling currents (Le Fèvre 1986; Franks 1992; Genin et al. 2005). Some fronts featuring convergent currents propagate together with the water mass, and in this way also transport the planktonic larvae that swim against the downwelling currents and remain aggregated in the front (for a review, see Metaxas 2001). Thus, by examining the behavioral response of larvae to vertical downwelling currents, ecologists may be able to assess whether a large number of hydrodynamic processes can efficiently transport larvae that exhibit such behavior.

Process reduction: focus on hydrodynamic processes that transport larvae onshore

In the case of cross-shore transport, we suggest that researchers first resolve the mechanisms that transport larvae and influence recruitment before focusing on the mechanisms that keep larvae away from their adult habitats. Marine invertebrate and fish have enormous fecundities but few individuals survive to reproduce. After reproduction and dispersal away from the nearshore, larvae can either be transported onshore or transported further offshore, a wastage for the population if larvae are unable to return to nearshore habitats (Johnson 1960). Marine ecologists have been interested in both—factors that transport larvae onshore and those that transport larvae offshore. Given the complexity of the larval transport problem, the enormous fecundity of marine invertebrates and fish, the lack of determination of the spatial domain over which the putative mechanisms operate, and limited research resources, it may be more fruitful to prioritize our emphasis on the processes that transport larvae onshore (e.g., sea breeze, transport by surface waves) rather than the mechanisms that cause larval wastage (e.g., wind-driven Ekman upwelling). Moreover, it is not always clear that processes such as Ekman upwelling cause wastage of larvae. For example, larvae may never abandon the very nearshore area, or have vertical distributions that negate offshore drift, and upwelling may actually enhance onshore larval transport, directly by influencing cross-shore circulation (Garland et al. 2002; Shanks and Brink 2005), or indirectly by producing shallowing of the thermocline that enhances cross-shore transport by internal bores in the nearshore zone (Pineda and López 2002). While larval wastage is an interesting problem, and researchers should be aware of this issue as it may partially explain the large fecundities in marine animal life-histories and the infrequent colonization events these organisms experience, the onshore larval processes may be more relevant for understanding population dynamics, because enormous mortality also occurs following settlement (Gosselin and Qian 1996; Hunt and Scheibling 1997). Ultimately, the individuals that survive to reproduce are the ones that sustain the population.

Process reduction: focus on the survivors to adulthood

The number of survivors in a given time period is the total number of individuals at the beginning of the time interval minus the number that die at the end of the time interval. Although survival and mortality are mathematical complements, the processes and interactions that affect survival may not be the same as those that affect mortality. Individuals that survive may share similar characteristics (e.g., lipid stores, genes, seasonal time of settlement, etc.) whereas mortality may come from a variety of factors (e.g., biotic or abiotic factors that may be random). The effectiveness of mortality factors (e.g., $\ll$1% survival for high-fecundity species) suggests that independent mortality agents may be redundant, that is, an individual that does not die due to factor *a* could die because of factors *b, c, d*, or *e*. Identifying the characteristics of survivors can reduce the list of potential factors that need to be studied. For example, by focusing on the factors common to survivors in barnacles, we can reduce the number of factors that affect recruitment in barnacles *Semibalanus balanoides* to three or four (Pineda et al. 2006).

It may be more fruitful to focus field and process studies of post-settlement survival to recruitment on the individuals that survive instead that on those that die (see also Fritz et al. 1990) because individuals that disperse, settle, and survive to adulthood are most likely to reproduce, and their traits may be selected for, while many individuals that die may not share those traits. Thus, focusing on the factors that collectively result in survivorship to adulthood is more in line with the way natural selection operates to maximize fitness, than focusing on the individual factors that cause mortality. Moreover, focusing on survivorship may reduce the complexity of the recruitment problem, as pointed above.

Population life history models that look at sensitivity and elasticity of parameters for a species can identify what stages or ages have the most affect on population growth. In demographic models of benthic invertebrates, survival probabilities at early stages are often the most sensitive term in the model (Levin et al. 1987; but see Caswell 2001). Population growth can also be highly sensitive to age at first reproduction (Wethey 1985). Thus, besides reducing the complexity of studying recruitment, identifying the factors that affect survival probabilities at the early stages can be most relevant to predicting population growth.

Empirical resolution: improved in-situ measurements

Successful coupled biophysical models to simulate dispersal and assess connectivity of marine populations need to:

1. parameterize sub-scale biophysical processes in the models; and
2. validate model results with field data.

To accomplish these two goals, more comprehensive larval behavior studies should be conducted in realistic field settings. Because larvae are relatively small and cryptic, and generally have low concentrations or patchy distributions in the ocean, they are inherently difficult to track in space and time. Thus, the development of new technologies will improve our ability to track larvae and obtain in-situ measures of larval behaviors and the surrounding physical environments they experience.

A number of methodological advances have been developed to track larvae in the ocean, including stains, radioactive labels, genetic markers, and trace elemental signatures in calcified structures (see reviews by Metaxas 2001; Levin 2006). While these techniques enable us to track how far larvae travel or determine origination sites with some success (Almany et al. 2007; Becker et al. 2007), larval behaviors and mortality have not been quantified using these approaches.

Currently, quantifying larval behaviors in the field can be accomplished using towed video camera systems with special magnifying optics to identify larvae and record their behavior (e.g., Video Plankton Recorder; Benfield et al. 2000; Gallager et al. 2004). One emerging technology that holds promise for the future, however, is the use of holographic particle image velocimetry (HPIV), by means of which an organism's behavior, and complex turbulent flows, can be simultaneously measured in 3D (Malkiel et al. 2003, 2006). This technology can successfully follow individual larvae, their prey, predators, and surrounding physical flows by taking repeated holographic images using a digital camera suspended by a fiber optic cable in the ocean (Malkiel et al. 2003, 2006). Additional ways in which larval behaviors can be quantified are to track individuals using SCUBA (method amenable for relatively large larvae like ascidian tadpoles, e.g., Olson 1985) or, for smaller larvae, by placing individuals in contained arenas that drift in-situ, with a video camera to record behaviors (e.g., orientation with no frame of reference system used with reef fish larvae; Paris et al. 2008). Thus, as larval imaging techniques become more advanced (i.e., more powerful digital video cameras, optics, and computers) better visualization of larvae in situ will be possible. Finally, the development of genetic probes should facilitate larval tracking during dispersal, at least for the purpose of identifying individual larvae to species (Goffredi et al. 2006).

Conclusions

To successfully describe and predict recruitment in benthic populations, greater empirical knowledge of the processes important to recruitment and knowledge of the relative importance of these processes at different temporal and spatial scales are needed to better choose variables and estimates to incorporate into models. The number of factors that are incorporated into models of recruitment must be reduced because models cannot include all details of natural systems if they are to contribute to understanding of fundamental processes. Modeling recruitment in benthic populations is complicated further because recruitment is subject to large environmental variability in different environments. What is the best way to simplify models? Adding single variables without information about how these variables interact with other variables can produce biased parameter estimates of recruitment. Excluding variables such as larval swimming behavior or larval transport, because of lack of knowledge about their importance, will also result in biased results.

First-order broad-brush approaches have contributed little to recent awareness of the importance of small-scale spatial and temporal processes in determining recruitment, from larval dispersal to survival to adulthood, and more specifically on the prevalence of restricted dispersal and self-recruitment. In fact, such approaches only reiterate the already generally accepted notion that large spatial and temporal variability characterizes recruitment of marine organisms. In particular, reduction of complexity by neglecting high-frequency small-scale processes has no empirical support: there appears to be no logical arguments supporting the primacy of large-scale and meso-scale processes. The recent shift in views (restricted vs. broad dispersal, open versus closed populations, etc.) are rooted in empirical studies. However, indiscriminate empirical studies are unlikely to resolve the problem of recruitment because the number of processes, interactions, and scales are vast, and empirical findings cannot be easily generalized. Beyond probabilistic descriptions, recruitment may only be understood mechanistically if a small number of processes and interactions are considered. We argue that empirical studies should discover processes such as swimming up, onshore larval transport, and survival to adulthood, and theoretical studies should use numerical and syllogistic abstraction to put these processes together to gain insight into the problem of recruitment.

The list of fundamental processes influencing recruitment in this contribution may be inexact, and other general processes not discussed here may be involved. For example, modulation of physical and behavioral processes by astronomical cycles (e.g., tidal, fortnightly, and lunar periodicity in settlement; Reyns and Sponaugle 1999; Cruz et al. 2005; Queiroga et al. 2006) are often observed, particularly in shallow water systems such as estuaries and coastal environments. The underlying mechanisms of these cycles remain unclear, however, and hopefully additional studies will enable more complete understanding such that these processes can be incorporated in syllogistic and quantitative abstractions. Additionally, this contribution was limited to nearshore invertebrate populations inhabiting open coastlines and the associated ecological and hydrodynamic processes. We consider, however, that our remarks apply to most invertebrate and fish benthic populations with pelagic larval phases inhabiting a variety of habitats, from estuaries to sea-mounts to hydrothermal vents. Indeed, a quick survey of the processes emphasized in this contribution and addressed by ecologists studying in other marine environments may reveal useful trends along the lines of our contribution. For example, students of sea-mounts and hydrothermal-vent benthos emphasize processes that retain larvae near the benthic hard substrate, and rarely study processes that disperse larvae away.

In summary, predicting recruitment by collating knowledge from multiple individual studies may not be possible, in a somehow similar way that numerical simulation models with many variables and parameters yield little fundamental understanding of the process and variables they attempt to model. Broad-brush approaches that assume primacy of processes with larger spatial and temporal scales (e.g., meso-scale vs. small-scale geophysical flows in larval transport), that neglect small-scale biological processes (e.g., larval behavior), and that overlook small temporal scales after larval settlement and metamorphosis may miss some of the most important processes in larval dispersal and survival to adulthood. Thus, these broad-brush approaches may contribute little to identification of the critical processes determining recruitment. We suggest that a reduced set of processes and rates, for example, swimming up behavior, onshore larval transport, survival to adulthood, and larval mortality, should be better determined empirically. From these key processes, abstractions including quantitative models (Eckman 1996) and syllogisms should be created. With a reduced set of better-determined processes, researchers may be better able to tackle the complex but important problem of recruitment.

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