



Causes of decoupling between larval supply and settlement and consequences for understanding recruitment and population connectivity

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ABSTRACT

Marine broadcast spawners have two-phase life cycles, with pelagic larvae and benthic adults. Larval supply and settlement link these two phases and are crucial for the persistence of marine populations. Mainly due to the complexity in sampling larval supply accurately, many researchers use settlement as a proxy for larval supply. Larval supply is a constraining variable for settlement because, without larval supply, there is no settlement. Larval supply and settlement may not be well correlated, however, and settlement may not consistently estimate larval supply.

This paper explores the argument that larval supply (i.e., larval abundance near settlement sites) may not relate linearly to settlement. We review the relationship between larval supply and settlement, from estimates and biases in larval supply sampling, to non-behavioral and behavioral components, including small-scale hydrodynamics, competency, gregarious behavior, intensification of settlement, lunar periodicity, predation and cannibalism. Physical and structural processes coupled with behavior, such as small-scale hydrodynamics and intensification of settlement, sometimes result in under- or overestimation of larval supply, where it is predicted from a linear relationship with settlement. Although settlement is a function of larval supply, spatial and temporal processes interact with larval behavior to distort the relationship between larval supply and settlement, and when these distortions act consistently in time and space, they cause biased estimates of larval supply from settlement data.

Most of the examples discussed here suggest that behavior is the main source of the decoupling between larval supply and settlement because larval behavior affects the vertical distribution of larvae, the response of larvae to hydrodynamics, intensification of settlement, gregariousness, predation and cannibalism. Thus, larval behavior seems to limit broad generalizations on the regulation of settlement by larval supply. Knowledge of the relationship is further hindered by the lack of a well founded theoretical relationship between the two variables. The larval supply–settlement transition may have strong general consequences for population connectivity, since larval supply is a result of larval transport, and settlement constrains recruitment. Thus, measuring larval supply and settlement effectively allows more accurate quantification and understanding of larval transport, recruitment and population connectivity.

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1. Introduction

Most bottom dwelling marine invertebrates produce pelagic larvae that disperse. The number of young recruiting to a local adult population may be uncorrelated to local reproductive effort. In benthic communities, the number of larvae settling and recruiting into the adult population may determine not only changes through time, but also how species interact. Researchers have appreciated the role of new recruits in population processes for a long time (e.g., Hjort, 1926; Hatton, 1938; Thorson, 1946; Ayers, 1956; Barnes, 1956; Loosanoff, 1964; Yoshioka, 1982). In the 1980's there was increased attention on the role of larval input on rocky shore community dynamics (Roughgarden et al., 1985), baptized "supply-side ecology" by Lewin, (Lewin, 1986; J. Roughgarden, pers. com.), a science journalist. The work by Roughgarden and colleagues catalyzed gestating interest (e.g., Lewis, 1977; Denley and Underwood, 1979; Underwood, 1979; Yoshioka, 1982; Underwood and Denley, 1984) and generated some controversy, and arguably, influenced the nature of current field work in benthic community ecology, from an emphasis in biological interactions and disturbance, to an emphasis on larval processes, particularly larval transport, in determining community structure. Moreover, this literature renewed interest on larval processes influencing population dynamics, a longstanding topic in benthic ecology (e.g., Underwood and Fairweather, 1989). Recently, larval dispersal and input into local and remote habitats have been considered in the context of population connectivity (Roberts, 1997), an important process in metapopulation dynamics, genetic diversity and fisheries management, including management through Marine Protected Areas (Cowen et al., 2007). Whereas larval dispersal is the spread of larvae from spawning grounds to a settlement location, reproductive population connectivity consists of dispersal of pelagic larvae among metapopulations and survival to reproduction of the benthic recruits (Pineda et al., 2007).

Understanding the role of new propagules on population dynamics, community structure, and population connectivity requires accurate estimates of larval supply. Recently, "larval supply" has been used broadly to describe abundance of available propagules. Operationally, researchers have measured larval supply as the number of planktonic larvae available near settlement sites (e.g., Minchinton and Scheibling, 1991; Bertness et al., 1992; Miron et al., 1995; Sponaugle and Cowen, 1996; Noda et al., 1998; Jeffery and Underwood, 2000; Doherty et al., 2004; Jonsson et al., 2004; Todd et al., 2006; Beaulieu et al., 2009), and we use this definition here. Researchers have used other terminology to refer to these available larvae (e.g., Porri et al., 2006).

For sessile species such as barnacles, per area settlement can be defined as the number of attached larvae N per unit area per time interval, $N \text{ area}^{-1} \text{ time}^{-1}$. Recruitment, a fisheries concept commonly used in the benthic literature, is generally defined as the number of settled individuals that survive after an arbitrary period of time per unit area. Although settlement and recruitment are straightforwardly defined, they are often confused (see Connell, 1985 for definitions and discussion). It is possible to measure settlement of sessile species over short time intervals with little error, because settlers accumulate on a given substrate area and do not move afterwards, although mortality shortly after settlement is great (Gosselin and Qian, 1996). There is some consensus that daily sampling of settlement is a good compromise between logistical difficulty and accuracy of estimate (Connell, 1985), but some researchers have sampled every semidiurnal tide (12.4 h, Wetthey, 1986; Cruz et al., 2005; Jacinto and Cruz,

2008), and automated sampling devices can sample for even shorter intervals (Whitlatch and Osman, 1998).

Estimating larval supply is more challenging than estimating settlement because planktonic larval abundance is notoriously variable in time and space (see "Quantifying larval supply"). Thus, many studies have used settlement and recruitment as proxies for larval supply. While larval supply is a constraining variable for settlement, since larval supply sets the lower bounds for settlement (that is, with zero supply there is no settlement), and settlement is more convenient to measure than larval supply, various processes can produce a lack of correlation between settlement and larval supply. This lack of correlation leads to misidentification of larval transport and dispersal processes and misjudgment of the relative importance of pre- versus post-settlement processes in influencing population and community processes (Pineda, 2000, for discussion). While in some studies settlement and larval supply appear to be correlated (Minchinton and Scheibling, 1991; Yund et al., 1991; Hurlbut, 1992; Jeffery and Underwood, 2000; Ross, 2001; Ma, 2005), other studies find no correlation (Miron et al., 1995; Olivier et al., 2000; Porri et al., 2006; Rilov et al., 2008), suggesting caution in interpreting settlement as proxy for larval supply.

The relationship between larval supply and settlement has been reported in various ways, including (1) qualitatively (e.g., Pineda et al., 2002), (2) as a regression of settlement or recruitment as function of larval abundance (e.g., Yoshioka, 1982; Noda et al., 1998), and more commonly, (3) as a parametric correlation coefficient between these two variables (e.g., Minchinton and Scheibling, 1991; Yund et al., 1991). The relationship has been depicted as time series plots of settlement or recruitment and larval concentration (e.g., Yoshioka, 1982), and as plots of settlement or recruitment as function of larval supply (Yund et al., 1991; Todd et al., 2006). Larval supply and settlement may correlate well, but in some sites and times settlement measured on experimental substrates may over- or underestimate supply relative to that in other locations and periods.

Other than potential scaling when values are reported as concentration for supply (cm^{-3}) and density for settlement, (cm^{-2}), it appears that there are no empirically well-justified theoretical expectations about the relationship between these two variables, at least for larvae with active settlement behavior. That is, how many of the larvae near settlement sites are expected to settle per unit area? What is the settlement to larval supply ratio? In early supply-side ecology models (Roughgarden and Iwasa, 1986), settlement per unit area of free space was assumed to be proportional to larval supply. More pragmatically, some researchers have suggested that settlement ought to be directly proportional to the period of submersion of the settlement substrate in intertidal locations (implying a directly-proportional relationship between larval supply and settlement), and settlement results have been standardized by period of submersion, but as Hatton discovered more than 70 years ago, there is no such proportionality (Hatton, 1938). Direct proportionality between submersion period and settlement implies no patchiness in the planktonic larval distribution, and that larvae act like passive particles, two assumptions that are often false. For example, Hills et al. (1998) found that settling cyprids responded quickly to settlement cues, implying that settlement would not be proportional to submersion period. While submersion period ultimately determines whether larvae can settle, it is likely that this constraint operates almost exclusively for very short submersion periods (see also Pineda, 2000 for discussion). In general, the lack of a well founded theoretical expectation of the relationship between larval supply and settlement makes field results difficult to interpret and compare.

Here we further identify and discuss the challenges in estimating larval supply and settlement, and the processes that should be considered when estimating these two variables. We discuss methods to estimate larval supply and potential biases in estimation. We review factors that influence the relationship between larval supply and settlement, highlighting cases where nonlinearities arise. Factors considered include competency, gregarious settlement, suitable area of substrate and intensification of settlement, larval predation and cannibalism, and hydrodynamics. Several of these processes involve behavior, but, for convenience, we discuss them separately. We also discuss the consequences of the decoupling between supply and settlement for understanding population connectivity. This review concentrates on invertebrates in general and barnacles in particular, with some examples about fish.

2. Factors influencing the correlation between larval supply and settlement

2.1. Quantifying larval supply

Applied ecologists have been interested in the empirical relationship between larval supply and settlement for years in part because, "...sets are heaviest in localities where the larvae had been most abundant" (quote from a misidentified source in [Korringa, 1941](#); see also [De Wolf, 1973](#)). Recent interest in estimating larval supply and settlement, as outlined in the "Introduction", is to gain understanding of how larval input modulates population and community processes. More pragmatically, current research seeks to define whether settlement and larval supply are correlated, and, specifically, whether settlement can be used as a proxy for larval supply. If so, predictions about the distribution and abundance of larvae near settlement sites can be made from settlement.

Larval supply has been measured discretely in time with plankton nets and pumps which sample water for a small proportion of time relative to the length of the settlement sampling interval, but water is in contact with the benthic settlement substrate for a much longer period (2 h of sampling, daily to every few days, [Bushek, 1988](#); [Minchinton and Scheibling, 1991](#); [Noda et al., 1998](#); [Olivier et al., 2000](#); [Satumanatpan and Keough, 2001](#); [Palma et al., 2006](#); [Porri et al., 2006](#)). Larval supply has also been measured at higher frequency with pumps, from discrete samples taken every 2–4 h for 1 day or daily for two weeks ([Hurlbut, 1992](#); [Ma, 2005](#)), to 1 to 60 samples per hour for up to a few days ([Pyefinch, 1949](#); [De Wolf, 1973](#); [Grosberg, 1982](#)). In addition to discrete sampling, researchers have sampled larval supply by integrating larval counts over long periods with (a) pumps (8–24 h samples, [Yoshioka, 1982](#)), (b) nets, including nets on reef crests, and at the entrance of semi-enclosed bodies of water ([Eggleston and Armstrong, 1995](#); [Moksnes and Wennhage, 2001](#); [Doherty et al., 2004](#); [Queiroga et al., 2006](#)), and (c) larval traps, including light traps ([Doherty, 1987](#); [Sponaugle and Cowen, 1996](#); [Reyns and Sponaugle, 1999](#)), and passive trapping devices ([Otaíza, 1989](#); [Yund et al., 1991](#); [Jeffery and Underwood, 2000](#); [Castilla et al., 2001](#); [Metaxas, 2001](#); [Yan et al., 2004](#); [Todd et al., 2006](#); [Rilov et al., 2008](#); [Dudas et al., 2009](#)). Debate over the methods used to sample pelagic larvae of benthic invertebrates started early, with the realization that, like other zooplankton (e.g., [Haury et al., 1978](#)), larval distributions are patchy ([Barnes and Marshall, 1951](#); [Cassie, 1957, 1959](#); [Natunewicz and Epifanio, 2001](#)). Furthermore, evasive behavior of some larvae, particularly crustaceans, was also recognized as a source of sampling bias (e.g., [Korringa, 1941](#); [De Wolf, 1973](#); [Singarajah, 1975](#); [Doherty and Butman, 1990](#)). These issues are still relevant when estimating larval supply.

Given planktonic patchiness and that settlement is the accumulation of benthic individuals over an area and time, discrete pump and net samples taken for a small fraction of time relative to the settlement measurement interval may not estimate accurately overall larval abundance ([Otaíza, 1989](#); [Yund et al., 1991](#); [Gaines and Bertness, 1993](#);

[Miron et al., 1995](#)). Some researchers sampling discretely and infrequently have, however, found some correlation between larval supply and settlement (e.g., [Minchinton and Scheibling, 1991](#); [Pineda et al., 2002](#)). These positive relationships suggest that larval patches are very large, and therefore, larval abundance is sampled well with discrete samples at a fixed point. Patchiness of pelagic zooplankton is thought to be a function of behavioral and hydrodynamic processes. Patches determined by purely behavioral processes have been reported in the ocean (e.g., [Haury and Wiebe, 1982](#)), and behavior interacting with hydrodynamics also results in patches, such as patches formed in ocean convergences where frontal and internal wave circulation interact with planktonic behavior (e.g., [Le Fèvre, 1986](#)). Seasonal layering of the coastal ocean, causing stratification of temperature, also enhances patchiness of plankton ([Haury et al., 1978](#); [Gallager et al., 2004](#); [Woodson et al., 2005](#)), and the onshore advection of offshore stratified water parcels produces nearshore horizontal heterogeneity in larval distribution (e.g., [Pineda, 1994b](#); [Leichter et al., 2005](#)). More stratification should result in more patchiness and therefore in more decoupling between settlement and discrete estimates of larval supply, a hypothesis that has never been tested.

Sampling devices such as stationary nets and passive larval traps that integrate over settlement sampling interval are appealing. Stationary nets on top of reef crests appear ideal for larvae settling on reef lagoons, because the net samples the entire water-column, mass transport is unidirectional (from the offshore larval pool to the adult lagoon habitat), and the period to be sampled is constrained for larval fish that cross the reef crest only at night ([Doherty and McIlwain, 1996](#)). Moreover, in some reef lagoons, almost all flow into the reef lagoon (forced by wind and waves) tends to pass on top of the reef crest, with only occasional inshore flows in the lagoon's channels ([Coronado et al., 2007](#)). Although channel nets may not fish over the entire water-column, they perform well in energetic flood tidal currents ([Eggleston and Armstrong, 1995](#)).

Researchers have used light traps to capture crab larvae, and numbers caught are interpreted as a proxy for larval settlement ([Reyns and Sponaugle, 1999](#)). Inspired by intuition ([Otaíza, 1989](#)) and by devices estimating sediment vertical flux ([Yund et al., 1991](#)), researchers have proposed passive larval traps to estimate integrated larval abundance near settlement sites (see also [Jeffery and Underwood, 2000](#); [Castilla et al., 2001](#); [Todd et al., 2006](#)). While generally positive linear relationships between settlement and number of trapped larvae are encouraging ([Yund et al., 1991](#); [Todd et al., 2006](#)) some comparisons of passive traps with other discrete and integrative measurements have found little or no correlation ([Rilov et al., 2008](#); [Beaulieu et al., 2009](#); [Dudas et al., 2009](#); see also [Todd et al., 2006](#)).

Some researchers have argued that larval supply should be measured as larval flux instead of concentration. It has also been argued that open-ended larval tubes can measure horizontal larval flux ([Yund et al., 1991](#); [Gaines and Bertness, 1993](#); [Todd, 2003](#)), similar to the way particle flux is measured from particle concentration and current velocity in manmade channels. Estimating larval flux in enclosed lagoons appears straightforward (e.g., [Doherty et al., 2004](#)), but estimating absolute horizontal larval flux near settlement sites with open-ended tubes traditionally designed to estimate vertical sedimentation flux may be problematic. First, traps can be biased samplers depending on their shape and opening size ([Butman, 1986](#)). Second, nets on reef crests are effective for measuring the time-averaged flux because mass transport is unidirectional and fixed nets only sample larvae going into the adult benthic habitat. On the other hand, in environments with oscillatory flows, such as the intertidal and shallow subtidal areas where wave-induced orbital motions are frequent, and multidirectional tidal currents the norm, open-ended traps would capture the larvae going towards, and away from the adult habitat, without differentiation. Few researchers have partitioned the in and out flux of larvae (e.g. [Moksnes and Wennhage,](#)

2001, using fixed trapping nets). Moreover, ecologists sometimes use weight loss of a soft substance such as plaster or chalk as a proxy for current speed in flux estimates. In sites with current reversals, current speed derived from weight loss of substances may overestimate the actual flux towards the benthic habitat because erosion would be influenced by oscillatory flows in all horizontal and vertical directions. Finally, but very importantly, when larval flux is taken as an estimate of larval supply, larval supply and settlement may not be linearly related. At zero velocity and in very fast currents, larvae may not be available or able to settle, and therefore settlement may be non-linearly related to larval supply (e.g., Pawlik and Butman, 1993; Qian et al., 2000; Larsson and Jonsson, 2006; see also Jonsson et al., 2004, for discussion). Indeed, researchers have observed less settlement in field sites with faster flow (Todd, 1998), while others found decreased contact with the substrate by larvae at increasing speed of flow (Jonsson et al., 2004). The effects of fast currents on settlement may be dependent on the specific abilities of the larvae to attach in a turbulent environment. At one end, it may increase turbulence and contact rate near the bottom, potentially enhancing settlement, but it may also increase resuspension, resulting in a reduction of settlement (see review in Koehl, 2007). Moreover, settlement in flow may relate to behavioral processes that supersede purely hydrodynamic arguments: larvae may choose to settle in moderate speed flows due to suboptimal feeding conditions for juveniles in fast flows (Larsson and Jonsson, 2006).

2.2. Hydrodynamics

The role of large-scale to microscale hydrodynamic processes on delivery, larval supply and settlement has been investigated for over five decades (e.g., Crisp, 1955). Coarse- to large-scale hydrodynamic features (10 to 100s km, sensu Haury et al., 1978) such as downwelling, relaxation events, internal tidal bores, and wind driven currents influence transport and larval supply of benthic invertebrate taxa (e.g., Bennell, 1981; Hawkins and Hartnoll, 1982; Farrell et al., 1991; Pineda, 1991; Poulin et al., 2002). The effects of coarse- to large-scale hydrodynamics on larval supply have been inferred from measurements of larval concentrations and time series of physical measurements that characterize the hydrodynamic processes (e.g., Garland et al., 2002; Shanks and Brink, 2005). In other studies, coarse- to large-scale hydrodynamic processes are correlated to time series of larval settlement, but larval concentrations in the water are not measured (e.g., Bertness et al., 1996; Jacinto and Cruz, 2008). Some studies have measured both larval concentrations and settlement (e.g., Jeffery and Underwood, 2000; Ma, 2005; Porri et al., 2006; Dudas et al., 2009), and recruitment (e.g., Palma et al., 2006; Rilov et al., 2008), to determine the relationship with hydrodynamics. Modelers have also explored the relationship between large-scale hydrodynamics, larval supply and settlement (e.g., Alexander and Roughgarden, 1996; Guizien et al., 2006; Ayata et al., 2009). It has been argued that, ultimately, coarse- to large-scale processes that bring larvae to shore may be more important to determining settlement than smaller scale processes because large-scale processes affect whether larvae are supplied near settlement sites. That is, larger scale processes constrain smaller scale processes (Pineda, 2000). Nevertheless, smaller scale hydrodynamic processes, including advection by surface gravity waves and turbulent mixing in the bottom boundary layer influence larval delivery to the settlement site, contact to the bottom substrate, attachment (e.g., Koehl, 2007; Reidenbach et al., 2009) and post-settlement mobility (e.g., Moksnes and Wennhage, 2001).

As larvae are transported from offshore waters to within 10–100's m of the shore, delivery of larvae to the bottom will be influenced by hydrodynamic forces such as surface gravity waves, through oscillatory flows, shoaling and breaking, and wave induced along-shore and cross-shore flows (e.g., Miller and Emler, 1997; Porri et al., 2006; Rilov et al., 2008; Dudas et al., 2009). A relationship

between larval supply and settlement is most likely to be detected when larval supply is measured within a few meters or less of the settlement substrate (e.g., Otaiza, 1989; Jeffery and Underwood, 2000; Todd et al., 2006; Tremblay et al., 2007). At these finer spatial scales, flow velocities and substrate characteristics, which determine the boundary layer, turbulent flows, and shear stress, will affect whether larvae attach or are re-suspended from a substrate (Koehl, 2007). For example, turbulence increases the settling of negatively buoyant phytoplankton cells (Ruiz et al., 2004), and some larvae use sinking behavior to promote settlement in turbulent flows (Fuchs et al., 2004). In fast flows with high turbulence, contact rate of larvae increases, resulting in higher settlement than in still water or in low flow conditions, whereas above certain flow speeds larvae are not able to make contact or adhere (e.g., Eckman et al., 1990; Pawlik and Butman, 1993; Qian et al., 2000; Pernet et al., 2003). Some species are stimulated by flow or shear to attach to surfaces (Crisp, 1955). For example, cyprids attach to pipette glass walls the moment flow starts.

Instantaneous stress events caused by wave driven flows may be a better predictor of larval settlement than mean stress (Crimaldi et al., 2002). Wave driven flows result in instantaneous high turbulent flow that increase shear stress and reduce the thickness of the viscous sublayer (Koehl, 2007). In these conditions, larval settlement probability will be highest if larvae settle quickly and adhere. Roughness elements enhance instantaneous turbulent flows that will result in decreased probability of settlement on surfaces such as corals (Reidenbach et al., 2009). Variability in roughness, however, creates microhabitats with reduced shear stress. In microhabitats such as rough subtidal surfaces (Walters, 1992) or within coral reefs (Reidenbach et al., 2009), and clam beds (Crimaldi et al., 2002), larvae will have longer contact times and have a greater opportunity to settle. Natural patchiness of roughness elements will result in greater variability in instantaneous stresses and events, and this may translate to greater variability in larval settlement.

Fine-scale hydrodynamics over settlement surfaces continually change over time, since settling larvae change the roughness elements of the substrate by creating more pits, peaks, and grooves that are experienced by subsequent settlers. If larvae settle more on substrates with pits and grooves, one could speculate that larval settlement rate may be greater on plates with high settlement than on plates with low settlement, as roughness increases with settlement (see Thomason et al., 1998 for effects of adult barnacles on flows). On the other hand, the type and spacing of roughness elements could decrease the chance of contact or attachment if turbulence is increased (Crimaldi et al., 2002). Larval response to fine-scale hydrodynamics in concert with a positive response to conspecific or other chemical cues could be predictors of a settlement increase.

In addition to the turbulence larvae experience in nature, larvae will experience hydrodynamic forces associated with collectors used to sample them, and this can affect the accuracy and reliability of larval supply and settlement estimates. Ideally, larval collectors and artificial substrates should minimize disturbance to the natural flow so that larvae approaching the collecting device are not carried away or attracted in a way to reduce or increase collection efficiency in an artificial way. Pumps have been designed to minimize flow disturbance in some field conditions (Doherty and Butman, 1990; Snelgrove et al., 1999), but it is difficult to evaluate the hydrodynamic effect of collectors in the field. Evaluations of sediment collectors (e.g., Hargrave and Burns, 1979; Black and Rosenberg, 1994) will not necessarily apply to larval collectors since they do not account for larval behavior in the presence of turbulence. To measure settlement and compare relative settlement measurements across sites, researchers use artificial substrates (e.g. tiles, grooved PVC plates, plates with non-skid surface, artificial turf, scouring pads) to reduce the confounding effects of natural substrate variability resulting from small-scale hydrodynamic factors. Size, shape, and surface texture of the substrate will affect larval settlement (Rittschof et al., 2007) since

these factors have direct effects on turbulence, and thus the bottom boundary layer (Mullineaux and Butman, 1991; Snelgrove, 1994; Field et al., 2007; Koehl, 2007).

Hydrodynamic conditions on settlement collectors will depend on location of collectors within a site. In the rocky intertidal, placement choices that will differ in delivery of larval and settlement, include vertical or horizontal surfaces, degree of exposure to waves, and tidal height (Porri et al., 2007, 2008b). These differences, however, are sometimes smoothed out by settlement larval behavior (Pineda, 1994a). Another approach has been to place settlement substrates on mooring lines (e.g., Dobrestov and Miron, 2001; Rilov et al., 2008; Dudas et al., 2009). Comparison of hydrodynamics on fixed versus moving settlement substrates has not been made although increased biomass of barnacles on rotating panels compared to fixed panels was attributed to differences in water flow (Glasby, 2001). It seems possible that coupling or decoupling of larval supply and settlement could be confounded with the effects of hydrodynamics on collectors, but this has yet to be shown.

In summary, hydrodynamics plays a role in determining larval supply and settlement, but identifying the hydrodynamics forces that result in decoupling between supply and settlement is difficult except, perhaps, in extremely high flows over surfaces on which larvae cannot attach and are re-suspended. Coarse- to large-scale hydrodynamic processes influence the rate of arrival of larvae to the shore, but fine-scale processes influence the precise location of contact with the substrate. Settlement response to local hydrodynamic forces is not likely to be linear. The methods we use to assess larval supply and settlement alter fine-scale hydrodynamics, and the consequences of these alterations are difficult to predict in the highly turbulent oscillatory flows that are characteristic of many shallow water environments. Although a sample taken to estimate settlement integrates over small-scale temporal variability, localized variability resulting from instantaneous changes in near-bed turbulence may reduce the reliability of estimates of settlement rate among replicate samples. Hence, delivery of larvae to the shore and larval settlement will be a consequence of the behavioral (directional swimming, sinking, active habitat selection, adhesiveness) or passive response of larvae interacting with hydrodynamics forces at multiple spatial and temporal scales. More importantly, larval response to the hydrodynamic forces they encounter will be mediated by biochemical (e.g., settlement inducers, presence of conspecifics, biofilms) and physical factors (e.g., light), biological interactions (e.g., cannibalism), and larval physiology (age, competency, energy reserves) (Olivier et al., 2000; Qian et al., 2000; Marshall and Keough, 2003; Koehl et al., 2007; Tremblay et al., 2007).

2.3. Competency

The proportion of competent to non competent larvae in larval samples may obscure a supply–settlement relationship (Miron et al., 1995; Rilov et al., 2008). Competency can be defined as “the capacity of a developing individual to initiate settlement and complete morphogenic transformation associated with metamorphosis” (Bishop et al., 2006). Competent larvae can also include those larvae that delay metamorphosis although they are developmentally ready to metamorphose (Swanson et al., 2007). We would expect that larval settlement would be more tightly coupled with supply of competent larvae than to a mixture including non-competent larval stages. Depending on the species, and the method and location of collection, samples of a species may be a combination of competent and non competent larvae. For example, vertical plankton net samples taken through the water-column are likely to obtain both types of larvae, while intertidal plankton traps (Castilla et al., 2001) should gather more competent larvae, since they are more likely to be positioned close to the adult habitat. If larvae become competent only near the adult habitat (e.g., crabs, Moreira et al., 2007; corals, Gilmour et al.,

2009), plankton samples taken away from the habitat may contain predominantly non-competent larvae. If competent and non-competent larvae can be distinguished, vertical location and method of collection can be improved to obtain better estimates of competent larval supply.

In some species, competency can be determined by morphological characters (e.g., tube feet in sea urchins, Swanson et al., 2004), physiological changes (buoyancy loss in corals Gilmour et al., 2009) and behavioral changes (e.g., swimming or sinking rate changes, Mann et al., 1991). In many species, (e.g., mussels, Rilov et al., 2008) competency must be assessed by testing whether larvae settle in the laboratory, although size has also been used as proxy (e.g., Porri et al., 2006). Sampling coral from different water depths in the field and testing whether larvae would settle in the laboratory, Gilmour et al. (2009) determined that competent larvae are found near the bottom. The precompetent period for corals was around 3 days. Precompetent period in other spawning coral is 2–4 days (Miller and Mundy, 2003).

Barnacle larvae are not all competent upon metamorphosis to the cyprid stage. Laboratory settlement experiments with *Balanus amphitrite* suggests that cyprid larvae are precompetent for up to three days after metamorphosis to a cyprid (Rittschof et al., 1984; Satuito et al., 1996) and up to two days after metamorphosis for cyprid larvae of *Balanus improvisus* (Zega et al., 2007). Vertical distribution of barnacle cyprid larvae with respect to competency is not known, but vertical distribution of cyprid larvae can differ between nearshore and offshore stations (Dudas et al., 2009). In Southern California, cyprid larvae of *Chthamalus* spp. are found near the adult intertidal habitat, while late-stage nauplii are found farther offshore (Tapia and Pineda, 2007). Because the position of larvae in the water-column may affect onshore delivery and subsequent settlement (Pineda, 2000, for discussion), researchers assessing larval supply should consider whether competent larvae are being sampled and what is the appropriate vertical location in the water-column for sampling them.

2.4. Gregarious settlement

Larvae of marine invertebrates can sense features of the environment and react in a pre-determined fashion. For example, a variety of cues induce larval settlement, including chemical, mechanical, hydrodynamic or biotic stimuli from the environment (Crisp, 1974). Therefore, larval settlement might be a quite ordered process in an apparently unstructured environment because larvae exhibit larval settlement behaviors.

The discovery of gregarious settlement in intertidal barnacles stimulated research on the proximate causes of larval behavior and its applicability in natural settings. Gregariousness in intertidal barnacles was first reported in field populations of *Elminius modestus* (Knight-Jones and Stevenson, 1950). A conspecific cue was identified and chemically characterized (Knight-Jones, 1953; Crisp and Meadows, 1962, 1963). Extracted from adult barnacles, this cue could be applied to experimental substrates to demonstrate its influence in settlement induction in the laboratory and in the wild (Larman and Gabbott, 1975; Jarrett, 1997). These discoveries allowed subsequent researchers to examine the role of the conspecific cue in natural settings. Field experiments show that larval settlement behavior is selective (Miron et al., 1996) and sensitive (Kent et al., 2003) to the cues produced by conspecific adults.

The broader ecological significance of settlement in response to conspecific cues can be demonstrated in two ways. First, multiple taxa may respond to conspecific cues. For example, gregariousness has been reported for some taxa (oysters, Crisp, 1967; Bayne, 1969; polychaetes, Knight-Jones, 1951; Scheltema et al., 1981). Second, larval settlement behavior may mediate the distribution and timing of settlement. For example, it may account for differential settlement determining the adult distribution within a shore (Raimondi, 1991;

Blythe and Pineda, 2009), and the distribution among shores (Jenkins, 2005). Field studies have also elucidated the influence of larval settlement behavior on timing of settlement (Bertness et al., 1992).

Attempts to quantify larval supply should explicitly take into account larval settlement behavior when measuring settlement variability in the field, as settlement may vary in response to conspecific cues. Controlling the concentration of a cue is complicated, because we do not completely understand the various sources of the conspecific cue and how the cue affects the behavior of larval barnacles in various natural settings. For example, contact with live adults may not be the only way a conspecific cue could influence barnacle settlement in the wild. Cyprids leave conspecific cues on surfaces when adhesive proteins are secreted from their antennules during exploration of the substrate (Yule and Walker, 1985; Clare et al., 1994). Fine-scale observations on distribution of cyprids suggest that they aggregate (Wetthey, 1984), which could be a response to secretions from the antennules or another source of conspecific cues. Juvenile barnacles may induce settlement (Knight-Jones, 1953), though it is unclear how common this is in the field (Wetthey, 1984; Jeffery, 2002). Additionally, adults that are removed from laboratory (Knight-Jones, 1953; Crisp, 1961) or natural (Minchinton and Scheibling, 1993; Miron et al., 1999) substrates leave behind conspecific cues, but these are apparently short-lived (Wetthey, 1984). Therefore, the loss of juveniles and adults due to natural disturbances could result in conspecific cues left on the disturbed surfaces. These cues could facilitate settlement and result in enhanced colonization. These observations continue to stimulate research on how the conspecific cue induces barnacle settlement and affects spatial and temporal variability in recruitment.

The largest spatial scale at which settlement behavior influences settlement is difficult to address empirically. Larval settlement behavior implicitly specifies a spatial scale that spans the distance at which a cue signal is produced and received by the larval sensory apparatus, and the subsequent responses by larvae to the cue. In intertidal barnacles, larvae respond immediately or a short time after direct contact with the conspecific cue. Therefore, the spatial scale is on the order of centimeters that a cyprid may explore a benthic habitat, before resuming its search for habitat by returning to the plankton, or adhering to the substrate (Knight-Jones, 1953; Crisp and Meadows, 1962). Before selecting a precise site for settlement, larvae exhibit even smaller-scale behavior, rocking back and forth to “test” the suitability of the settlement site (Crisp, 1961). Small-scale larval settlement behavior has, however, been implied in much larger scale ecological phenomena, like the aggregation of larvae between locations separated by more than several meters (Berntsson et al., 2004). Larval settlement behavior may also have consequences for settlement variability on geographic scales, since different cues may induce metamorphosis across a species’ range (Strathmann et al., 1981). Inter-habitat patterns result primarily from the absence of cues on the substrate preventing any proximally located larvae from completing metamorphosis. Paradoxically, the consequences of larval settlement behavior at the largest spatial scales might result from a lack of induction of settlement (for example, in the absence of conspecific cues). Complex processes, including larval transport (Kingsford et al., 2002) and optimal behavioral variability (Raimondi and Keough, 1990; Stamps et al., 2005; Toonen and Tyre, 2007), may, instead, determine patterns of settlement at these larger scales.

The argument that larval behavior modulates larval supply, influencing settlement distribution, is well supported by the literature on gregarious settlement presented here. Larval settlement behavior is particularly interesting because behavioral interventions at this stage have the greatest potential to carry over to juvenile and adult stages of the life cycle (Giménez, 2004; Blythe and Pineda, 2009). However, the spatial scales of influence of conspecific cues may be quite limited. It is an open question what are the impacts of the conspecific cues on the distribution of juvenile and adult barnacles,

and whether similar processes apply to other marine invertebrates (Porri et al., 2007). Finally, it is intriguing to speculate whether gregarious larval settlement behavior could influence connectivity of benthic invertebrate populations.

2.5. Suitable area of substrate and intensification of settlement

Imagine that sea-breeze driven circulation transports barnacle larvae onshore ready to settle, exactly half to site A, a sandy shore with only a few uncovered rocks and little free space for larvae to settle, and the other half to site B, a rocky shore with abundant habitat to settle (i.e., abundant such that settlement does not saturate all habitat in B). Researcher “Nve” wants to test the hypothesis that an approximately equal number of larvae are transported to sites A and B by the circulation caused by the sea-breeze. Researcher Nve has read several papers where larval supply is inferred from settlement data, so to test this hypothesis, replicated tiles are fixed to the substrate in each site. Every day at low tide, tiles are replaced with new ones, and settled larvae counted. Many larvae settle in each locality and numbers vary with time, but Nve is surprised to find consistently more settlers at site A. Nve concludes erroneously that the hypothesis being tested is false and considers an alternative hypothesis that involves different supply of larvae at the two locations. His conclusion is, however, incorrect because similar numbers are brought to each location by the circulation generated by the sea-breeze. If competent cyprid larvae act like passive particles, the number of cyprids contacting the tiles in each site would be about the same. Where larvae “behave” and search for substrate on which to settle, more would settle on tiles at site A because less natural substrate is available for settlement. So, searching larvae must settle more intensively per unit area available (Pineda, 1994a; Pineda and Caswell, 1997).

Intensification of settlement has been discussed by Pineda (2000). Field and laboratory research supports that settlement of barnacles and mussels intensifies where there is less area of suitable substrate (Bertness et al., 1992; Pineda, 1994a; Osman and Whitlatch, 1995a; Hunt and Scheibling, 1996; Pineda and Caswell, 1997; Berntsson et al., 2004; Rilov et al., 2008). No evidence of intensification was found, however, where adult density was low and settlement sparse (Jeffery, 2000). In addition to responding to the availability of suitable substrate, settlers respond to other stimuli, such as the presence of other settlers (Crisp, 1974) and potential mates. Therefore, cyprid larvae may respond to free suitable substrate by increasing their settlement only in sites where density of potential mates is large, and there is little free suitable substrate (see also Kent et al., 2003).

Thus, in sites with small numbers of barnacles and abundant free space for settlement, there may be few settlers on settlement plates relative to larval supply because settlers do not find cues from conspecifics to settle nearby, and settlers have ample choice to settle in adjacent areas. In these sites, settlement may underestimate larval supply. In sites with large numbers of barnacles, and little free space, settlement may intensify. In these sites, settlement may overestimate larval supply. Suitable substrate in a site can vary seasonally and at scales from 10s of m (Pineda, 1994a) to 10s of km (pers. obs. JP, see also Rilov et al., 2008). Thus, in some circumstances, particularly in areas with great adult density and high settlement, settlement may overestimate larval supply.

2.6. Lunar periodicity

Lunar periodicity in reproduction and settlement is a widespread phenomenon in coastal fish and invertebrates, and may be a factor in decoupling larval supply and settlement (e.g. for examples of lunar periodicity in reproduction see Korringa, 1947, and for lunar settlement see Sponaugle and Cowen, 1996; Reyns and Sponaugle, 1999; Jacinto and Cruz, 2008). Fortnightly (spring to neap) settlement

variability in coastal lagoons may be related larval transport, since tidal currents can be energetic in lagoon channels, and more mass transport is expected in spring tides. However, in more open coastal environments, onshore tidal currents are generally weak, and are unlikely to always explain lunar patterns in settlement. Further, tidal larval transport does not parsimoniously explain why different invertebrate taxa peak at different phases of the moon (e.g., [Reyns and Sponaugle, 1999](#)). We speculate that larval settlement in some lunar phases could be related to a behavioral response to some tidally related cue (see also [Wetthey, 1986](#); [Reyns and Sponaugle, 1999](#) for discussion). Little is known of behaviorally induced lunar settlement patterns in barnacles, however, and this hypothesis has been considered implausible ([Pineda, 2000](#), p.95). Nonetheless, we speculate that it could potentially influence the relationship between larval supply and settlement for some species when available larvae settle disproportionately at some phase of the moon (e.g. larvae near settlement sites settling preferentially at certain time).

2.7. Larval predation

Ecological interactions and environmental variables can determine community structure through a complex network of species connections ([Menge and Sutherland, 1987](#); [Polis and Strong, 1996](#)). Understanding the dynamics and scales of these interactions is therefore essential to discover and predict patterns in community ecology ([Leibold et al., 2004](#)). Although greatly debated, local processes may also be important in explaining metapopulation and regional variability ([Lawton, 1999](#); [Simberloff, 2004](#)). Local disturbance, in conjunction with recovery patterns, can drive regional variability and dynamics in marine metapopulations ([Gouhier and Guchard, 2007](#)). Predation can act as a local disturbance that has the potential to govern local population dynamics of benthic systems with larger scale repercussions. While predation on post-settlement stages and its critical contribution to community dynamics have been documented for several taxa ([Osman and Whitlatch, 1995a](#); [David et al., 1997](#); [Osman and Whitlatch, 2004](#)), the effect of planktonic (pre-settlement) predation on shallow water benthic population dynamics is not often recognized ([Woodin, 1976](#); [Osman and Whitlatch, 1995a](#); [Doherty et al., 2004](#)). Predation on pelagic larvae potentially mediates population structure through inhibition of settlement.

Predation on invertebrate larvae has been described for several species (reviewed in [Young and Gotelli, 1988](#)), but documenting its significance on regulation of recruitment in the field is difficult. Laboratory and field studies on ascidians show that planktonic mortality due to predation is variable with values of pre-settlers ranging between 18%, 50% and 87% ([Olson and McPherson, 1987](#); [Davis and Butler, 1989](#); [Stoner, 1990](#)). In a coral reef fish, pre-settlement mortality just a few hours before settlement was density-independent and about 61% of larvae died. Such great mortality due to predation has been interpreted as a potential bottleneck for reef fish populations, and suggested to be a reason for evolution of strategies to avoid predation, such as mass nocturnal onset of settlement ([Doherty et al., 2004](#)).

Other factors such as hydrodynamics may reduce the number of sessile organisms settling. For example, an alteration to the structural complexity of a habitat can affect the hydrodynamics at a settlement site and which may change settlement (see “Hydrodynamics” section). Empirical support for the effects of hydrodynamics on settlement is, however, not consistent and the effects of predation and hydrodynamics on sessile communities may be scale-dependent. [Holloway and Keough \(2002\)](#) found a 50% decrease of larvae of several invertebrate taxa under the canopy of an adult invasive fan worm. This pattern was explained by mechanical alteration of flow around the polychaetes, overruling predation at the scale of the experimental plates. At larger scales (pier pilings), predation was suggested to have an important effect on some taxa. Thus, the effect of

predation and hydrodynamics on sessile communities may be scale-dependent ([Holloway and Keough, 2002](#)).

The role of predation on population dynamics can be masked by variability in recruitment ([Young and Gotelli, 1988](#)) and in occupation of primary space by adults ([Osman and Whitlatch, 1995b](#)). Pre-settlement resistance and vulnerability to predators, is regulated by behavior ([Leis and Carson-Ewart, 2001](#); [Doherty et al., 2004](#)), larval morphology ([Morgan and Christy, 1996](#)), larval quality traits ([Giménez, 2004](#)) and chemical defense of early life stages ([Johnson and Strathmann, 1989](#); [Lindquist, 2002](#), for a review), with consequences for success of settlement. Chemical response varies strongly among species and is generally lacking among most meroplankton, with morphological and physical resistance often more common features than chemical defense itself ([Bullard et al., 1999](#)). Consequently, individual taxa should be considered separately when assessing the role of predation on the coupling between larval supply and settlement and on overall community assemblages.

Active selection of habitat during settlement and recruitment often dictates the initial distribution of juveniles ([Fernández et al., 1993](#); [Levin et al., 1997](#)), but the distribution of juveniles may be reinforced by predation. [Moksnes \(2002\)](#) found that predation of settlers was the greatest cause of mortality for shore crabs, regardless of the type of habitat (open sand and structurally complex refuges). Yet, this source of mortality did not have a significant effect on the initial distribution of the population. The stability and boundaries of dense, discrete infaunal assemblages may rely on larval mortality by adult ingestion ([Woodin, 1976](#)). In sedimentary systems, polychaete recruitment success may be limited by adults, through direct predation ([Ambrose, 1984](#)) and through physical disturbance ([Woodin, 1976](#)). Browsing on adults (which causes temporal damage of adult appendages) reverts this pattern and increases settlement of worms, even if only temporarily ([Lindsay et al., 1996](#)). The type of predator can interfere with population dynamics, since some predators only affect adults, while others impact recruits ([Lindsay et al., 1996](#)).

The effect of predation on assemblages depends on larval dispersal. Under low dispersal (comparable to closed systems), predation shapes assemblages because local species prey on larvae produced locally, but when dispersal is high the local effect of predation is masked by the larger scale movement of larvae amongst local patches ([Palmer et al., 1996](#)). Overall, in marine systems, the dynamics of connectivity ([Menge, 1991](#); [Lagos et al., 2005](#)), the capability of predators to influence the import and export of larval prey, the different behavioral strategies of prey ([André et al., 1993](#)), and the degree of disturbance, might determine whether a system is under regional or local control, or under a mixture of the two. Since intertidal systems experience elevated levels of unpredictable disturbance and many intertidal invertebrate larvae are long lived lecithotrophs or planktotrophs with potentially high dispersal, these systems may be governed by regional, unpredictable processes. Therefore, the localized effects of predation may be less influential in the regulation of communities ([Palmer et al., 1996](#)). Recent studies suggest, however, that the scales of larval transport and dispersal of many coastal species may be smaller than originally thought ([McQuaid and Phillips, 2000](#); [Pineda et al., 2007](#) for discussion and references), suggesting that predation of local larvae may have a role in the dynamics of communities.

An indirect effect of predation as mediator between larval supply and settlement is set by the interactions between predators and prey at dispersal ([White, 2008](#)). The delivery of prey and predators is likely to be driven by common, nearshore oceanographic mechanisms resulting in persistent patterns of settlement and recruitment ([Lagos et al., 2005](#); [Hamilton et al., 2006](#); [White, 2007](#); [Navarrete et al., 2008](#)). If larvae of predators and prey are delivered consistently to certain patches, spatial variability of predation, coupled with patterns of settlement, will influence the characteristics of community assemblages (“coupled settlement effect”, [White, 2008](#)). Although this

model was suggested for post-settlement regulation of metapopulations of reef fish (White, 2007, 2008), it could be extended to pre-settlement regulation of benthic invertebrates, given the following: (1) The pre-settlement exposure of invertebrate planktonic larvae to predation (Young and Gotelli, 1988; Moksnes, 2002). (2) The density-dependent role of predation on invertebrates at the local scale (Seitz et al., 2001; Menge et al., 2004). (3) The small size of many planktonic invertebrate larvae, which makes them possibly more susceptible than fish larvae to be transported by purely physical processes transport (McQuaid and Phillips, 2000). (4) The consistency of larval delivery to sites separated by hundreds of meters (Pineda, 1994a; Porri et al., 2006; Rilov et al., 2008). Systems characterized by “coupled settlement” mechanisms would generally experience density-dependent mortality of prey (White, 2007) and are more likely to be strongly regulated by predation on early stages (at settlement, White, 2008).

2.8. Larval predation: cannibalism

Cannibalism is an intraspecific trophic interaction (Fox, 1975) that occurs frequently, with important consequences for population dynamics, and implications for population stability and selection of cannibalistic traits (Fox, 1975; Polis, 1981; Claessen et al., 2004, for review). Cannibalistic dynamics are complex (Polis, 1981; Moksnes, 2004), often strongly dependent on the opportunistic nature of cannibals, prey–cannibal interference, temporal variability of prey–cannibal interactions, and on density-dependent characteristics of the population (Moksnes, 2004). Few studies have explained the link between cannibalism and the stabilizing dynamics in marine populations (Luppi et al., 2001).

Cannibalistic interactions in aquatic systems mostly involve fish (Wespestad et al., 2000; Olson et al., 2005) or post-settlement cannibalistic interactions among crabs (Moksnes, 2004), with little information on the regulatory role of cannibalism in benthic broadcast spawners at settlement (Luppi et al., 2001; Tamburri et al., 2007). Cannibalism often contributes towards mortality at settlement (Luppi et al., 2001; Porri et al., 2008a) and, therefore, alters recruitment and controls population dynamics (Fox, 1975; Polis, 1981). In some species, evolutionary adaptations at settlement can limit mortality caused by cannibalism (Tamburri et al., 2007). Mortality at settlement, however, could generally have a crucial effect on settlement success and, inherently, on population regulation (Pineda et al., 2007).

In highly cannibalistic organisms, such as shore crabs, population dynamics seem to be driven by a sigmoid functional response (reviewed in Real, 1977) of cannibals at settlement, where the amount of consumed prey per predator depends nonlinearly on prey density. This pattern might be crucial for population regulation, especially at low settlement, as cannibalism may reduce variability in recruitment and balance the effect of variable dispersal and stabilize recruitment (Moksnes, 2004).

Recruitment of mobile benthic organisms is frequently determined by active selection of habitat (see several examples in crabs and lobsters in Fernández et al., 1993; Moksnes et al., 1997). Since inter-cohort cannibalism is often the main source of mortality at settlement (although intra-cohort cannibalism may also be density-dependent, Moksnes et al., 1997; Sainte-Marie and Lafrance, 2002; Moksnes, 2004), ontogenetic post-settlement redistribution of postlarvae from nursery refuges to epibenthic juvenile and adult habitats reduces settlement mortality and may decrease cannibalism (Moksnes et al., 1997; Stevens and Swiney, 2005 and references therein). In intra-cohort interactions, density dependent antagonistic behavior can also affect mortality (Sainte-Marie and Lafrance, 2002), and an adaptive response to this behavior is emigration to unoccupied areas which will limit intra-cohort cannibalism (Iribarne et al., 1994) and mortality during recruitment. Ontogenetic niche shifts by organisms

between refuges may be the major factor regulating population persistence (Moksnes et al., 1997).

Many intertidal systems are dominated by sessile and sedentary species (especially mussels) that are important consumers of biomass, capable of depleting the water-column of nutrients (Norén et al., 1999), phytoplankton, and often playing the role of opportunistic carnivores (Lehane and Davenport, 2002; Alfaro, 2006). Thus, a substantial source of invertebrate settler mortality may be due to benthic inter- and intra-specific predation (Alfaro, 2006; Tamburri et al., 2007; Porri et al., 2008a). In sedentary and sessile filter-feeder species, the active behavioral component of cannibalism is reduced however, because mutual interference is minimal. Cannibals do not aggregate in response to prey patchiness, antagonistic behavior is reduced, and cannibals and prey do not emigrate. Thus, the effect of cannibalism as a regulating mechanism of local population dynamics and overall structure of sedentary and sessile filter-feeding assemblages may be simplified.

The effect of cannibalism on the relationship between larval supply and settlement may vary with the species considered, the degree of patchiness, and the fragmentation and size of adult habitat. In benthic invertebrates, cannibalism could alter the potential positive relationship between larval supply and settlement depending on the intensity of larval supply and tidal level. For example, in mussels, larval mortality induced by adult predation almost halves potential settlement regardless of the intensity of larval supply (Porri et al., 2008a). These results are more conservative than the 70% loss of larvae due to ingestion by adults found by Alfaro (2006). In the first instance, however, the 50% loss of the potential larval pool is persistent in time, and mortality was independent of intensity of settlement. The relationship between mussel larval supply and settlement would be positive, but with a dramatic change in slope due to a 50% or greater loss of potential settlers as a consequence of cannibalism by adults. On the other hand, in barnacles, cannibalism removes between 65 and 100% of available larvae only during low settlement. At high settlement, cannibalism does not significantly lower the success of larval settlement (Navarrete and Wieters, 2000). Even if this study considered nauplii loss instead of settling cyprids, it could be speculated that feeding rates change with density resulting in overall depletion of settlement. Thus, in this case, the larval supply–settlement relationship would change, depending on the rates of settlement, and perhaps would reach a plateau due to filtration saturation.

Accurate measurements of larval mortality are difficult to obtain and field estimates are variable. Thus, models of dispersal are often inaccurate and tend to overestimate dispersal (Pineda et al., 2009). The role of cannibalism has not been incorporated into models of dispersal, and it has often been underestimated in models of population dynamics because oversimplified models do not take into account the spatio-temporal heterogeneity of cannibalism, the habitats in which it occurs, and rate of cannibalism for different size and age classes (Fox, 1975; Dercole and Rinaldi, 2002). Models of population dynamics that include cannibalism, especially in size and age-structured populations, predict a series of effects, from destabilization of populations, to regulation, chaos, bistability (through the creation of local states that are driven by the final size of cannibals), and size-dependent effects (Costantino et al., 1997; Claessen and De Roos, 2003; Claessen et al., 2004; Shurin et al., 2004). These effects of cannibalism on populations depend on which factors are included in the models: (1) mortality of prey, (2) feeding rates of predators (Fox, 1975), (3) energy gain at the individual and at the population level (Persson et al., 2003), (4) size-dependent interactions, and (5) intraspecific competition (Polis, 1981; Claessen and De Roos, 2003). To date, the majority of models that include cannibalism in aquatic systems address fish community structure (Persson et al., 2003; Olson et al., 2005).

Cannibalism may be a predictive factor for the dynamics of marine benthic broadcast spawners if the spatio-temporal heterogeneity and

species-specific behavioral characteristics of cannibals and their prey are considered. While we recognize the potential role of cannibalism in decoupling larval supply and settlement and in the overall regulation of assemblages, we suggest that predictions of population structure that incorporate the effects of cannibalism should be made at the local population level, with a well-established understanding of the dynamics within the system. Future studies should aim at including the effects of larval supply and biological interactions within and among species. Lastly, and more generally, to assess the realistic mediating role of cannibalism on population regulation, the explicit effect of cannibalism should be integrated in multi life-stages studies, to estimate the “actual” impact of this process as a regulatory mechanism of populations.

3. Discussion and conclusions

Intellectual maturity, experimental manipulation, ease of access to field sites, and inexpensive off-the-shelf gear have been the hallmarks of intertidal and shallow water benthic ecology, arguably the marine field that contributed most to the general field of ecology in the late 20th century. Some problems brought by the recent reappraisal of supply-side ecology, such as identification of larval transport and accurate estimation of larval mortality, may defy simple solutions in systems where larval behavior is unknown, hydrodynamic transport phenomena not fully understood, and mortality of larvae difficult to estimate; that is, the vast majority of marine systems. Likewise, some technical problems brought by this re-evaluation of supply-side ecology, such as estimation of larval flux in environments where oscillatory flow is common (discussed above in “Quantifying larval supply”), may defy simplicity. Researchers should decide whether the value in obtaining unbiased estimates of larval flux as a measure of larval supply justify the expense of developing and building an unbiased sampling device. While some difficult problems in supply-side ecology may be worth the effort, others may be so intricate that no reasonable research program could resolve them mechanistically in their entirety.

The high variability in plankton abundance (Cassie, 1959; Haury et al., 1978) creates challenges in estimating larval abundance near settlement sites. Following and sampling plankton patches on the go, as opposed to sampling water at a fixed location, reduces variability when estimating pelagic larval concentration. Settlement can be imagined as the benthic habitat sampling the waters at a fixed point, and were it not for larval behavior, abundance of settlers in some microhabitats would be even more variable. While devices that sample larval supply appear optimal for some systems, such as reef nets in reef lagoons where total larval flux into the lagoon can be estimated (e.g., Doherty et al., 2004; Coronado et al., 2007), no such panacea exists for unclosed systems such as the intertidal, shallow subtidal, hydrothermal, and open sedimentary environments where total larval flux cannot be as easily estimated. Trapping tubes are useful devices for measuring larval concentration, and appear to work in various systems. It is not clear, however, that they measure flux towards the benthic habitat, as discussed in “Quantifying larval supply”, and how larval concentrations and water velocity scale in various field conditions. Other trap designs are also appealing (Otaíza, 1989; Castilla et al., 2001), though no studies have compared the different devices in variable field conditions. Settlement, on the other hand, is easily measured in natural and artificial substrata, at least in hard substrate environments, and as long as sampling interval is short, a day or less, mortality may not be an issue (e.g., Connell, 1985).

If settlement sampling underestimates or overestimates larval supply, knowledge of physical transport processes derived from settlement time series may be flawed. Larvae may transport to a site, but a large portion may be preyed upon before settlement (Alfaro, 2006; Porri et al., 2008a), and fewer larvae may settle in sites where there are no settlement cues (Knight-Jones and Stevenson, 1950; Hills

et al., 1998). Similarly, consistent temporal (seasonal, Bertness et al., 1992; Pineda, 1994a) and spatial variability in settlement among sites separated from meters to tens of kilometers (Pineda, 1994a and pers. obs.; Rilov et al., 2008, see also Berntsson et al., 2004) may be the result of settlement intensification due to variability in suitable area at commensurate scales (Pineda and Caswell, 1997), instead of differential physical transport, supply, or reproductive patterns during the season and among sites. Among nearby sites with similar larval supply but differing availability or quality of substrate area for settlement (i.e., sites separated 10's m, Pineda, 1994a), intensification could be predictable at some temporal and spatial scales, and consistency in species interactions at those scales may also be expected.

The relationship between larval supply and settlement includes correlation, and the ratio of these two variables (i.e., estimation of the settlement to larval supply ratio). First, does larval supply and settlement correlate (as measured by r), that is, do they scale directly proportionally and monotonically? Correlation may degrade when (1) larval patches are small since, for example, the larval patch may be sampled by a larval trap but not by an experimental settlement substrate. (2) Benthic predator patches are large, that is, larvae could be sampled by the trap but preyed upon before settlement. (3) Gregariousness and intensification are strong, since larvae would settle disproportionately near adults and in small patches of free substrate, creating nonlinearities in the larval concentration–settlement density relationship. (4) Residence time of plankton patches near settlement sites is short, preventing larvae from settling (a factor that may relate with 1). Second, what is the ratio of settlement to larval supply? Although there are no well justified theoretical models to assess whether settlement over or underestimates larval supply, empirical comparisons of settlement-to-supply ratio for observed values among experimental units may help reveal a mean and a range of values for this ratio (e.g., Noda et al., 1998). Gregariousness and intensification in experimental quadrats may result in settlement overestimating supply (relative to quadrats with no gregariousness and intensification effects), similar to experimental quadrats in micro hydrodynamic regimes that may increase retention time near settlement substrates. Alternatively, adverse hydrodynamic settings (e.g., very fast currents) and absence of settlement cues, such as settled adults, may result in settlement underestimating larval supply.

Our hypothetical researcher, “Nve”, wonders whether the correlation between larval supply and settlement may improve at larger spatial scales. That is, does averaging over increasingly large spatial scales improve the correlation? The answer is not clear, because the slope and sign of this relationship depend on the processes that degrade the relationship itself, including dimensions of the larval patches, scales of the larval search behavior, scales of patches of benthic larval predators, and residence time of water parcels near the settlement habitat. Moreover, these processes may interact and may not be stationary, due to seasonal reproduction (larval availability), benthic disturbance (e.g., seasonal sand inundation of rocky habitats influencing substrate availability), and presumably seasonal variability in larval patchiness due to seasonal changes in water-column stratification. If spatial averaging smoothes out small-scale variability, correlations and estimation of the settlement to larval-supply ratio may improve with spatial scale. Yet, this appears unlikely at scales larger than 10s of m, because larval behavior and the characteristics of the benthic landscape (larval predator patch size, adult density for gregarious settlement and settlement intensification) tend to vary at scales smaller than 10s of m. In any event, no empirical studies have addressed these speculations.

A recent trend in shallow water benthic ecology are recruitment studies at coarse to large scales (i.e., a few to 100s km, see Haury et al., 1978). While population and community ecology problems can be resolved elegantly at the small scale (e.g., Hatton, 1938; Dayton, 1971), other problems necessarily require contemplation of large temporal and spatial domains distinctive of the geophysical sciences

(e.g., larval transport, Johnson, 1939; Roughgarden et al., 1986). Indeed, some of the most pressing problems in marine ecology, such as conservation, fisheries, population connectivity, and determining how meso- and large-scale circulation modulate natural communities, must be addressed at 10 to 100s km scales. It is commendable that, despite intellectual and logistical challenges, shallow water benthic marine ecologists are addressing large-scale problems. This follows trends in pelagic ecology in particular, and oceanography in general, fields where scale issues have been a longstanding concern (e.g., Haury et al., 1978). Overall, attention to large-scale processes has benefited benthic ecology enormously. With more space and time to cover, however, researchers are forced to dilute their efforts, and in the quest to address large-scale issues, ecologists have used coarse approaches, including estimating larval supply from recruitment data. Unfortunately, attempts to address large spatial scales with broad brush measurements may bias our view of key processes, such as overestimating the scales of larval transport and dispersal in benthic populations (e.g., Pineda et al., 2009).

In addition to muddling inferences of larval transport and dispersal, the decoupling between larval supply and settlement has implications for understanding recruitment and population connectivity. Larvae may disperse among metapopulations, but not all larvae that disperse recruit and survive to reproduction (discussed in Bhaud, 1998; Pineda et al., 2007). Larvae that transport from spawning sources to waters near adult habitats still may not settle, or settle disproportionately on portions of the habitat due to the factors discussed above, hydrodynamics, competency, gregariousness, intensification, and predation. In cases where settlement is larger than predicted by larval supply, increased settlement and recruitment due to gregariousness (e.g., Knight-Jones and Stevenson, 1950; Kent et al., 2003) and intensification (Pineda, 1994a) implies that individuals may realize higher population connectivity (measured, for example, as number of individuals from site a and population A that disperse to site b, containing population B and reproduce e.g., Pineda et al., 2007). This is because settling in high density and near settled conspecifics results in more potential mates and enhanced reproductive potential. Alternatively, in cases where strong currents reduce settlement (e.g., Qian et al., 2000), or larvae are preyed upon (Porri et al., 2008a), waters near settlement sites may “break” population connectivity. Thus, decoupling of larval supply and settlement has consequences for recruitment and population connectivity. Better measurements of settlement and larval supply will result in more realistic estimates of larval transport, dispersal, recruitment, and population connectivity and greater understanding of the factors that affect these processes.

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