

1 **Causes of decoupling between larval supply and settlement and**
2 **consequences for understanding recruitment and population**
3 **connectivity**
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1 **Abstract**

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

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

20 Most of the examples discussed here suggest that behavior is the main source of the decoupling
21 between larval supply and settlement because larval behavior affects the vertical distribution of

1 larvae, the response of larvae to hydrodynamics, intensification of settlement, gregariousness,
2 predation and cannibalism. Thus, larval behavior seems to limit broad generalizations on the
3 regulation of settlement by larval supply. Knowledge of the relationship is further hindered by
4 the lack of a well founded theoretical relationship between the two variables.

5 The larval supply- settlement transition may have strong general consequences for population
6 connectivity, since larval supply is a result of larval transport, and settlement constrains
7 recruitment. Thus, measuring larval supply and settlement effectively allows more accurate
8 quantification and understanding of larval transport, recruitment and population connectivity.

9

1 **Introduction**

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

1 population connectivity consists of dispersal of pelagic larvae among metapopulations and
2 survival to reproduction of the benthic recruits (Pineda et al., 2007).

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

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

1 tide (12.4 h, Wetthey, 1986; Cruz et al., 2005; Jacinto and Cruz, 2008), and automated sampling
2 devices can sample for even shorter intervals (Whitlatch and Osman, 1998).

3 Estimating larval supply is more challenging than estimating settlement because planktonic
4 larval abundance is notoriously variable in time and space (see “Quantifying larval supply”).
5 Thus, many studies have used settlement and recruitment as proxies for larval supply. While
6 larval supply is a constraining variable for settlement, since larval supply sets the lower bounds
7 for settlement (that is, with zero supply there is no settlement), and settlement is more convenient
8 to measure than larval supply, various processes can produce a lack of correlation between
9 settlement and larval supply. This lack of correlation leads to misidentification of larval transport
10 and dispersal processes and misjudgment of the relative importance of pre- versus post-
11 settlement processes in influencing population and community processes (Pineda, 2000, for
12 discussion). While in some studies settlement and larval supply appear to be correlated
13 (Minchinton and Scheibling, 1991; Yund et al., 1991; Hurlbut, 1992; Jeffery and Underwood,
14 2000; Ross, 2001; Ma, 2005), other studies find no correlation (Miron et al., 1995; Olivier et al.,
15 2000; Porri et al., 2006; Rilov et al., 2008), suggesting caution in interpreting settlement as proxy
16 for larval supply.

17 The relationship between larval supply and settlement has been reported in various ways,
18 including (1) qualitatively (e.g., Pineda et al., 2002), (2) as a regression of settlement or
19 recruitment as function of larval abundance (e.g., Yoshioka, 1982; Noda et al., 1998), and more
20 commonly, (3) as a parametric correlation coefficient between these two variables (e.g.,
21 Minchinton and Scheibling, 1991; Yund et al., 1991). The relationship has been depicted as time
22 series plots of settlement or recruitment and larval concentration (e.g., Yoshioka, 1982), and as

1 plots of settlement or recruitment as function of larval supply (Yund et al., 1991; Todd et al.,
2 2006). Larval supply and settlement may correlate well, but in some sites and times settlement
3 measured on experimental substrates may over- or underestimate supply relative to that in other
4 locations and periods.

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

1 discussion). In general, the lack of a well founded theoretical expectation of the relationship
2 between larval supply and settlement makes field results difficult to interpret and compare.
3 Here we further identify and discuss the challenges in estimating larval supply and settlement,
4 and the processes that should be considered when estimating these two variables. We discuss
5 methods to estimate larval supply and potential biases in estimation. We review factors that
6 influence the relationship between larval supply and settlement, highlighting cases where
7 nonlinearities arise. Factors considered include competency, gregarious settlement, suitable area
8 of substrate and intensification of settlement, larval predation and cannibalism, and
9 hydrodynamics. Several of these processes involve behavior, but, for convenience, we discuss
10 them separately. We also discuss the consequences of the decoupling between supply and
11 settlement for understanding population connectivity. This review concentrates on invertebrates
12 in general and barnacles in particular, with some examples about fish.

13 **Factors influencing the correlation between larval supply and** 14 **settlement**

15 ***Quantifying larval supply***

16 Applied ecologists have been interested in the empirical relationship between larval supply and
17 settlement for years in part because, "...sets are heaviest in localities where the larvae had been
18 most abundant" (quote from a misidentified source in Korringa, 1941; see also De Wolf, 1973).
19 Recent interest in estimating larval supply and settlement, as outlined in the "Introduction", is to
20 gain understanding of how larval input modulates population and community processes. More

1 pragmatically, current research seeks to define whether settlement and larval supply are
2 correlated, and, specifically, whether settlement can be used as a proxy for larval supply. If so,
3 predictions about the distribution and abundance of larvae near settlement sites can be made
4 from settlement.

5 Larval supply has been measured discretely in time with plankton nets and pumps which sample
6 water for a small proportion of time relative to the length of the settlement sampling interval, but
7 water is in contact with the benthic settlement substrate for a much longer period (2 hours of
8 sampling, daily to every few days, Bushek, 1988; Minchinton and Scheibling, 1991; Noda et al.,
9 1998; Olivier et al., 2000; Satumanatpan and Keough, 2001; Palma et al., 2006; Porri et al.,
10 2006). Larval supply has also been measured at higher frequency with pumps, from discrete
11 samples taken every 2-4 hours for 1 day or daily for two weeks (Hurlbut, 1992; Ma, 2005), to 1
12 to 60 samples per hour for up to a few days (Pyefinch, 1949; De Wolf, 1973; Grosberg, 1982). In
13 addition to discrete sampling, researchers have sampled larval supply by integrating larval counts
14 over long periods with (a) pumps (8-24 h samples, Yoshioka, 1982), (b) nets, including nets on
15 reef crests, and at the entrance of semi-enclosed bodies of water (Eggleston and Armstrong,
16 1995; Moksnes and Wennhage, 2001; Doherty et al., 2004; Queiroga et al., 2006), and (c) larval
17 traps, including light traps (Doherty, 1987; Sponaugle and Cowen, 1996; Reynolds and Sponaugle,
18 1999), and passive trapping devices (Otaíza, 1989; Yund et al., 1991; Jeffery and Underwood,
19 2000; Castilla et al., 2001; Metaxas, 2001; Yan et al., 2004; Todd et al., 2006; Rilov et al., 2008;
20 Dudas et al., 2009). Debate over the methods used to sample pelagic larvae of benthic
21 invertebrates started early, with the realization that, like other zooplankton (e.g., Haury et al.,
22 1978), larval distributions are patchy (Barnes and Marshall, 1951; Cassie, 1957; 1959;

1 Natunewicz and Epifanio, 2001). Furthermore, evasive behavior of some larvae, particularly
2 crustaceans, was also recognized as a source of sampling bias (e.g., Korringa, 1941; De Wolf,
3 1973; Singarajah, 1975; Doherty and Butman, 1990). These issues are still relevant when
4 estimating larval supply.

5 Given planktonic patchiness and that settlement is the accumulation of benthic individuals over
6 an area and time, discrete pump and net samples taken for a small fraction of time relative to the
7 settlement measurement interval may not estimate accurately overall larval abundance (Otaíza,
8 1989; Yund et al., 1991; Gaines and Bertness, 1993; Miron et al., 1995). Some researchers
9 sampling discretely and infrequently have, however, found some correlation between larval
10 supply and settlement (e.g., Minchinton and Scheibling, 1991; Pineda et al., 2002). These
11 positive relationships suggest that larval patches are very large, and therefore, larval abundance
12 is sampled well with discrete samples at a fixed point. Patchiness of pelagic zooplankton is
13 thought to be a function of behavioral and hydrodynamic processes. Patches determined by
14 purely behavioral processes have been reported in the ocean (e.g., Haury and Wiebe, 1982), and
15 behavior interacting with hydrodynamics also results in patches, such as patches formed in ocean
16 convergences where frontal and internal wave circulation interact with planktonic behavior (e.g.,
17 Le Fèvre, 1986). Seasonal layering of the coastal ocean, causing stratification of temperature,
18 also enhances patchiness of the plankton (Haury et al., 1978; Gallagher et al., 2004; Woodson et
19 al., 2005), and the onshore advection of offshore stratified water parcels produces nearshore
20 horizontal heterogeneity in larval distribution (e.g., Pineda, 1994b; Leichter et al., 2005). More
21 stratification should result in more patchiness and therefore in more decoupling between
22 settlement and discrete estimates of larval supply, a hypothesis that has never been tested.

1 Sampling devices such as stationary nets and passive larval traps that integrate over settlement
2 sampling interval are appealing. Stationary nets on top of reef crests appear ideal for larvae
3 settling on reef lagoons, because the net samples the entire water-column, mass transport is
4 unidirectional (from the offshore larval pool to the adult lagoon habitat), and the period to be
5 sampled is constrained for larval fish that cross the reef crest only at night (Doherty and
6 McIlwain, 1996). Moreover, in some reef lagoons, almost all flow into the reef lagoon (forced by
7 wind and waves) tends to pass on top of the reef crest, with only occasional inshore flows in the
8 lagoon's channels (Coronado et al., 2007). Although channel nets may not fish over the entire
9 water-column, they perform well in energetic flood tidal currents (Eggleston and Armstrong,
10 1995).

11 Researchers have used light traps to capture crab larvae, and numbers caught are interpreted as a
12 proxy for larval settlement (Reyns and Sponaugle, 1999). Inspired by intuition (Otaíza, 1989)
13 and by devices estimating sediment vertical flux (Yund et al., 1991), researchers have proposed
14 passive larval traps to estimate integrated larval abundance near settlement sites (see also Jeffery
15 and Underwood, 2000; Castilla et al., 2001; Todd et al., 2006). While generally positive linear
16 relationships between settlement and number of trapped larvae are encouraging (Yund et al.,
17 1991; Todd et al., 2006) some comparisons of passive traps with other discrete and integrative
18 measurements have found little or no correlation (Rilov et al., 2008; Beaulieu et al., 2009; Dudas
19 et al., 2009; see also Todd et al., 2006).

20 Some researchers have argued that larval supply should be measured as larval flux instead of
21 concentration. It has also been argued that open-ended larval tubes can measure horizontal larval

1 flux (Yund et al., 1991; Gaines and Bertness, 1993; Todd, 2003), similar to the way particle flux
2 is measured from particle concentration and current velocity in manmade channels. Estimating
3 larval flux in enclosed lagoons appears straightforward (e.g., Doherty et al., 2004), but
4 estimating absolute horizontal larval flux near settlement sites with open-ended tubes
5 traditionally designed to estimate vertical sedimentation flux may be problematic. First, traps can
6 be biased samplers depending on their shape and opening size (Butman, 1986). Second, nets on
7 reef crests are effective for measuring the time-averaged flux because mass transport is
8 unidirectional and fixed nets only sample larvae going into the adult benthic habitat. On the other
9 hand, in environments with oscillatory flows, such as the intertidal and shallow subtidal areas
10 where wave-induced orbital motions are frequent, and multidirectional tidal currents the norm,
11 open-ended traps would capture the larvae going towards, and away from the adult habitat,
12 without differentiation. Few researchers have partitioned the in and out flux of larvae (e.g.
13 Moksnes and Wennhage, 2001, using fixed trapping nets). Moreover, ecologists sometimes use
14 weight loss of a soft substance such as plaster or chalk as a proxy for current speed in flux
15 estimates. In sites with current reversals, current speed derived from weight loss of substances
16 may overestimate the actual flux towards the benthic habitat because erosion would be
17 influenced by oscillatory flows in all horizontal and vertical directions. Finally, but very
18 importantly, when larval flux is taken as an estimate of larval supply, larval supply and
19 settlement may not be linearly related. At zero velocity and in very fast currents, larvae may not
20 be available or able to settle, and therefore settlement may be non-linearly related to larval
21 supply (e.g., Pawlik and Butman, 1993; Qian et al., 2000; Larsson and Jonsson, 2006; see also
22 Jonsson et al., 2004, for discussion). Indeed, researchers have observed less settlement in field

1 sites with faster flow (Todd, 1998), while others found decreased contact with the substrate by
2 larvae at increasing speed of flow (Jonsson et al., 2004). The effects of fast currents on
3 settlement may be dependent on the specific abilities of the larvae to attach in a turbulent
4 environment. At one end, it may increase turbulence and contact rate near the bottom, potentially
5 enhancing settlement, but it may also increase resuspension, resulting in a reduction of
6 settlement (see review in Koehl, 2007). Moreover, settlement in flow may relate to behavioral
7 processes that supersede purely hydrodynamic arguments: larvae may choose to settle in
8 moderate speed flows due to suboptimal feeding conditions for juveniles in fast flows (Larsson
9 and Jonsson, 2006).

10 ***Hydrodynamics***

11 The role of large-scale to microscale hydrodynamic processes on delivery, larval supply and
12 settlement has been investigated for over five decades (e.g., Crisp, 1955). Coarse- to large-scale
13 hydrodynamic features (10 to 100s km, sensu Haury et al., 1978) such as downwelling,
14 relaxation events, internal tidal bores, and wind driven currents influence transport and larval
15 supply of benthic invertebrate taxa (e.g., Bennell, 1981; Hawkins and Hartnoll, 1982; Farrell et
16 al., 1991; Pineda, 1991; Poulin et al., 2002). The effects of coarse- to large-scale hydrodynamics
17 on larval supply have been inferred from measurements of larval concentrations and time series
18 of physical measurements that characterize the hydrodynamic processes (e.g., Garland et al.,
19 2002; Shanks and Brink, 2005). In other studies, coarse- to large-scale hydrodynamic processes
20 are correlated to time series of larval settlement, but larval concentrations in the water are not
21 measured (e.g., Bertness et al., 1996; Jacinto and Cruz, 2008). Some studies have measured both
22 larval concentrations and settlement (e.g., Jeffery and Underwood, 2000; Ma, 2005; Porri et al.,

1 2006; Dudas et al., 2009), and recruitment (e.g., Palma et al., 2006; Rilov et al., 2008), to
2 determine the relationship with hydrodynamics. Modelers have also explored the relationship
3 between large-scale hydrodynamics, larval supply and settlement (e.g., Alexander and
4 Roughgarden, 1996; Guizien et al., 2006; Ayata et al., 2009). It has been argued that, ultimately,
5 coarse- to large-scale processes that bring larvae to shore may be more important to determining
6 settlement than smaller scale processes because large-scale processes affect whether larvae are
7 supplied near settlement sites. That is, larger scale processes constrain smaller scale processes
8 (Pineda, 2000). Nevertheless, smaller scale hydrodynamic processes, including advection by
9 surface gravity waves and turbulent mixing in the bottom boundary layer influence larval
10 delivery to the settlement site, contact to the bottom substrate, attachment (e.g., Koehl, 2007;
11 Reidenbach et al., 2009) and post-settlement mobility (e.g., Moksnes and Wennhage, 2001).

12 As larvae are transported from offshore waters to within 10 -100's meters of the shore, delivery
13 of larvae to the bottom will be influenced by hydrodynamic forces such as surface gravity waves,
14 through oscillatory flows, shoaling and breaking, and wave induced along-shore and cross-shore
15 flows (e.g., Miller and Emlet, 1997; Porri et al., 2006; Rilov et al., 2008; Dudas et al., 2009). A
16 relationship between larval supply and settlement is most likely to be detected when larval
17 supply is measured within a few meters or less of the settlement substrate (e.g., Otaíza, 1989;
18 Jeffery and Underwood, 2000; Todd et al., 2006; Tremblay et al., 2007). At these finer spatial
19 scales, flow velocities and substrate characteristics, which determine the boundary layer,
20 turbulent flows, and shear stress, will affect whether larvae attach or are re-suspended from a
21 substrate (Koehl, 2007). For example, turbulence increases the settling of negatively buoyant
22 phytoplankton cells (Ruiz et al., 2004), and some larvae use sinking behavior to promote

1 settlement in turbulent flows (Fuchs et al., 2004). In fast flows with high turbulence, contact rate
2 of larvae increases, resulting in higher settlement than in still water or in low flow conditions,
3 whereas above certain flow speeds larvae are not able to make contact or adhere (e.g., Eckman et
4 al., 1990; Pawlik and Butman, 1993; Qian et al., 2000; Pernet et al., 2003). Some species are
5 stimulated by flow or shear to attach to surfaces (Crisp, 1955). For example, cyprids attach to
6 pipette glass walls the moment flow starts.

7 Instantaneous stress events caused by wave driven flows may be a better predictor of larval
8 settlement than mean stress (Crimaldi et al., 2002). Wave driven flows result in instantaneous
9 high turbulent flow that increase shear stress and reduce the thickness of the viscous sublayer
10 (Koehl, 2007). In these conditions, larval settlement probability will be highest if larvae settle
11 quickly and adhere. Roughness elements enhance instantaneous turbulent flows that will result in
12 decreased probability of settlement on surfaces such as corals (Reidenbach et al., 2009).

13 Variability in roughness, however, creates microhabitats with reduced shear stress. In
14 microhabitats such as rough subtidal surfaces (Walters, 1992) or within coral reefs (Reidenbach
15 et al., 2009), and clam beds (Crimaldi et al., 2002), larvae will have longer contact times and
16 have a greater opportunity to settle. Natural patchiness of roughness elements will result in
17 greater variability in instantaneous stresses and events, and this may translate to greater
18 variability in larval settlement.

19 Fine-scale hydrodynamics over settlement surfaces continually change over time, since settling
20 larvae change the roughness elements of the substrate by creating more pits, peaks, and grooves
21 that are experienced by subsequent settlers. If larvae settle more on substrates with pits and

1 grooves, one could speculate that larval settlement rate may be greater on plates with high
2 settlement than on plates with low settlement, as roughness increases with settlement (see
3 Thomason et al., 1998 for effects of adult barnacles on flows). On the other hand, the type and
4 spacing of roughness elements could decrease the chance of contact or attachment if turbulence
5 is increased (Crimaldi et al., 2002). Larval response to fine-scale hydrodynamics in concert with
6 a positive response to conspecific or other chemical cues could be predictors of a settlement
7 increase.

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

1 the bottom boundary layer (Mullineaux and Butman, 1991; Snelgrove, 1994; Field et al., 2007;
2 Koehl, 2007).

3 Hydrodynamic conditions on settlement collectors will depend on location of collectors within a
4 site. In the rocky intertidal, placement choices that will differ in delivery of larval and settlement,
5 include vertical or horizontal surfaces, degree of exposure to waves, and tidal height (Porri et al.,
6 2007; Porri et al., 2008b). These differences, however, are sometimes smoothed out by
7 settlement larval behavior (Pineda, 1994a). Another approach has been to place settlement
8 substrates on mooring lines (e.g., Dobrestov and Miron, 2001; Rilov et al., 2008; Dudas et al.,
9 2009). Comparison of hydrodynamics on fixed versus moving settlement substrates has not been
10 made although increased biomass of barnacles on rotating panels compared to fixed panels was
11 attributed to differences in water flow (Glasby, 2001). It seems possible that coupling or
12 decoupling of larval supply and settlement could be confounded with the effects of
13 hydrodynamics on collectors, but this has yet to be shown.

14 In summary, hydrodynamics plays a role in determining larval supply and settlement, but
15 identifying the hydrodynamics forces that result in decoupling between supply and settlement is
16 difficult except, perhaps, in extremely high flows over surfaces on which larvae cannot attach
17 and are re-suspended. Coarse- to large-scale hydrodynamic processes influence the rate of arrival
18 of larvae to the shore, but fine-scale processes influence the precise location of contact with the
19 substrate. Settlement response to local hydrodynamic forces is not likely to be linear. The
20 methods we use to assess larval supply and settlement alter fine-scale hydrodynamics, and the
21 consequences of these alterations are difficult to predict in the highly turbulent oscillatory flows

1 that are characteristic of many shallow water environments. Although a sample taken to estimate
2 settlement integrates over small-scale temporal variability, localized variability resulting from
3 instantaneous changes in near-bed turbulence may reduce the reliability of estimates of
4 settlement rate among replicate samples. Hence, delivery of larvae to the shore and larval
5 settlement will be a consequence of the behavioral (directional swimming, sinking, active habitat
6 selection, adhesiveness) or passive response of larvae interacting with hydrodynamics forces at
7 multiple spatial and temporal scales. More importantly, larval response to the hydrodynamic
8 forces they encounter will be mediated by biochemical (e.g., settlement inducers, presence of
9 conspecifics, biofilms) and physical factors (e.g., light), biological interactions (e.g.,
10 cannibalism), and larval physiology (age, competency, energy reserves) (Olivier et al., 2000;
11 Qian et al., 2000; Marshall and Keough, 2003; Koehl et al., 2007; Tremblay et al., 2007)

12 ***Competency***

13 The proportion of competent to non competent larvae in larval samples may obscure a supply-
14 settlement relationship (Miron et al., 1995; Rilov et al., 2008). Competency can be defined as
15 “the capacity of a developing individual to initiate settlement and complete morphogenic
16 transformation associated with metamorphosis” (Bishop et al., 2006). Competent larvae can also
17 include those larvae that delay metamorphosis although they are developmentally ready to
18 metamorphose (Swanson et al 2007). We would expect that larval settlement would be more
19 tightly coupled with supply of competent larvae than to a mixture including non-competent
20 larval stages. Depending on the species, and the method and location of collection, samples of a
21 species may be a combination of competent and non competent larvae. For example, vertical
22 plankton net samples taken through the water-column are likely to obtain both types of larvae,

1 while intertidal plankton traps (Castilla et al., 2001) should gather more competent larvae, since
2 they **are** more likely to be positioned close to the adult habitat. If larvae become competent only
3 near the adult habitat (e.g., crabs, Moreira et al., 2007; corals, Gilmour et al., 2009), plankton
4 samples taken away from the habitat may contain predominantly non-competent larvae. If
5 competent and non-competent larvae can be distinguished, vertical location and method of
6 collection can be improved to obtain better estimates of competent larval supply.

7 In some species, competency can be determined by morphological characters (e.g., tube feet in
8 sea urchins, Swanson et al., 2004), physiological changes (buoyancy loss in corals Gilmour et al.,
9 2009) and behavioral changes (e.g., swimming or sinking rate changes, Mann et al., 1991). In
10 many species, (e.g., mussels, Rilov et al., 2008) competency must be assessed by testing whether
11 larvae settle in the laboratory, although size has also been used as proxy (e.g., Porri et al., 2006).
12 Sampling coral from different water depths in the field and testing whether larvae would settle in
13 the laboratory, Gilmour et al. (2009) determined that competent larvae are found near the
14 bottom. The precompetent period for corals was around 3 days. Precompetent period in other
15 spawning coral is 2-4 days (Miller and Mundy, 2003).

16 Barnacle larvae are not all competent upon metamorphosis to the cyprid stage. Laboratory
17 settlement experiments with *Balanus amphitrite* suggests that cyprid larvae are precompetent for
18 up to three days after metamorphosis to a cyprid (Rittschof et al., 1984; Satuito et al., 1996) and
19 up to two days after metamorphosis for cyprid larvae of *Balanus improvisus* (Zega et al., 2007).
20 Vertical distribution of barnacle cyprid larvae with respect to competency is not known, but
21 vertical distribution of cyprid larvae can differ between nearshore and offshore stations (Dudas et

1 al., 2009). In Southern California, cyprid larvae of *Chthamalus* spp. are found near the adult
2 intertidal habitat, while late-stage nauplii are found farther offshore (Tapia and Pineda, 2007).
3 Because the position of larvae in the water-column may affect onshore delivery and subsequent
4 settlement (Pineda, 2000, for discussion), researchers assessing larval supply should consider
5 whether competent larvae are being sampled and what is the appropriate vertical location in the
6 water-column for sampling them.

7 ***Gregarious settlement***

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

13 The discovery of gregarious settlement in intertidal barnacles stimulated research on the
14 proximate causes of larval behavior and its applicability in natural settings. Gregariousness in
15 intertidal barnacles was first reported in field populations of *Elminius modestus* (Knight-Jones
16 and Stevenson, 1950). A conspecific cue was identified and chemically characterized (Knight-
17 Jones, 1953; Crisp and Meadows, 1962; 1963). Extracted from adult barnacles, this cue could be
18 applied to experimental substrates to demonstrate its influence in settlement induction in the
19 laboratory and in the wild (Larman and Gabbott, 1975; Jarrett, 1997). These discoveries allowed
20 subsequent researchers to examine the role of the conspecific cue in natural settings. Field

1 experiments show that larval settlement behavior is selective (Miron et al., 1996) and sensitive
2 (Kent et al., 2003) to the cues produced by conspecific adults.

3 The broader ecological significance of settlement in response to conspecific cues can be
4 demonstrated in two ways. First, multiple taxa may respond to conspecific cues. For example,
5 gregariousness has been reported for some taxa (oysters, Crisp, 1967; Bayne, 1969; polychaetes,
6 Knight-Jones, 1951; Scheltema et al., 1981). Second, larval settlement behavior may mediate the
7 distribution and timing of settlement. For example, it may account for differential settlement
8 determining the adult distribution within a shore (Raimondi, 1991; Blythe and Pineda, 2009), and
9 the distribution among shores (Jenkins, 2005). Field studies have also elucidated the influence of
10 larval settlement behavior on timing of settlement (Bertness et al., 1992).

11 Attempts to quantify larval supply should explicitly take into account larval settlement behavior
12 when measuring settlement variability in the field, as settlement may vary in response to
13 conspecific cues. Controlling the concentration of a cue is complicated, because we do not
14 completely understand the various sources of the conspecific cue and how the cue affects the
15 behavior of larval barnacles in various natural settings. For example, contact with live adults may
16 not be the only way a conspecific cue could influence barnacle settlement in the wild. Cyprids
17 leave conspecific cues on surfaces when adhesive proteins are secreted from their antennules
18 during exploration of the substrate (Yule and Walker, 1985; Clare et al., 1994). Fine-scale
19 observations on distribution of cyprids suggest that they aggregate (Wethey, 1984), which could
20 be a response to secretions from the antennules or another source of conspecific cues. Juvenile
21 barnacles may induce settlement (Knight-Jones, 1953), though it is unclear how common this is

1 in the field (Wethey, 1984; Jeffery, 2002). Additionally, adults that are removed from laboratory
2 (Knight-Jones, 1953; Crisp, 1961) or natural (Minchinton and Scheibling, 1993; Miron et al.,
3 1999) substrates leave behind conspecific cues, but these are apparently short-lived (Wethey,
4 1984). Therefore, the loss of juveniles and adults due to natural disturbances could result in
5 conspecific cues left on the disturbed surfaces. These cues could facilitate settlement and result
6 in enhanced colonization. These observations continue to stimulate research on how the
7 conspecific cue induces barnacle settlement and affects spatial and temporal variability in
8 recruitment.

9 The largest spatial scale at which settlement behavior influences settlement is difficult to address
10 empirically. Larval settlement behavior implicitly specifies a spatial scale that spans the distance
11 at which a cue signal is produced and received by the larval sensory apparatus, and the
12 subsequent responses by larvae to the cue. In intertidal barnacles, larvae respond immediately or
13 a short time after direct contact with the conspecific cue. Therefore, the spatial scale is on the
14 order of centimeters that a cyprid may explore a benthic habitat, before resuming its search for
15 habitat by returning to the plankton, or adhering to the substrate (Knight-Jones, 1953; Crisp and
16 Meadows, 1962). Before selecting a precise site for settlement, larvae exhibit even smaller-scale
17 behavior, rocking back and forth to “test” the suitability of the settlement site (Crisp, 1961).

18 Small-scale larval settlement behavior has, however, been implied in much larger scale
19 ecological phenomena, like the aggregation of larvae between locations separated by more than
20 several meters (Berntsson et al., 2004). Larval settlement behavior may also have consequences
21 for settlement variability on geographic scales, since different cues may induce metamorphosis
22 across a species’ range (Strathmann et al., 1981). Inter-habitat patterns result primarily from the

1 absence of cues on the substrate preventing any proximally located larvae from completing
2 metamorphosis. Paradoxically, the consequences of larval settlement behavior at the largest
3 spatial scales might result from a lack of induction of settlement (for example, in the absence of
4 conspecific cues). Complex processes, including larval transport (Kingsford et al., 2002) and
5 optimal behavioral variability (Raimondi and Keough, 1990; Stamps et al., 2005; Toonen and
6 Tyre, 2007), may, instead, determine patterns of settlement at these larger scales.

7 The argument that larval behavior modulates larval supply, influencing settlement distribution, is
8 well supported by the literature on gregarious settlement presented here. Larval settlement
9 behavior is particularly interesting because behavioral interventions at this stage have the
10 greatest potential to carry over to juvenile and adult stages of the life cycle (Giménez, 2004;
11 Blythe and Pineda, 2009). However, the spatial scales of influence of conspecific cues may be
12 quite limited. It is an open question what are the impacts of the conspecific cues on the
13 distribution of juvenile and adult barnacles, and whether similar processes apply to other marine
14 invertebrates (Porri et al., 2007). Finally, it is intriguing to speculate whether gregarious larval
15 settlement behavior could influence connectivity of benthic invertebrate populations.

16 ***Suitable area of substrate and intensification of settlement***

17 Imagine that sea-breeze driven circulation transports barnacle larvae onshore ready to settle,
18 exactly half to site A, a sandy shore with only a few uncovered rocks and little free space for
19 larvae to settle, and the other half to site B, a rocky shore with abundant habitat to settle (i.e.,
20 abundant such that settlement does not saturate all habitat in B). Researcher “Nve” wants to test
21 the hypothesis that an approximately equal number of larvae are transported to sites A and B by

1 the circulation sea-breeze. Researcher Nve has read several papers where larval supply is
2 inferred from settlement data, so to test this hypothesis, replicated tiles are fixed to the substrate
3 in each site. Every day at low tide, tiles are replaced with new ones, and settled larvae counted.
4 Many larvae settle in each locality and numbers vary with time, but Nve is surprised to find
5 consistently more settlers at site A. Nve concludes erroneously that the hypothesis being tested is
6 false and considers an alternative hypothesis that involves different supply of larvae at the two
7 locations. His conclusion is, however, incorrect because similar numbers are brought to each
8 location by the circulation generated by the sea-breeze. If competent cyprid larvae act like
9 passive particles, the number of cyprids contacting the tiles in each site would be about the same.
10 Where larvae “behave” and search for substrate on which to settle, more would settle on tiles at
11 site A because less natural substrate is available for settlement. So, searching larvae must settle
12 more intensively per unit area available (Pineda, 1994a; Pineda and Caswell, 1997).

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

1 Thus, in sites with small numbers of barnacles and abundant free space for settlement, there may
2 be few settlers on settlement plates relative to larval supply because settlers do not find cues
3 from conspecifics to settle nearby, and settlers have ample choice to settle in adjacent areas. In
4 these sites, settlement may underestimate larval supply. In sites with large numbers of barnacles,
5 and little free space, settlement may intensify. In these sites, settlement may overestimate larval
6 supply. Suitable substrate in a site can vary seasonally and at scales from 10s of m (Pineda,
7 1994a) to 10s of km (pers. obs. JP, see also Rilov et al., 2008). Thus, in some circumstances,
8 particularly in areas with great adult density and high settlement, settlement may overestimate
9 larval supply.

10 ***Lunar periodicity***

11 Lunar periodicity in reproduction and settlement is a widespread phenomenon in coastal fish and
12 invertebrates, and may be a factor in decoupling larval supply and settlement (e.g. for examples
13 of lunar periodicity in reproduction see Korrynga, 1947, and for lunar settlement see Sponaugle
14 and Cowen, 1996; Reynolds and Sponaugle, 1999; Jacinto and Cruz, 2008). Fortnightly (spring to
15 neap) settlement variability in coastal lagoons may be related larval transport, since tidal currents
16 can be energetic in lagoon channels, and more mass transport is expected in spring tides.
17 However, in more open coastal environments, onshore tidal currents are generally weak, and are
18 unlikely to always explain lunar patterns in settlement. Further, tidal larval transport does not
19 parsimoniously explain why different invertebrate taxa peak at different phases of the moon
20 (e.g., Reynolds and Sponaugle, 1999). We speculate that larval settlement in some lunar phases
21 could be related to a behavioral response to some tidally related cue (see also Wethey, 1986;
22 Reynolds and Sponaugle, 1999 for discussion). Little is known of behaviorally induced lunar

1 settlement patterns in barnacles, however, and this hypothesis has been considered implausible
2 (Pineda, 2000, p.95). Nonetheless, we speculate that it could potentially influence the
3 relationship between larval supply and settlement for some species when available larvae settle
4 disproportionately at some phase of the moon (e.g. larvae near settlement sites settling
5 preferentially at certain time).

6 ***Larval predation***

7 Ecological interactions and environmental variables can determine community structure through
8 a complex network of species connections (Menge and Sutherland, 1987; Polis and Strong,
9 1996). Understanding the dynamics and scales of these interactions is therefore essential to
10 discover and predict patterns in community ecology (Leibold et al., 2004). Although greatly
11 debated, local processes may also be important in explaining metapopulation and regional
12 variability (Lawton, 1999; Simberloff, 2004). Local disturbance, in conjunction with recovery
13 patterns, can drive regional variability and dynamics in marine metapopulations (Gouhier and
14 Guchard, 2007). Predation can act as a local disturbance that has the potential to govern local
15 population dynamics of benthic systems with larger scale repercussions. While predation on
16 post-settlement stages and its critical contribution to community dynamics have been
17 documented for several taxa (Osman and Whitlatch, 1995a; David et al., 1997; Osman and
18 Whitlatch, 2004), the effect of planktonic (pre-settlement) predation on shallow water benthic
19 population dynamics is not often recognized (Woodin, 1976; Osman and Whitlatch, 1995a;
20 Doherty et al., 2004). Predation on pelagic larvae potentially mediates population structure
21 through inhibition of settlement.

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

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

1 The role of predation on population dynamics can be masked by variability in recruitment
2 (Young and Gotelli, 1988) and in occupation of primary space by adults (Osman and Whitlatch,
3 1995b). Pre-settlement resistance and vulnerability to predators, is regulated by behavior (Leis
4 and Carson-Ewart, 2001; Doherty et al., 2004), larval morphology (Morgan and Christy, 1996),
5 larval quality traits (Giménez, 2004) and chemical defense of early life stages (Johnson and
6 Strathmann, 1989; Lindquist, 2002, for a review), with consequences for success of settlement.
7 Chemical response varies strongly among species and is generally lacking among most
8 meroplankton, with morphological and physical resistance often more common features than
9 chemical defense itself (Bullard et al., 1999). Consequently, individual taxa should be considered
10 separately when assessing the role of predation on the coupling between larval-supply and
11 settlement and on overall community assemblages.

12 Active selection of habitat during settlement and recruitment often dictates the initial distribution
13 of juveniles (Fernández et al., 1993; Levin et al., 1997), but the distribution of juveniles may be
14 reinforced by predation. Moksnes (2002) found that predation of settlers was the greatest cause
15 of mortality for shore crabs, regardless of the type of habitat (open sand and structurally complex
16 refuges). Yet, this source of mortality did not have a significant effect on the initial distribution
17 of the population. The stability and boundaries of dense, discrete infaunal assemblages may rely
18 on larval mortality by adult ingestion (Woodin, 1976). In sedimentary systems, polychaete
19 recruitment success may be limited by adults, through direct predation (Ambrose, 1984) and
20 through physical disturbance (Woodin, 1976). Browsing on adults (which causes temporal
21 damage of adult appendages) reverts this pattern and increases settlement of worms, even if only

1 temporarily (Lindsay et al., 1996). The type of predator can interfere with population dynamics,
2 since some predators only affect adults, while others impact recruits (Lindsay et al., 1996).

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

19 An indirect effect of predation as mediator between larval supply and settlement is set by the
20 interactions between predators and prey at dispersal (White, 2008). The delivery of prey and
21 predators is likely to be driven by common, nearshore oceanographic mechanisms resulting in

1 persistent patterns of settlement and recruitment (Lagos et al., 2005; Hamilton et al., 2006;
2 White, 2007; Navarrete et al., 2008). If larvae of predators and prey are delivered consistently to
3 certain patches, spatial variability of predation, coupled with patterns of settlement, will
4 influence the characteristics of community assemblages (“coupled settlement effect”, White,
5 2008). Although this model was suggested for post-settlement regulation of metapopulations of
6 reef fish (White, 2007; 2008), it could be extended to pre-settlement regulation of benthic
7 invertebrates, given the following: (1) The pre-settlement exposure of invertebrate planktonic
8 larvae to predation (Young and Gotelli, 1988; Moksnes, 2002). (2) The density-dependent role of
9 predation on invertebrates at the local scale (Seitz et al., 2001; Menge et al., 2004). (3) The small
10 size of many planktonic invertebrate larvae, which makes them possibly more susceptible than
11 fish larvae to be transported by purely physical processes transport (McQuaid and Phillips,
12 2000). (4) The consistency of larval delivery to sites separated by hundreds of meters (Pineda,
13 1994a; Porri et al., 2006; Rilov et al., 2008). Systems characterized by “coupled settlement”
14 mechanisms would generally experience density-dependent mortality of prey (White, 2007) and
15 are more likely to be strongly regulated by predation on early stages (at settlement, White, 2008).

16 ***Larval predation: cannibalism***

17 Cannibalism is an intraspecific trophic interaction (Fox, 1975) that occurs frequently, with
18 important consequences for population dynamics, and implications for population stability and
19 selection of cannibalistic traits (Fox, 1975; Polis, 1981; Claessen et al., 2004, for review).
20 Cannibalistic dynamics are complex (Polis, 1981; Moksnes, 2004), often strongly dependent on
21 the opportunistic nature of cannibals, prey-cannibal interference, temporal variability of prey-
22 cannibal interactions, and on density-dependent characteristics of the population (Moksnes,

1 2004). Few studies have explained the link between cannibalism and the stabilizing dynamics in
2 marine populations (Luppi et al., 2001).

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

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

18 Recruitment of mobile benthic organisms is frequently determined by active selection of habitat
19 (see several examples in crabs and lobsters in Fernández et al., 1993; Moksnes et al., 1997).

20 Since inter-cohort cannibalism is often the main source of mortality at settlement (although intra-
21 cohort cannibalism may also be density-dependent, Moksnes et al., 1997; Sainte-Marie and

1 Lafrance, 2002; Moksnes, 2004), ontogenetic post-settlement redistribution of postlarvae from
2 nursery refuges to epibenthic juvenile and adult habitats reduces settlement mortality and may
3 decrease cannibalism (Moksnes et al., 1997; Stevens and Swiney, 2005 and references therein).
4 In intra-cohort interactions, density dependent antagonistic behavior can also affect mortality
5 (Sainte-Marie and Lafrance, 2002), and an adaptive response to this behavior is emigration to
6 unoccupied areas which will limit intra-cohort cannibalism (Iribarne et al., 1994) and mortality
7 during recruitment. Ontogenetic niche shifts by organisms between refuges may be the major
8 factor regulating population persistence (Moksnes et al., 1997).

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

20 The effect of cannibalism on the relationship between larval supply and settlement may vary
21 with the species considered, the degree of patchiness, and the fragmentation and size of adult

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

17 Accurate measurements of larval mortality are difficult to obtain and field estimates are variable.
18 Thus, models of dispersal are often inaccurate and tend to overestimate dispersal (Pineda et al.,
19 2009). The role of cannibalism has not been incorporated into models of dispersal, and it has
20 often been underestimated in models of population dynamics because oversimplified models do
21 not take into account the spatio-temporal heterogeneity of cannibalism, the habitats in which it
22 occurs, and rate of cannibalism for different size and age classes (Fox, 1975; Dercole and

1 Rinaldi, 2002). Models of population dynamics that include cannibalism, especially in size and
2 age-structured populations, predict a series of effects, from destabilization of populations, to
3 regulation, chaos, bistability (through the creation of local states that are driven by the final size
4 of cannibals), and size-dependent effects (Costantino et al., 1997; Claessen and De Roos, 2003;
5 Claessen et al., 2004; Shurin et al., 2004). These effects of cannibalism on populations depend on
6 which factors are included in the models: (1) mortality of prey, (2) feeding rates of predators
7 (Fox, 1975), (3) energy gain at the individual and at the population level (Persson et al., 2003),
8 (4) size-dependent interactions, and (5) intraspecific competition (Polis, 1981; Claessen and De
9 Roos, 2003). To date, the majority of models that include cannibalism in aquatic systems address
10 fish community structure (Persson et al., 2003; Olson et al., 2005).

11 Cannibalism may be a predictive factor for the dynamics of marine benthic broadcast spawners if
12 the spatio-temporal heterogeneity and species-specific behavioral characteristics of cannibals and
13 their prey are considered. While we recognize the potential role of cannibalism in decoupling
14 larval supply and settlement and in the overall regulation of assemblages, we suggest that
15 predictions of population structure that incorporate the effects of cannibalism should be made at
16 the local population level, with a well-established understanding of the dynamics within the
17 system. Future studies should aim at including the effects of larval supply and biological
18 interactions within and among species. Lastly, and more generally, to assess the realistic
19 mediating role of cannibalism on population regulation, the explicit effect of cannibalism should
20 be integrated in multi life-stages studies, to estimate the “actual” impact of this process as a
21 regulatory mechanism of populations.

1 **Discussion and conclusions**

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

16 The high variability in plankton abundance (Cassie, 1959; Haury et al., 1978) creates challenges
17 in estimating larval abundance near settlement sites. Following and sampling plankton patches
18 on the go, as opposed to sampling water at a fixed location, reduces variability when estimating
19 pelagic larval concentration. Settlement can be imagined as the benthic habitat sampling the
20 waters at a fixed point, and were it not for larval behavior, abundance of settlers in some
21 microhabitats would be even more variable. While devices that sample larval supply appear
22 optimal for some systems, such as reef nets in reef lagoons where total larval flux into the lagoon

1 can be estimated (e.g., Doherty et al., 2004; Coronado et al., 2007), no such panacea exists for
2 unclosed systems such as the intertidal, shallow subtidal, hydrothermal, and open sedimentary
3 environments where total larval flux cannot be as easily estimated. Trapping tubes are useful
4 devices for measuring larval concentration, and appear to work in various systems. It is not clear,
5 however, that they measure flux towards the benthic habitat, as discussed in “Quantifying larval
6 supply”, and how larval concentrations and water velocity scale in various field conditions.
7 Other trap designs are also appealing (Otaíza, 1989; Castilla et al., 2001), though no studies have
8 compared the different devices in variable field conditions. Settlement, on the other hand, is
9 easily measured in natural and artificial substrata, at least in hard substrate environments, and as
10 long as sampling interval is short, a day or less, mortality may not be an issue (e.g., Connell,
11 1985).

12 If settlement sampling underestimates or overestimates larval supply, knowledge of physical
13 transport processes derived from settlement time series may be flawed. Larvae may transport to a
14 site, but a large portion may be preyed upon before settlement (Alfaro, 2006; Porri et al., 2008a),
15 and fewer larvae may settle in sites where there are no settlement cues (Knight-Jones and
16 Stevenson, 1950; Hills et al., 1998). Similarly, consistent temporal (seasonal, Bertness et al.,
17 1992; Pineda, 1994a) and spatial variability in settlement among sites separated from meters to
18 tens of kilometers (Pineda, 1994a and pers. obs.; Rilov et al., 2008, see also Berntsson et al.,
19 2004) may be the result of settlement intensification due to variability in suitable area at
20 commensurate scales (Pineda and Caswell, 1997), instead of differential physical transport,
21 supply, or reproductive patterns during the season and among sites. Among nearby sites with
22 similar larval supply but differing availability or quality of substrate area for settlement (i.e.,

1 sites separated 10's m, Pineda, 1994a), intensification could be predictable at some temporal and
2 spatial scales, and consistency in species interactions at those scales may also be expected.

3 The relationship between larval supply and settlement includes correlation, and the ratio of these
4 two variables (i.e., estimation of the settlement to larval supply ratio). First, does larval supply
5 and settlement correlate (as measured by r), that is, do they scale directly proportionally and
6 monotonically? Correlation may degrade when (1) larval patches are small since, for example,
7 the larval patch may be sampled by a larval trap but not by an experimental settlement substrate.
8 (2) Benthic predator patches are large, that is, larvae could be sampled by the trap but preyed
9 upon before settlement. (3) Gregariousness and intensification are strong, since larvae would
10 settle disproportionately near adults and in small patches of free substrate, creating nonlinearities
11 in the larval concentration-settlement density relationship. (4) Residence time of plankton
12 patches near settlement sites is short, preventing larvae from settling (a factor that may relate
13 with 1). Second, what is the ratio of settlement to larval supply? Although there are no well
14 justified theoretical models to assess whether settlement over or underestimates larval supply,
15 empirical comparisons of settlement-to-supply ratio for observed values among experimental
16 units may help reveal a mean and a range of values for this ratio (e.g., Noda et al., 1998).

17 Gregariousness and intensification in experimental quadrats may result in settlement
18 overestimating supply (relative to quadrats with no gregariousness and intensification effects),
19 similar to experimental quadrats in micro hydrodynamic regimes that may increase retention
20 time near settlement substrates. Alternatively, adverse hydrodynamic settings (e.g., very fast
21 currents) and absence of settlement cues, such as settled adults, may result in settlement
22 underestimating larval supply.

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

16 A recent trend in shallow water benthic ecology are recruitment studies at coarse to large scales
17 (i.e., a few to 100s km, see Haury et al., 1978). While population and community ecology
18 problems can be resolved elegantly at the small scale (e.g., Hatton, 1938; Dayton, 1971), other
19 problems necessarily require contemplation of large temporal and spatial domains distinctive of
20 the geophysical sciences (e.g., larval transport, Johnson, 1939; Roughgarden et al., 1986).
21 Indeed, some of the most pressing problems in marine ecology, such as conservation, fisheries,
22 population connectivity, and determining how meso- and large-scale circulation modulate natural

1 communities, must be addressed at 10 to 100s km scales. It is commendable that, despite
2 intellectual and logistical challenges, shallow water benthic marine ecologists are addressing
3 large-scale problems. This follows trends in pelagic ecology in particular, and oceanography in
4 general, fields where scale issues have been a longstanding concern (e.g., Haury et al., 1978).
5 Overall, attention to large-scale processes has benefited benthic ecology enormously. With more
6 space and time to cover, however, researchers are forced to dilute their efforts, and in the quest to
7 address large-scale issues, ecologists have used coarse approaches, including estimating larval
8 supply from recruitment data. Unfortunately, attempts to address large spatial scales with broad
9 brush measurements may bias our view of key processes, such as overestimating the scales of
10 larval transport and dispersal in benthic populations (e.g., Pineda et al., 2009).

11 In addition to muddling inferences of larval transport and dispersal, the decoupling between
12 larval supply and settlement has implications for understanding recruitment and population
13 connectivity. Larvae may disperse among metapopulations, but not all larvae that disperse recruit
14 and survive to reproduction (discussed in Bhaud, 1998; Pineda et al., 2007). Larvae that transport
15 from spawning sources to waters near adult habitats still may not settle, or settle
16 disproportionately on portions of the habitat due to the factors discussed above, hydrodynamics,
17 competency, gregariousness, intensification, and predation. In cases where settlement is larger
18 than predicted by larval supply, increased settlement and recruitment due to gregariousness (e.g.,
19 Knight-Jones and Stevenson, 1950; Kent et al., 2003) and intensification (Pineda, 1994a) implies
20 that individuals may realize higher population connectivity (measured, for example, as number
21 of individuals from site a and population A that disperse to site b, containing population B and
22 reproduce e.g., Pineda et al., 2007). This is because settling in high density and near settled

1 conspecifics results in more potential mates and enhanced reproductive potential. Alternatively,
2 in cases where strong currents reduce settlement (e.g., Qian et al., 2000), or larvae are preyed
3 upon (Porri et al., 2008a), waters near settlement sites may “break” population connectivity.
4 Thus, decoupling of larval supply and settlement has consequences for recruitment and
5 population connectivity. Better measurements of settlement and larval supply will result in more
6 realistic estimates of larval transport, dispersal, recruitment, and population connectivity and
7 greater understanding of the factors that affect these processes.

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