

LINKING LARVAL SETTLEMENT TO LARVAL TRANSPORT: ASSUMPTIONS, POTENTIALS, AND PITFALLS

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I ABSTRACT

Settlement rate time series of nearshore invertebrate taxa can be helpful for posing questions about larval transport processes. However, the potential of these time series remains mostly unexplored, and the assumptions in this inquiring process are rarely identified. This contribution discusses the potentials and pitfalls of using settlement rate time series in posing questions about larval transport. I discuss why physical processes are distinct in the nearshore, up to ~30 m depth, as compared to the offshore, and briefly consider the likely problems in uncritically transferring meso-scale (~100's km) arguments to nearshore discussions. I consider the assumptions of available and shared larval pools often used in shoreward larval transport studies, and then the hierarchical nature of the different processes influencing settlement-rate, developing an argument about their relative importance. Large-scale offshore processes operate first on more larvae than small-scale nearshore processes, which operate last on fewer larvae; it is argued that large-scale offshore processes are disproportionately important in determining population fluctuations. Many field studies using settlement plates or larval collectors assume that settlement rate is only influenced by the rate of arrival of larvae. I discuss how the sampling interval, and the "settlement environment", the background where plates or larval collectors are installed, can influence settlement rate. Settlement often does not correlate directly with larval supply, and settlement interval should be kept as short as possible as settlement and time do not scale proportionally. Finally, I discuss the processes that generate smooth and peaked settlement time series, and the use of settlement time-series in identifying the temporal and spatial scales of physical transport.

II INTRODUCTION

The majority of benthic organisms inhabiting the nearshore, roughly the zone from 0 to 30 m water depth, have planktonic larvae that inhabit the pelagic environment, where larvae accumulate in an offshore larval pool away from their adult habitats. After a period of time ranging from minutes to years, with a 3 - 4 week mode for temperate species (Levin & Bridges,

1995), these larvae must return shoreward in order to complete their life cycle.

Translocation of larvae from offshore to nearshore waters is an interesting problem that stands on its own as a research field. Results of research in this area have important implications for understanding such issues as population dynamics, species geographical ranges, fisheries management, spread of invading species, and the design of marine reserves. Larval transport is often studied to elucidate population and community ecology of nearshore benthic species. In

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particular, larval transport is a key component of settlement rate, the rate at which planktonic larvae establish permanent contact with the substrate (Connell, 1985) (see also Keough & Downes, 1982), and a key component of recruitment rate, the rate at which juveniles join the population. Settlement rate can be defined in several ways (e.g. Pineda & Caswell, 1997). Here it is defined as the number of larvae attaching to the substrate per unit area per time:

$$s = n / t \bullet a \quad (1)$$

with units of n individuals, a area, and t time. Settlement has been observed cumulatively in the field, and these measurements often address the issue of recruitment. Here, the number of larvae arriving to the site in a sampling period is observed without manipulation, and available suitable substrate in the study quadrat is variable. Settlement is also studied on “fresh” plates or sites that offer the same amount of area in each sampling date, and these observations often address the question of the number of larvae arriving from the plankton. “Fresh” and cumulative settlement are different essentially because while in cumulative settlement *area* is a variable which may change with time, and settler mortality increases with time, in “fresh-substrate settlement” *area* is a constant (but see below, under “VII.h.2 Settlement rate does not scale up directly proportional in time”), and mortality is minimized. Connell (1985) recognized that settlement rate was influenced by the number of propagules arriving, the site-specific hydrodynamic conditions, and larval behavior. Other factors may also affect settlement rate (see below, under “V Hierarchy of larval settlement processes”, and “VII.h.2 Settlement rate does not scale up directly proportional in time”).

Settlement measurements are particularly useful because they integrate over a period of time (e.g. Gaines & Bertness, 1993), overcoming to a certain extent the problem of high variability in punctual sampling related to plankton patchiness (e.g. Haury *et al.*, 1978). For studying the number of larvae arriving from the plankton, however, this integration may be a liability if sampling interval is very long as mortality may increase, and available suitable substrate becomes a variable influencing the process (see below, under “VII.h.2 Settlement rate does not scale up directly proportional in time”).

Previous studies have demonstrated that invertebrate settlement time-series are valuable for posing and contrasting hypotheses on larval transport processes. The role of settlement series in identifying mechanisms of larval transport, however, has not been explicitly addressed, and the assumptions made when using settlement series to identify mechanisms have not been evaluated. The purpose of this contribution is to clarify issues about invertebrate larval settlement pertinent to larval transport, and to discuss the links between settlement and physical transport in open-coast populations.

III NEARSHORE AND OCEANIC TRANSPORT SCALES

Several studies have emphasized the importance of large-scale (100 to 1000's km) currents, such as the California Current or the North and South Atlantic Gyres, in offshore larval advection and larval dispersal (Johnson, 1939; 1960; Scheltema, 1968; 1971; Efford, 1970; Ebert, 1983). However, the problem of shoreward larval return by smaller scale flows has received less attention.

Shoreward larval transport is distinct from transport in deeper oceanic regions because of the physical consequences of the constricting presence of shallow depths and the shoreline “barrier”, different stratification, and other hydrodynamic phenomena unique to shallow depths. Those features both restrict the physical mechanisms that can transport larvae and also offer new possibilities. For example, the presence of the coastline modifies tidal currents. In deep waters, components of horizontal tidal currents would tend to be isomorphic, while in shallow seas current components are anisomorphic, with currents in the alongshore direction much more energetic than in the cross-shore direction. This is illustrated in Alvarez *et al.* (1990) study, which found that along-shore diffusion was on average ten times larger than cross-shore diffusion. Obvious exceptions are estuaries and coastal lagoon mouths, where cross-shore flows are energetic. In addition, the currents generated by the wind in deep seas are often balanced by the Eckman upwelling component (rotation), while in shallow well-mixed seas, wind currents could be balanced by bottom friction. The implication is that in well-mixed shallow-seas,

Eckman transport would be less pervasive than in deep seas. Offshore Ekman transport estimates often do not translate well to the nearshore. In the case of the Southern California Bight, offshore Ekman estimates tend to predict energetic offshore transport and upwelling. However, observations demonstrate that Ekman upwelling is very weak in this region (Jackson, 1986). Tidal fronts, which have been correlated to larval accumulation (Epifanio, 1988; Clancy & Epifanio, 1989), occur in shallow and not in deep waters. Shallow waters are also a requisite of an important mechanism of larval transport, internal tidal bores, because the internal tide is only likely to produce mass transport in shallow water. Finally, stratification in shallow and deep waters differ because freshwater discharges in the nearshore, not in the deep sea, and because in some coastal oceans, such as the coast east of the California Current, the thermocline tends to uplift in shallow seas as response to the large scale flow (Hickey, 1979). Salinity (Lagadeuc, 1992; Thièbaut *et al.*, 1992; 1994) and thermal stratification (Pineda, 1991; Shanks, 1995; Pineda and López, in prep.) are both important in larval transport processes.

IV LARVAL POOL ASSUMPTIONS

The life cycle of approximately 70% of temperate nearshore benthic invertebrates includes the production of eggs and larvae that then advect and diffuse offshore. Some shoreward larval transport studies assume “an available larval pool”, an idealized condition where larvae are assumed to accumulate in an offshore region or water mass, available to be transported to their adult nearshore habitats. In this view, the process of accumulation is dependent on the addition of larvae of different ages to the pool of competent larva. The period where competent larvae can delay metamorphosis, here called the competency window, becomes the factor that controls accumulation, as larvae that originally differed in age are now aggregated into a single pool of competent larvae. It is clear that for larvae with short or no competency window, the process of accumulation would be negligible. The great variability in the larval competency periods of nearshore invertebrate species (e.g. Scheltema, 1986; Levin & Bridges, 1995) implies that the accumulation period vary.

This available larval pool assumption ignores larval birthplace, how the larvae joined the larval pool, and

the processes occurring in the larval pool. Where do the larvae come from? How were the eggs and larvae transferred to the larval pool? How are meta-populations connected? What proximate processes influence the planktonic larvae in the pelagic environment? The larval pool assumption is a useful simplification because it separates problems that even individually often defeat nearshore ecologists. Consider that the journey from egg to settled larva include the problems of fertilization (Levitan, 1995), nearshore diffusion (e.g. Koehl *et al.*, 1993), offshore diffusion and advection (Johnson, 1939; 1960; Roughgarden *et al.*, 1988), predation (e.g. Morgan, 1995a), nutrition (e.g. Boidron-Métairon, 1995; Jarrett, 1997; Jarrett & Pechenick, 1997; Pechenick *et al.*, 1998), onshore advection (Bennell, 1981; Ebert, 1983; Shanks, 1983; Epifanio, 1988; Farrell *et al.*, 1991; Pineda, 1991; Stoner *et al.*, 1996), and settlement (Hatton, 1938; Connell, 1961; Connell, 1985; Gaines & Roughgarden, 1985; Raimondi, 1990). A justification for ignoring larval birthplace is that, for solving the problem of how an offshore larva translocates onshore, larval birthplace is generally irrelevant. This is in part because one really does not need to know the origin of the larvae transported shoreward, and in part because, for populations in open coasts, the probability of a larva returning to its birthplace after 3-4 weeks in the plankton must be very small. Conversely, it is obvious that the location of larval birthplace is extremely important for problems in population genetics, meta-population dynamics (Botsford *et al.*, 1994), fisheries management, design of reserves, and zoogeography.

As with any other simplification, the larval pool assumption has limitations that must be made explicit. It is obvious that this assumption would be incorrect when addressing problems such as species geographical ranges or metapopulation dynamics. For shoreward transport problems the assumption of an extant larval pool would be a liability when for some reason larval pool abundance is zero. In such circumstances, no larval transport would occur even in the presence of physical transport processes (see discussion below, under VII.h.3).

Another assumption in regional settlement studies is a shared larval pool. Studies contrasting settlement rate in several sites have sometimes attributed all differences among sites to differences in water column

hydrodynamic processes. The implicit assumption is that the several sites share a common larval pool, with common larval abundance. Settlement rate is influenced by larval supply, and, as discussed below, by the amount of suitable substrate for settlement and the sampling interval. Larval supply is dependent not only on physical transport, but also on the local larval pool abundance, as indirectly exemplified by Gaines and Bertness (1992). If larval pool abundance is influenced by, for example, local adult density, then settlement rate differences may relate to local adult abundance rather than to water-column physical processes. This would imply “retention” of larvae on scales smaller than the separation of the settlement sites.

A related issue is the enhancement of differences in settlement rate among shore sites separated tens of kilometers or more. This would apply for typical

temperate invertebrates with a four-week larval period, and would result from a combination of factors including differences in onshore larval transport, local adult densities, and site exposure to the “local” larval pool. Persistent differences in larval transport among sites may eventually produce different adult abundances, with sites with more energetic larval transport yielding higher population abundance. Higher benthic population densities would enhance settlement rate due to (a) reduced substrate area for settlement and (b) gregarious settlement (see below, under VI). Higher population abundance would in turn produce more larvae, which would be then subjected to more energetic larval transport. This positive feedback mechanism would exacerbate regional differences in settlement and adult population density (Figure 1).

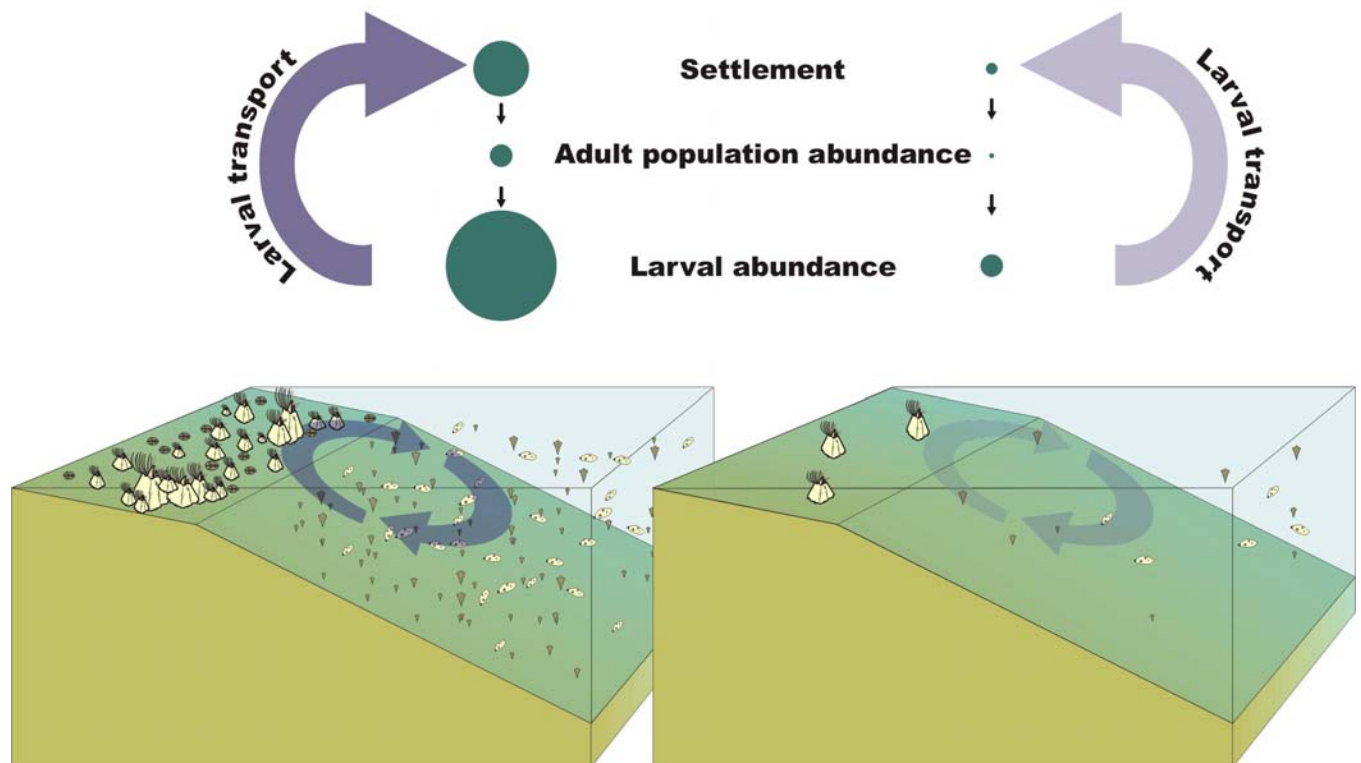


Figure 1. Schematic representation of the positive feedback that may exacerbate regional differences in settlement rate. In the left, stronger onshore physical transport results in increased settlement rate, which in turn produces larger adult population abundance. Larger adult populations would produce more larvae that would be in turn exposed to more energetic onshore physical transport. For a given area, larger adult populations will result in reduced suitable substrate for settlement, resulting in intensification of per-area settlement in the available space. Per-capita per-area settlement may be enhanced in the high settlement site due to gregarious settlement. The site to the left would eventually have disproportionately larger settlement rates than the site to the right, disproportionate to the effects of only more physical transport, or only higher larval abundance, or only less suitable area for settlement.

V HIERARCHY OF LARVAL SETTLEMENT PROCESSES

Phenomena influencing settlement include (1) processes influencing the larval pool (2), physical transport (3), micro-hydrodynamics, substrate availability, and behavior (e.g. Pineda, 1994). These processes are hierarchical in more than one axis. They are both *serial*, and *ordered in space*, starting with processes in the larval pool, far from the settlement site, and ending in processes occurring around the settlement site. There is also a *scale correspondence*, with large spatial scale processes occurring in the larval pool and during physical transport processes, but generally absent at the settlement site (Figure 2). Larger scale hydrodynamic (“oceanographic”) factors tend to be more pervasive in the larval pool and transport stages, with smaller-scale processes more pervasive during transport (e.g. accumulation processes) or settlement

(substrate availability; micro-hydrodynamics). It is obvious, however, that smaller scale processes occur at all stages. Finally, there is also an *abundance* relationship, where processes in the larger scales operate on a larger number of individuals than processes in the smaller scales. *Large-scale offshore oceanographic processes operate first and impact higher abundances than the small-scale nearshore processes that operate last and impact relatively fewer individuals.* An important consequence of this hierarchy is that variation in larger scale oceanographic processes is likely to produce large fluctuations in the number of larvae that may result in large variation in the adult population density, a phenomenon noted by Hjort (1926) (See also Thorson, 1950).

The fact that larval pool and physical transport processes have in general larger spatial and temporal scales than micro-hydrodynamic processes close to the

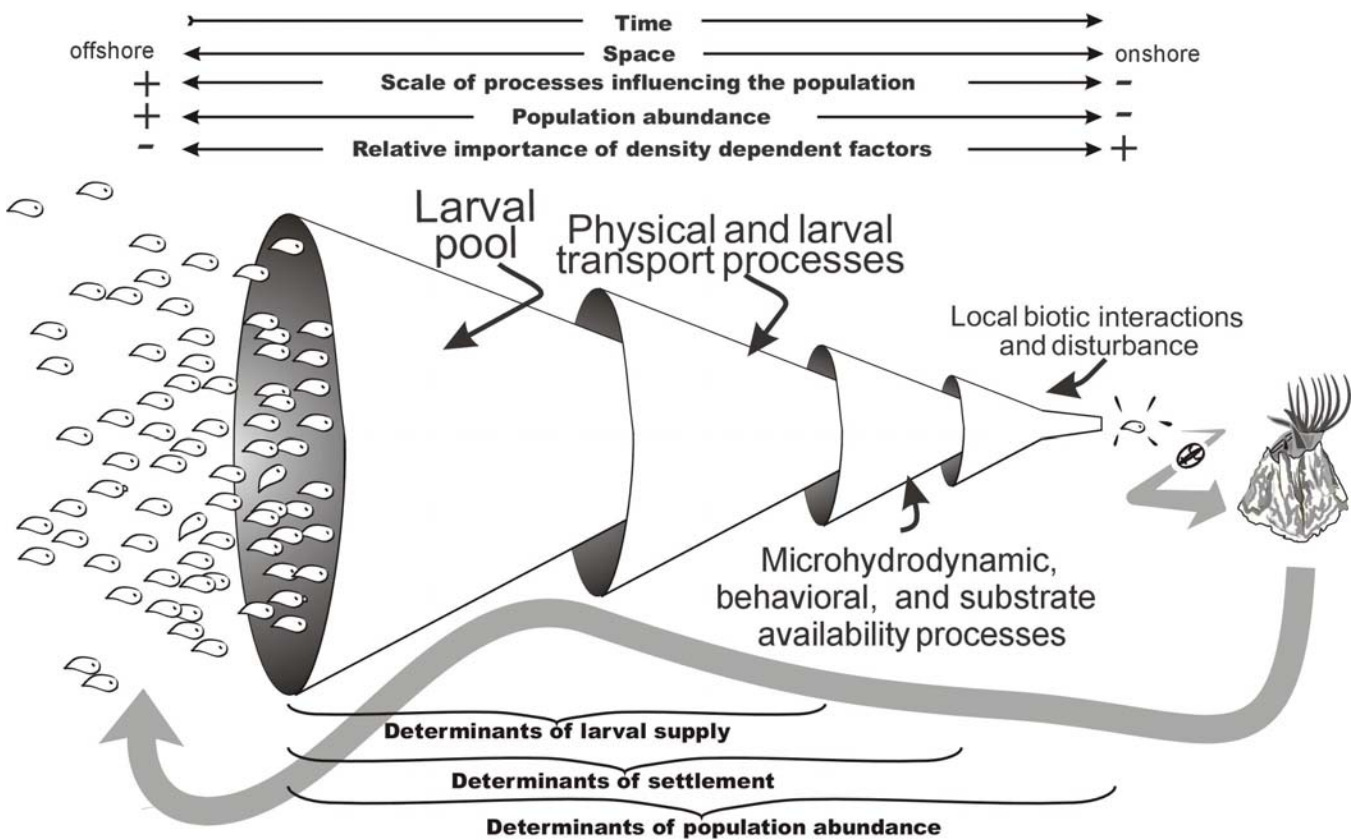


Figure 2. Representation of the proximate processes that influence settlement rate and population density. The number of larvae is larger than the number of adults, as each adult produces a myriad of larvae. Larvae are often found offshore, and before they can settle successfully at the coast, several conditions must be fulfilled. In each case, the proportion of larvae moving to the next set of processes is smaller. Small changes in the proportion of larvae that pass from one step to the next can produce large population changes. Redrawn from Pineda (1994).

settlement sites has some predictable consequences for the relative importance of larger and smaller scale processes in determining settlement. These can be illustrated with a hypothetical example.

Consider the spatial and temporal scales of the micro-hydrodynamic environment influencing settlement along a 1-km long rocky shore. A typical 1-km segment of rocky shore has a variety of micro-current environments separated from mm's to m's which may influence settlement patterns: surface roughness, rock cracks, sessile individuals, clumped sessile organisms (viewed as flow modifiers), pools, channels, protected ledges, exposed ledges, horizontal substrates, vertical substrates, etc. Adequate settlement sites may be found only mm to m's apart from unfavorable sites (Figure 3 left). Temporal scales of the micro-currents are also very short. For example, in a semidiurnal (~12.4 h)

tidal cycle, currents vary with the temporal scale of the waves and wave sets ("surf beat" frequencies, seconds to minutes, Inman & Jenkins, 1989), "beach" edge-waves (minutes, Oltman-Shay & Guza, 1987), and tides (hours). Currents produced by the breaking waves vary with the scales of the period of the wind waves, and the period of the sets of waves (e.g. sets of smaller and larger waves), from a few seconds to several minutes ("surf beat" frequency). Breaking waves also produce transport of mass, which in a topographically complex environment may produce flows with longer times scales than the period of the waves (e.g. a tide pool emptying slower than the period of the waves). Sea level changes also modify the flow environment because, for example, lower sea levels may leave areas unexposed to breaking waves, and "beach" edge-waves-the phenomenon of "trapped" wind waves along the beach- may produce alongshore differences in sea level

Temporal and spatial variability in micro-hydrodynamic conditions influencing settlement

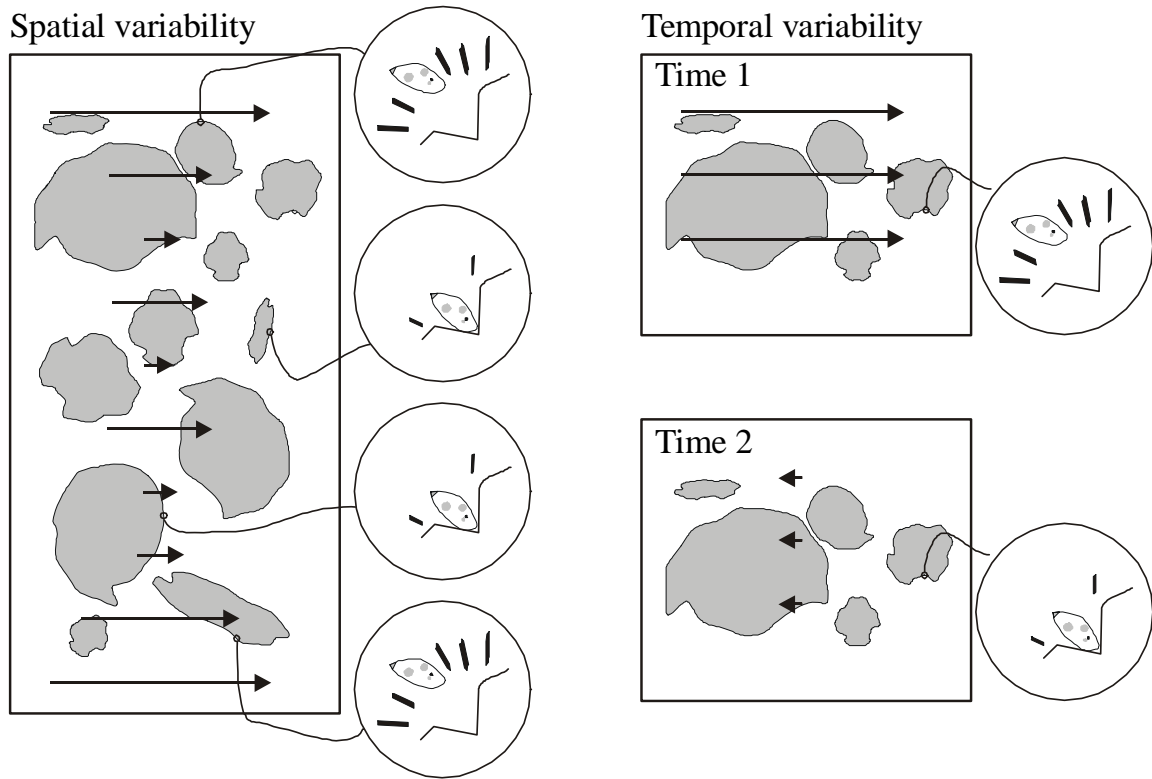


Figure 3. Representation of the effects of small spatial and temporal variability on settlement in a rocky shore. Boxes depict current variability over rocks (gray bodies), while circular windows represent barnacle cyprids approaching settlement sites (cracks). Circular windows connect to the rectangular boxes with different current environments, and show the case where cyprids in sites with stronger currents may have more difficult approaching the settlement site.

(Oltman-Shay & Guza, 1987), while the tide influences flow environment temporally. In such an environment, settling larvae may face several different flow conditions at the same site. One site that is unavailable for settlement at one time, because a wave is breaking and the currents are strong, may be available seconds later when the water is calm, a few minutes later when a change in sea-level is produced by surf beat, or a few hours later when the tide is receding and waves break further offshore (Figure 3 right). Larval behavior and small-scale currents and spatial heterogeneity are very important in determining settlement (Eckman, 1983; 1990; Butman, 1987; Chabot & Bourget, 1988; LeTourneaux & Bourget, 1988; Raimondi, 1990; Mullineaux & Butman, 1991; Mullineaux & Garland, 1993; Hills & Thomason, 1996). Larval substrate choice varies among cohorts, presumably related to the time spent in the plankton, and this could also impact settlement (Jarrett, 1997). However, because currents vary at very small spatial and temporal scales, there may always be an opportunity to settle in the area, or a second opportunity to settle in a given site, if larvae are close to the settling site. *Larger scale processes responsible for bringing larvae ready to settle close to the rocky shore may then be relatively more important than smaller scale processes in determining settlement magnitude.* These processes responsible for the number of larvae in the shore are, in fact, shoreward-transport and larval-pool processes.

VI SETTLEMENT RATE INTENSIFICATION: AMOUNT OF SUITABLE SUBSTRATE AND GREGARIOUS SETTLEMENT

Field studies using settlement panels and other larval collectors whose objectives are measuring the rate of larval arrival have implicitly assumed that settlement rate is only a function of the number of larvae arriving to the collectors. However, settlement per unit area is a function of the rate of supply of larvae, the settlement measuring interval, and the amount of suitable substrate, a property of the spatial environment where larvae settle (Bertness *et al.*, 1992; Pineda, 1994; Osman & Whitlatch, 1995a; Hunt & Scheibling, 1996; Pineda & Caswell, 1997). *Settlement rate, measured per unit area per time (Equation 1) may intensify as the amount of suitable substrate decreases,* and this phenomenon is scale dependent (Pineda, 1994; Pineda & Caswell,

1997). (The effects of gregariousness on settlement are discussed below.) For example, assume 100 larvae ready to settle in 3 settling environments with 1, 2, and 4-cm² suitable substrate for settling. If the residence time of the water parcel containing the larvae is long (for example, because there are no currents), then all the larvae will eventually encounter the substrate and settle. While each environment contained an equal number of larvae, settlement per unit area in the environments with 1, 2, and 4 cm² will differ, with 100, 50, and 25 larvae · cm⁻². Increasing settlement area linearly yields a geometric decrease in the settlement per unit area (Pineda, 1994; Osman & Whitlatch, 1995a; Pineda & Caswell, 1997).

An important consequence is that differences in settlement rates at different sites or times may be related to the amount of suitable substrate rather than to the rate of larval arrival to the shore. This is relevant for settlement differences among sites separated 10's of m (Pineda, 1994), 10's of km (Pineda and López, ms.), and more. To accurately measure the dependency of settlement rate on the amount of suitable substrate for settlement, researchers would have to (1) measure discrete (point) larval mean concentration and variance in the water, (2) estimate all the suitable settlement substrate, (3) calculate the residence time of the water, and (4) obtain observations of behavior and estimates of the swimming capabilities of the larvae (1 to 3 in field conditions, Pineda & Caswell, 1997). This task appears formidable and obviously impractical. When one is measuring regional differences in settlement, and interested in observing differences in the of supply of larvae due to regional variability in hydrodynamics, this problem can somehow be mitigated by (1) installing several collectors (v.g. 6-20) in each shore and obtaining a median settlement for the site, and (2) installing the collectors in compatible background environments (e.g. ceramic plates in rocky shores, mud trays in muddy environments, etc.). In a site with diverse settlement environments, a central tendency estimate which is not heavily influenced by the extremes (such as the median) would remove the influence of the upper extreme values that would result from the intensification phenomenon. Settlement substrates compatible with the background environment would diminish the possibility of intensification by removing the possibility of concentrated suitable settlement substrate in an unsuitable background environment. For example, while

a ceramic plate in a rocky-background settlement environment would reduce the possibility of intensification, the same substrate placed in a muddy plain would increase it. Of course, the intensification effect is not an artifact, and by ignoring it or trying to remove it, one would be ignoring a pervasive process with important yet largely unexplored consequences for the recruitment and dynamics of benthic populations.

Gregarious settlement behavior may also produce settlement intensification (Osman & Whitlatch, 1995b; Minchinton, 1997; Pineda & Caswell, 1997) (See also Raimondi, 1990). Based on observations that settlement intensifies when space was reduced, Osman and Whitlatch (1995b) suggested that gregarious settlement could produce settlement intensification, and created a model to account for this effect. Pineda and Caswell (1997) suggested that reduced suitable substrate could interact with gregarious settlement behavior, producing an even stronger intensification effect. Minchinton (1997) observed settlement intensification in the field in small (5 x 5 cm) cleared plots as compared to larger (15 x 15 cm) plots, and explained intensification as being due to gregarious settlement alone. Unfortunately, this study did not consider the fact that reduced suitable substrate could also produce settlement intensification, and the relative effects of reduced area and gregarious settlement cannot be separated in this study. In nature, it is likely that gregarious set and reduced suitable substrate interact positively to produce a stronger intensification effect.

VII BUILDING LARVAL-TRANSPORT

HYPOTHESES FROM SETTLEMENT-RATE TIME-SERIES

A great deal of knowledge about transport mechanisms can be gained from a settlement-rate time-series (Thorson, 1950; Coe, 1956; Loosanoff, 1964; 1966; De Wolf, 1973; Bennell, 1981; Yoshioka, 1982; Shanks, 1983; Wethey, 1984; Connell, 1985; Gaines *et al.*, 1985; Roughgarden *et al.*, 1988; Pineda, 1991; Bertness *et al.*, 1996; Miller and Emler, 1997). However, it should be obvious that there is no logical procedure to rigorously identify a shoreward transport mechanism from settlement data alone. This is because rigorous testing requires actual observation of larval transport in the water column. Settlement-rate

time-series can help in formulating transport hypotheses that could then be rigorously tested. The characteristics of the settlement-rate time-series that are most useful for gaining knowledge about transport processes include the *smoothness* of the settlement curve, the *number* of peaks of the curve, the *frequency* of the peaks, the *timing* of the peaks, and the *correlation* between series of different species, or series at different sites. Some of these features play important roles in identifying phenomena in geophysical time-series, and can help in deciding among alternative hypotheses of larval transport. Probably the characteristic of a single settlement-rate time-series most often used to gain information about transport relates to the smoothness of the time-series. A settlement-rate time-series that changes smoothly with time would be consistent with a diffusive process, while a series dominated by one or a few peaks would agree with transport by advective events or behavior.

VII.a Relationship between settlement and larval abundance close to the settlement site

Attempts to infer cross-shore larval transport from settlement time-series assume that settlement correlates with larval abundance in waters close to the settlement sites, a result found in several studies (Gaines *et al.*, 1985; Miron *et al.*, 1995; Noda *et al.*, 1998). Gaines *et al.* (1985) found that “sites switched rank in their settlement rates” from one year to another, and that ...”this change in settlement ranking matched a switch in rankings for cyprid concentration.” Miron *et al.* (1995) found the relationship to be statistically significant only when comparing low intertidal settlement with near-bottom larval abundance, with other comparisons non-significant. This relationship is not to be expected in cases where there is settlement intensification, as in this case settlement is somehow uncoupled to larval abundance (see under “VI Settlement rate intensification: amount of suitable substrate and gregarious settlement”). Another issue is that studies examining this relationship and employing discrete sampling for quantifying larval abundance (e.g. sampling larvae for a few minutes in a day) may underestimate or overestimate larval abundance if the larval distribution is patchy, leading to a lack of correlation between larval abundance and settlement. Larval sampling in the water column is a

temporally discrete estimate, while settlement integrates over a certain period of time (e.g. Gaines & Bertness, 1993). Studies concluding that settlement is correlated or uncorrelated to larval abundance near to the settlement sites should carefully evaluate the issue of water-column larval patchiness, and obtain better estimates of water-column larval abundance by, for example, sampling multiple times through the settlement-plate sampling interval.

The relationship between settlement and current speed is another issue that demands caution. Some researchers have argued that larval supply to benthic sites is a positive linear function of larval abundance and advection rates (Yund *et al.*, 1991; Bertness *et al.*, 1992; Gaines & Bertness, 1993). Moreover, those studies have found a positive correlation between settlement and larval supply near the settlement sites. This would suggest that settlement rate would increase with current speed. However, other studies that investigated the relationship between settlement rate and flow speed found that settlement rates of several invertebrate taxa *decreased* with higher current speeds (Todd, 1998). The problem in assuming that settlement rate increases with larval supply is that larvae may not be able to settle at high current speeds (e.g. Butman, 1987; Todd, 1998). Furthermore, high current speeds may advect the larvae away from the settlement sites, resulting in lower settlement rates. For example, in Pineda and Caswell's (1997) model, settlement rate decreases as the probability of being washed away from the system increases. These findings suggest that larval settlement may not be a simple directly-proportional function of larval abundance x current velocity; this relationship may be instead non-linear.

VII.b Larval translocation to the shoreline: "larval bath" or transporting events?

Larval return to open-coast adult habitats can potentially occur passively by *eddy diffusion* from an offshore larval pool to shallow water, *semi-continuous advection*, and *advective transporting events*, which may involve vertical swimming behavior, while active transport can potentially be achieved through *swimming* shoreward. Non-decapod marine invertebrate larvae are generally small, with limited swimming ability (Chia

et al., 1984), and therefore, those larvae must probably be transported back by diffusion or advection (Okubo, 1994). Swimming as a means of shoreward return is a hypothesis that requires further testing, but published work and scaling arguments suggest that swimming is unimportant for most invertebrate species (Shanks, 1995), although it is a possibility for certain larger decapod larvae, and other large short-lived larvae (e.g. Olson, 1985).

Diffusion and advective shoreward transport may have different impacts on several processes, from settlement and settler competition and mortality, to population dynamics. Specifically, settlement rates would differ for larvae returning by diffusion compared to larvae returning by advective events. Relatively high settlement can be generated by advective events, where a portion of the larval pool returns shoreward, but not by diffusion, where the larval pool is transported in a gradual manner. The high settlement rates associated with advection can also have an impact on spat competition and mortality. It has been fortuitously observed that when settlement of the barnacle *Pollicipes polymerus* is very high, cyprids of this species set in the base of < 1-day old barnacle *Chthamalus* spat, leading to dislodgment of the spat. It has also been observed that very high settlement rates of *Chthamalus* appear to elicit a functional response of the spat-predator crab *Pachygrapsus crassipes* (Pineda, 1994). For cases where settlement correlates with recruitment (e.g. Connell, 1985), diffusion and transport by events may have consequences for many other processes such as the positive and negative effects of crowding (Bertness, 1989), and gregarious settlement (WetHEY, 1984). Interannual variation in transport processes may also have long-term impacts on populations by causing interannual variation in settlement and recruitment intensity, which may result in dominant cohorts (Hjort, 1926).

VII.c Settlement rates for larvae diffused shoreward and for larvae transported by semi-persistent advection

Starting with an offshore larval pool, a smooth settlement time-series curve that increases as larvae diffuse shoreward, continues to increase as more larvae

from different positions in the larval pool arrive to the shore, and then decreases as the larval pool is depleted, is consistent with a diffusive process, as shown in Figure 4a. As pointed by Efford (1970) and Okubo (1994), eddy diffusion is most probably insufficient to transport the larvae shoreward. To my knowledge, this process has not been demonstrated in nature.

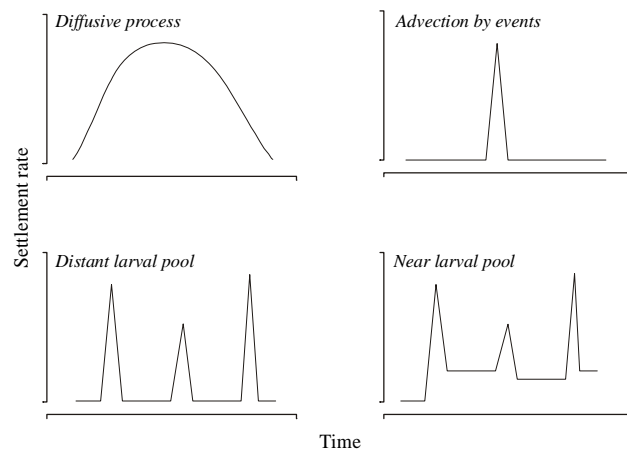


Figure 4. Hypothetical settlement-rate time-series resulting from (A) a diffusive process, (B) advection by events (C) a distant larval pool and (D) a near larval pool.

A smooth settlement curve would also result from persistent advection of larvae by shoreward persistent or semi-persistent flow as opposed to event-driven flow. This assumes that larvae are transported as they accumulate in the larval pool. To my knowledge, there is no observational evidence supporting this mechanism in open coastlines. One reason that this mode of transport is not very common is that because of the shoreline barrier discussed above, there are few *persistent* physical mechanisms energetic in the cross-shore direction. However, two important exceptions are the flow generated by the Stokes drift and the sea breeze. Semi-continuous advection is probably more common in small bays and other inland enclosures, etc. where tidal residual currents are pervasive.

VII.d Peaked settlement: advective events

Larvae transported by advective events would produce a “peaked” settlement function (Hawkins & Hartnoll, 1982) (Figure 4b). Other options to explain

pulsed settlement include larval behavior and synchronous egg release, and Figure 5 shows some assumptions of the different options discussed below.

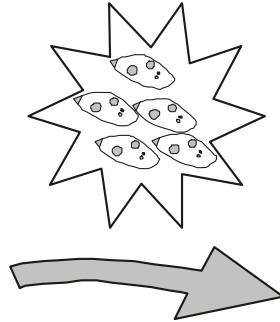
In peaked settlement by advective events, the increase portion of the peak is explained as the result of the larvae arriving to the settlement sites “en masse” (Figure 5 top). The decrease results from disappearance of the larvae from around the settlement sites, potentially due to (1) nearshore waters deplete of larvae as a result of all larvae settling, (2) predation of the remaining larvae (e.g. Young, 1988), or (3) diffusion or advection away from the set sites (e.g. Pineda, 1994). If all the larvae in the larval pool transport and settle successfully in the suitable substrate, this would yield a single peak, while several peaks would result if only a fraction of the larval pool is transported in each transporting event, or if the larval pool is replenished each time after all the larval pool settles successfully, or a combination of the two.

Several studies interpret a peaked settlement time-series as transporting events, with no distinction for the increase and decrease portions of the peaks (Hawkins & Hartnoll, 1982; Shanks, 1983; Pineda, 1991). As discussed above, transport would only explain the increase portion of the peaks. The decrease portion of the peaks has received little attention, with Pineda (1994) suggesting that abrupt decreases in barnacle settlement-rate could be explained as the sinking and disappearance of the water parcel containing the larvae from the nearshore settlement areas.

VII.e Peaked settlement: synchronous egg release

Synchronous release of invertebrate eggs or larvae by adults could also explain peaks in settlement in open-coast populations (Connell, 1961), although, to my knowledge, unambiguous evidence supporting this hypothesis is lacking. The idea is that (1) adults release propagules synchronously, possibly related to an environmental trigger, (2) the pulse of propagules remains coherent in the water column during the length of larval development, and that either (3A) larvae somehow remain close to the adult habitat, become competent, and the synchronously settle, or (3B) the cohort of larvae remains coherent, moves offshore, and an advective event transports the larvae back to the adult

Peaks caused by advective events: Synchronous transport of larvae, from the larval pool to the nearshore sites



Peaks caused by settlement behavior: Synchronous settlement of larvae already present around settlement sites



Peaks caused by synchronous egg release: Synchronous egg or larval release, and coherence of the larval patch, from larval release to settlement

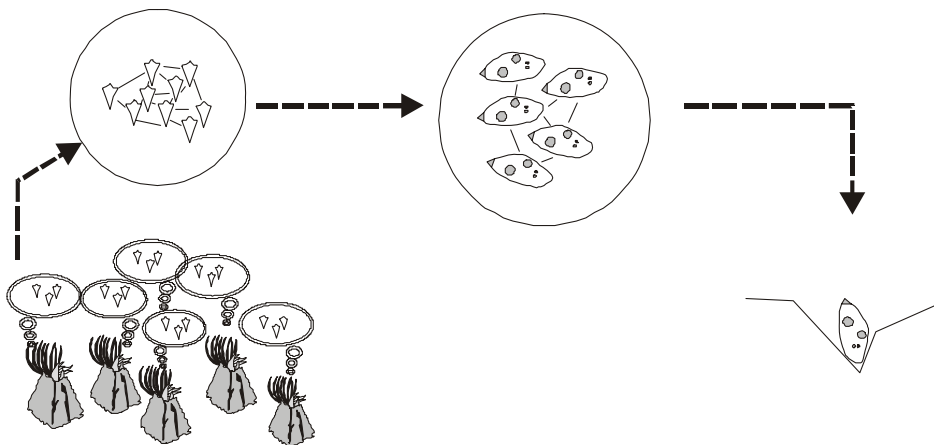


Figure 5. Representation of the assumptions in peaked settlement resulting from transport of larvae by events (top drawing), behavior (mid drawing), and synchronous egg release (bottom drawing).

habitat, in which case, 3B is equivalent to the process discussed in “VII.d Peaked settlement: advective events”. This hypothesis is presented in Figure 5, bottom.

Authors have reported synchronous release of propagules in temperate and tropical habitats (e.g. Christy, 1978; Oliver & Willis, 1987; Wolanski *et al.*, 1989; Starr *et al.*, 1990a; 1990b; Willis & Oliver, 1990).

For the coral-reef case, it has been observed that eggs remain coherent for some time in surface slicks, fulfilling above assumptions (1) and (2). However, many larvae in these slicks abandon the surface layer and then dive to deeper waters, and to my knowledge, the slicks have not been correlated with pulsed settlement. Several authors have explicitly argued against synchronous release of eggs or larvae explaining pulsed settlement (Kendall *et al.*, 1982; Farrell *et al.*, 1991). Reyns and Sponaugle (1999) found that while some brachyuran crabs apparently released their larvae synchronously in the first lunar quarter, this did not explain the subsequent peak in postlarval settlement. Thus far this hypothesis appears unlikely for open coast populations because of the apparently small probability of the fulfillment of the conditions outlined above. For coral-reef systems, however, conditions 1 and 2 could be satisfied, and it is plausible that a single peak in settlement may correlate to synchronous egg-release.

VII.f Peaked settlement: behavior

Larval behavior could also explain a peaked settlement time-series, although evidence for behavioral explanations is lacking, and this idea appears implausible (but see discussion in p. 102 of Sponaugle & Cowen, 1997). Assuming (1) larvae in the nearshore water-column very close to settlement sites, and (2) settlement triggered by a given environmental condition such as the phase of the moon or the temperature of the water, then a peaked settlement curve would result from the occurrence of the environmental trigger (Figure 5 middle). While this scenario would certainly explain peaked settlement, studies invoking this explanation would have to address how the larval pool either got transported shoreward or was retained in the nearshore, as well as issues about the selective advantages or “hard-wired” design (*e.g.* non-adaptationist) of remaining in the water until the occurrence of the settlement trigger. In cases where the putative settlement trigger is a phase of the moon, as sometimes is argued, studies would need also to falsify the alternative explanation that the settlement peak was caused by a physical transport mechanism with lunar periodicity. Wetthey (1986) suggested that synchronous larval settlement in the barnacle *Semibalanus balanoides* could be triggered by behavior. However, he pointed out that there was not an obvious behavioral mechanism.

For further considering the plausibility of peaked settlement resulting from larval behavior, it is useful to consider the concept of spatial and temporal settlement triggers. A time trigger would be when a larval aggregation would initiate settlement after perceiving an environmental clue, “the right phase of the moon”, or the “right temperature”. A spatial trigger, on the other hand, is a clue in the environment that would initiate a settling response; a larva would delay settlement until finding the “right spot”. To my knowledge, there is no published work showing conclusively field settlement initiated by an environmental event that could explain *peaks in invertebrate settlement separated by several days*. While there are several examples of adults releasing reproductive products synchronously associated to some environmental clues (*e.g.* Christy, 1978; Oliver & Willis, 1987; Wolanski *et al.*, 1989; Morgan, 1995b, for a review), and this synchronization may somehow suggest synchronization in larval settlement, the selective pressures are different, the two phenomena independent, and thus the analogy spurious. On the other hand, there are multiple examples of spatial triggers initiating settlement in field conditions. Examples include larvae responding to adults (*e.g.* Scheltema *et al.*, 1981), to other biota (*e.g.* Strathmann *et al.*, 1981), habitat heterogeneity, or small-scale intensification of currents (Pineda, 1994). In this case, the selective pressures appear to be clear: habitat quality is key for fitness.

In summary, the hypothesis that peaked settlement is caused by larval behavior at settlement requires strong evidence and falsification of alternative hypotheses.

VII.g Background level of settlement

Another characteristic that could be drawn from a settlement time-series is related to the distance of the larval pool from the settlement sites. If a settlement time-series drops to zero levels after a settlement peak, one may infer that the center of distribution of the larvae is far from shore, with no larvae in the nearshore diffusing to the settlement sites. If peaks tend to fall to some background level different from zero, this may be related to the larval pool being closer to the shore, with some larvae always close to the settlement sites (Figure 4d). This idea appears plausible; however, it has never been tested.

VII.h Identifying scales of the physical mechanism from settlement time-series

Spatial scale is, intuitively “the distance one must travel before some quantity of interest changes significantly”, and temporal scale, “that period over which one waits to see a significant change in some quantity of interest” (Powell, 1989). Another similar but more technical definition used in the geophysical sciences equates temporal scale to the period of a time-series (e.g. interval among peaks), and spatial scale to its equivalent in a transect, the wavelength (e.g. Marquet *et al.*, 1993) (See also Schneider, 1994, for other definition). Physical oceanographic phenomena have characteristic spatial and temporal scales, and period and spatial extent are therefore important criteria for demarcating hydrodynamic phenomena in physical oceanography (e.g. Stommel, 1963). Because hydrodynamic forcing is so pervasive in pelagic planktonic communities, studies in pelagic ecology have maintained that temporal and spatial scales in physical variability force time and spatial scales in biological variability (Kamykowski, 1972; Haury *et al.*, 1978; Steele, 1978; 1985). Non-linear phenomena may break this direct-proportional relationship between physical and biological scales (Denman & Powell, 1984; Denman, 1994), but to my knowledge, it remains to be observed whether this breakage in physical and ecological scales occurs in nature.

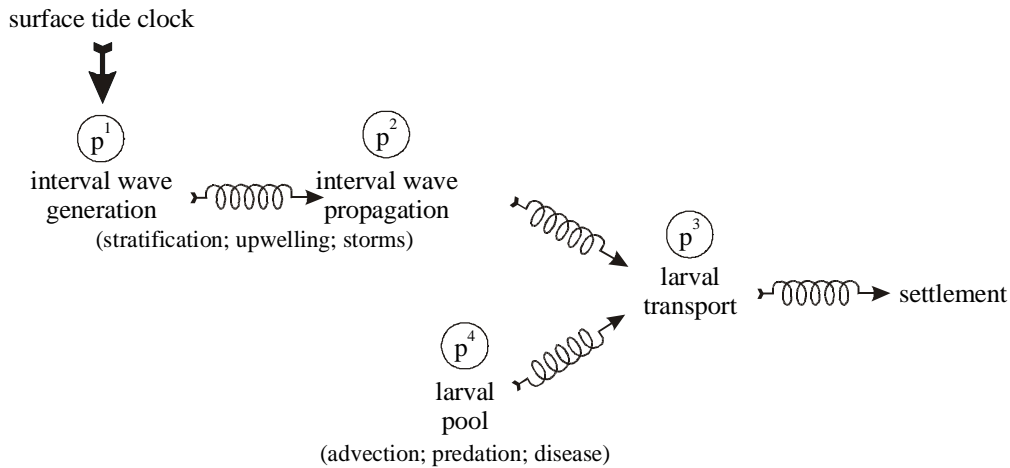
Time scale arguments have also been used in studies of shoreward larval transport. For example Shanks (1983) observed fortnightly (= semilunar, spring to neap cycle, ≈ 14.7 d) periodicity in the settlement of crab and barnacle larvae. These and other data, as well as the author’s conjecture that internal waves would also have fortnightly variability, led the author to infer that surface-slicks over internal waves were responsible for the shoreward transport of larvae. Pineda (1991) used semi-diurnal, diurnal, and fortnightly periodicity in surface water temperature to identify a larval transport mechanism.

Time scale arguments are valuable, but are a double-edged sword that demands caution because (1) periodicity in settlement may be caused by other phenomena with identical periods, (2) non-linear processes may break this physical-biological scale correspondence, and (3) the linkage between the

physical phenomenon with a given characteristic periodicity in settlement is a chain that can break at several linkages. For an example of the latter, consider the linkage between the surface tide, internal wave generation, propagation, the larval pool, larval transport, and settlement. Figure 6 shows a conceptual representation of the relationship among these processes. The forcing mechanism, the surface tide, is a predictable process with fortnightly periodicity (≈ 14.5 d) that may generate internal waves or tides that may propagate shoreward. If there are larvae in the larval pool, propagating internal bores may then carry larvae shoreward and these larvae may settle. Because the surface tide has fortnightly periodicity, this periodicity would transfer to the settlement signal (Figure 6b). However, as the reader may already suspect, this relationship can break at several links. For example, while the surface tide is predictable, the water column conditions may not be appropriate for internal wave generation or propagation because it could be well mixed due to wind-driven upwelling (Rosenfeld, 1990) or a storm system (Winant, 1980). Even if the ocean climate is appropriate for internal wave generation and propagation, larval transport may not occur if there are no larvae in the larval pool because, for example, advection, predation, or disease. There are multiple steps where the transfer of the spring-to-neap rhythm may break, producing lunar periodicity at times, and no periodicity on other occasions. Paraphrasing and amending a popular saying, “the periodicity-transfer-chain hypothesis is as strong as the weakest of its links”.

Another important characteristic of a settlement rate time series is the timing of the peaks relative to a given astronomical cycle such as the seasonal cycle ($\gg 365$ d) or the lunar cycle ($\gg 29.5$ d). That is, peaks in settlement in a given season or a given day of the lunar cycle may also help suggest the particular mechanism. For example, because internal motions are more energetic when the water column is strongly stratified, and the nearshore water column is well stratified in spring and summer, peaks in settlement in these seasons may well be related to internal motions (Pineda, 1991). However, if these peaks occur in fall and winter, when internal motions are weak (Winant & Bratkovich, 1981), one may question internal motions as the source of larval transport. Peaks in barnacle settlement observed in ~ November - January in Southern California (J. Pineda, unpub.), when the water column is weakly stratified,

A



B

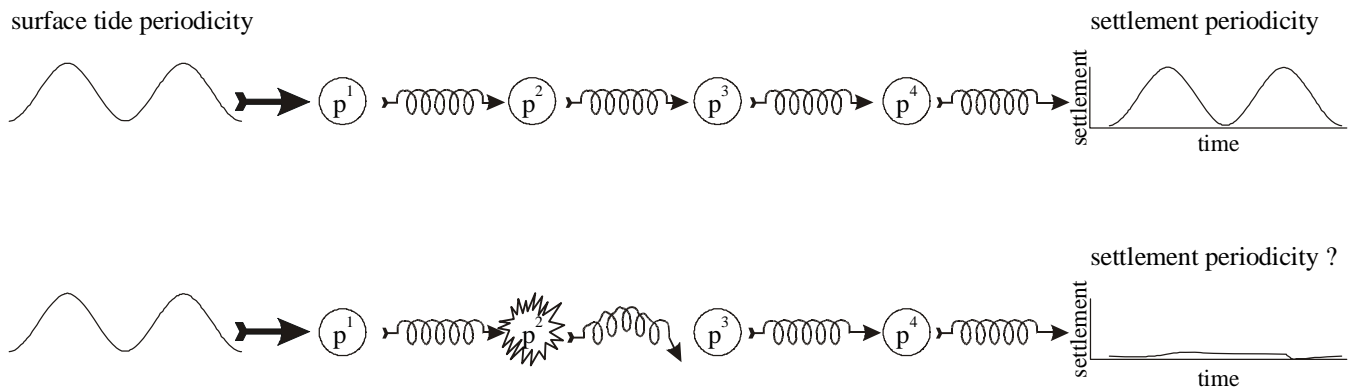


Figure 6. Representation of the periodicity-transfer chain hypothesis. p represents processes. The A drawing represents the processes involved in the transfer of periodicity, from the surface tide to the settlement, while the B drawings represent a case where all the processes “work” and transfer the periodicity (B upper), and a case in which one of the processes, internal wave propagation, did not work with no periodicity transfer (B lower).

may be due to processes other than those which require strong water column stratification.

VII.h.1 Settlement sampling interval

When attempting to gain knowledge about transport from settlement time-series, it is important to shorten sampling interval (e.g. to sample more frequently). Connell (1985) noted that measurement of settlement should be frequent, and that the “closest to the ideal” in normal conditions would be daily. Connell argued that frequent settlement measurements are needed “to avoid missing any larva that attach and then become detached within a short period”. Long sampling interval allows for mortality of the settled larvae, and inferring transport

events using long sample intervals introduces uncertainty. For example, Power *et al.* (1999) found that settlement (cyprid abundance) did not correlate with recruitment (~30 day sampling period) in the barnacle *Chthamalus montagui*, albeit the correlation was positive in *C. stellatus*. Booth (1991) suggested that frequent sampling would be a measure of “true settlement rate”, while less frequent sampling would estimate “the size of the recruit cohort that will enter the juvenile population”.

Other important reasons for sampling frequently are that (1) in long sampling intervals, the area *a* in equation (1) transforms from a constant to a variable, as discussed in the next section, and simply that (2) sampling interval –and time series length– determine

the phenomena that one can identify from a time-series. The relationship between sampling interval and temporal-scale in time-series is called the Nyquist frequency (Chatfield, 1989), and expressed in cycles per unit time is

$$f_N = 1/2\Delta t \quad (2)$$

where Δt is sampling interval. The important consequence is that the smallest time scale of a phenomenon one can identify with a time-series is twice the sampling interval. For example, weekly samples would only serve to identify phenomena with scales of 2 weeks and longer, while monthly samples would be capable of identifying temporal scales of 2 months and longer.

In order to further understand the importance of sampling interval, consider the following hypothetical example (see also Figure 4 in Michener & Kenny, 1991). Assume two settlement plates sampling the same population of larvae. One is sampled daily, while the other is sampled weekly. Figure 7 shows two possible curves. The settlement time-series for the plates that were sampled daily shows three different peaks. One lasted 3 days, other 2 day, and other 6 days. This suggests that the scale of the offshore transporting mechanism or the size of the larval patch advected onshore was 3 days in the first peak, 1 day in the second and 6 days in the last one. On the weekly time-series it is impossible to decide whether the peaks are weeks or days long.

Small sampling-intervals allow detection of the temporal scale of the transporting event, and because the temporal scale of physical phenomena is an important characteristic, may help in identifying mechanisms and eliminating alternatives for peaked settlement. It may be argued that long intervals (weeks to months) are adequate for inferring settlement based on the idea that meso-scale (100 km's) oceanographic processes are more pervasive than their coarse scale (10 km's) counterparts in affecting the distribution or transport of larvae. Since meso-scale processes would have longer temporal scales, it has been argued that a coarser settlement sampling-rate would be adequate for identifying the hydrodynamic processes influencing the distribution and transport of larvae. This is an illusion

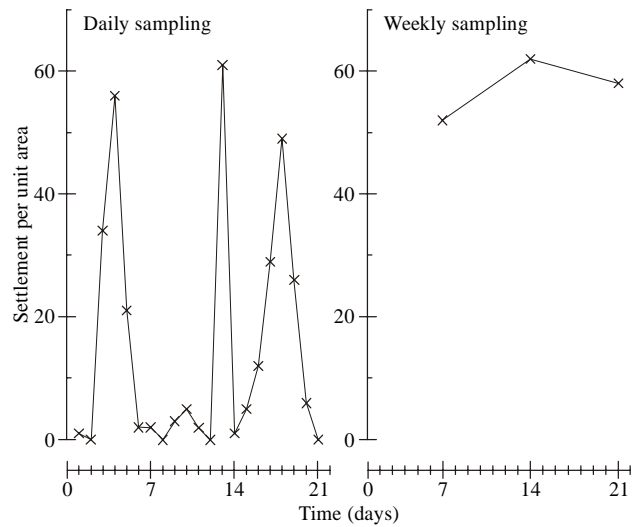


Figure 7. Hypothetical settlement time-series obtained at different sampling intervals (For an observed example, see Michener & Kenny, 1991).

rooted in the earlier traditions of oceanography, the lure of satellite-oceanography, and the documented importance of meso-scale processes in pelagic ecology (e.g. Haury *et al.*, 1978; Mann & Lazier, 1996). While it is true that meso-scale processes are important in open - ocean pelagic systems, it does not necessarily follow that the meso-scale is the most important scale in nearshore systems. As discussed above under “III Nearshore and oceanic transport scales”, the way water moves in the nearshore is very different from the way it moves in the open or coastal ocean (> 60 m depth). Friction, stratification, and topography in the nearshore transform the larger scale flows into smaller features, and give rise to new, smaller phenomena, such as buoyancy flows, rips, etc. In short, there are no logical arguments or observations supporting the primacy of the meso-scale in the nearshore.

Nearshore ecologists wishing to understand larval distribution and transport face a challenging task because nearshore hydrodynamics is currently poorly understood. Translating hydrodynamic arguments from the meso-scale to the nearshore is logically untenable. Since the nearshore dynamics are not well known, nearshore ecologists should try to derive their knowledge largely from their own observations, and not to try to infer dynamics from published arguments only.

VII.h.2 Settlement rate does not scale up directly proportional in time

Assume that the number of larvae settled in a given substrate increases linearly with sampling interval:

$$\frac{n_1}{t_1} = \frac{n_x}{t_x} \quad (3)$$

where t_1 is the lowest “natural” sampling interval, usually one day (but could also represent other periods such as one tidal cycle), and n_1 is set larvae at time t_1 . The variable t_x is a positive integer $t_x > t_1$ multiple of t_1 , and n_x is set larvae at time t_x . An important yet little appreciated observation regarding sampling interval is that settlement rate does not scale directly proportionally in time (Michener & Kenny, 1991) (See also Booth, 1991; Minchinton & Scheibling, 1993). Observations suggests that:

$$\frac{n_1}{t_1} k = \frac{n_x}{t_x} \quad (4)$$

where the proportionality coefficient $k \neq 1$, a non directly proportional relationship. (The settlement function may instead be non-linear, that is, the relationship between set at time t_x and set at time t_1 would involve exponential or higher order terms; for simplicity, here I treat only the linear case). If $k > 1$, the number of larvae set in t_x is *disproportionally higher* than those set within a sampling interval of t_1 . For example, the number of larvae set in 2 days is *larger* than two times the number of larvae set in 1 day. For $k < 1$, the number of larvae set in t_x is disproportionately smaller than those set with t_1 sampling interval (v.g. the number of larvae set in 2 days is *smaller* than two times the number of larvae setting in 1 day) (Figure 8).

There are various hypotheses explaining the phenomenon that $k \neq 1$. The most obvious are space limitation, mortality of early settlers, and settlement behavior. (1) If settlement space is filled early, longer sampling interval would not yield more larvae; as the available space is filled, there is no more space to settle, and $k < 1$. (2) If there is mortality of settled larvae, then $k < 1$, because the longer the sampling interval, the more the mortality (unless mortality is inversely density-dependent). Small sampling interval would yield

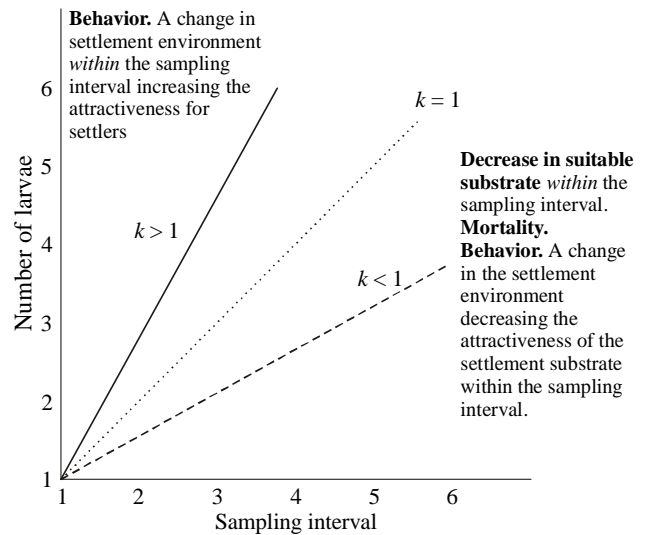


Figure 8. Schematic representation of the different values and explanations for the proportionality coefficient k in equation (4).

higher set rates because mortality would operate over a short period (Booth, 1991; Michener & Kenny, 1991; Minchinton & Scheibling, 1993). (See Hunt & Scheibling, 1998, for a similar interpretation.) (3) Behavior of settling larvae in the presence of settled spat would also explain this inequality. Early settlers or a more attractive substrate within a *sampling interval* attracting late settlers would result in $k > 1$ (Booth, 1991; Michener & Kenny, 1991). On the other hand, early settlers or a less attractive substrate repelling late settlers would yield $k < 1$. There is also the possibility that k varies with time and area, and that some of the above processes interact.

Michener and Kenny (1991) observed oyster settlement in subtidal horizontal asbestos set-plates. They found that $k < 1$ and suggested that this resulted from mortality associated to siltation or predation. On vertical plastic tubes on the intertidal, $k > 1$, which they suggested could be explained by gregarious settlement behavior.

Observations on intertidal barnacle-set on plastic plates show that $k < 1$ in intertidal plates (Pineda, unpub.). For a hypothetical example, on average 10 larvae would settle on plates sampled every day, yielding a rate of 10 larvae per day, while 15 would settle on plates sampled every other day, yielding 7.5 larvae per day. This result has been obtained for low and high settlement areas, and in plates where there is abundant

space for settlement (Pineda, pers. obs.), suggesting that space limitation as a cause of $k < 1$ is unlikely. It is plausible then that this inequality is related to mortality of early settlers, with behavior as a second or complimentary hypothesis.

A related phenomenon is that settlement rate does not scale *directly proportionally* with settlement-plate immersion time (Hatton, 1938):

“Y a-t-il proportionnalité entre le nombre de larves fixées sur un chantier et le temps pendant lequel ce chantier est couvert d'eau? En aucune façon...” (P. 264)

(Is the number of larvae set over a rock proportional to the time that the rock is covered by water? Not at all...)

For example, one plate immersed by the tide 6 hours will not have twice as many settlers as a plate immersed in the water 3 hours. This is also demonstrated by field results showing little or no differences in settlement-rate in plates at different vertical levels in the intertidal (e.g. Hatton, 1938; Pineda, 1994). Of course, differences in settlement must arise at some level, and eventually one should find more settlers per sampling interval in plates immersed longer than in plates immersed only a fraction of the time (e.g. Michener & Kenny, 1991). It seems arbitrary, however, to scale settlement measurements linearly to immersion time, as some studies have done in the past.

VII.h.3 Spatial and temporal correlation in settlement time-series, and lagged correlation in settlement

Following Pineda (1994), *spatial correlation* “is used for correlation over some time of the individual species among time (irrespective of other species), while *temporal correlation* is the correlation...” among two or more species “within one site, independent of other sites”.

Assume a larval transporting event with alongshore scale L . Settlement plates spaced equal or less than L would all receive settlers, resulting in spatially correlated settlement peaks. Correlated “settlement” peaks measured daily have been observed at several scales, ranging from 100’ m (Wetthey, 1986; Pineda, 1994) to

10’s km (Wetthey, 1986, J. Pineda and M. López in prep.) to 100’s of km (Caffey, 1985). Spatial correlation in settlement may then result from common transporting events, and the scale of the settlement may help reveal the scale of the transporting mechanism. Shanks and Wright (1987) correlated barnacle settlement with number of drifters returned by what they interpreted as linear internal waves. Farrell *et al.* (1991) measured settlement in several sites separated by various distances; unfortunately, in this last study, settlement data for all sites were not presented. Ebert *et al.* (1994) measured weekly settlement of seurchins for three years in ten sites along the West Coast of the US separated up to 8°. They found that *S. purpuratus* settlement was geographically coherent, with correlated patterns among northern, central, and southern sites.

The correlation scale between settlement and physical transport events can be upset by several factors. For example, consider a hypothetical oceanic front 10 km long with a large number larvae arriving to the shore. One would expect correlated settlement along 10 km of the coastline. However, this correlation scale may be upset by at least 3 factors: (1) Differential mortality of settlers may obscure the spatial correlation. For example settlers arriving in one section of the front may die due to local factors, potentially reducing the observed settlement scale. (2) Along-shore surf-zone currents may increase the settlement scale by extending the larval patch farther along the shore. That is, the larval patch is stretched beyond the size of the front and then produces a settlement scale larger than the front. For example, the 10-km front that arrives to the shoreline could be stretched an additional 5 km before settlement is quantified. This would produce a longer settlement scale (15 km) than the scale of the front (10 km). (3) Larval patchiness in the front may reduce the observed settlement scale. For example, larvae are present in only 1/10 of the 10 km front, producing a settlement scale of 1 km only. Both 2 and 3 are dependent on the sampling interval. The longer the sampling interval, the further the patch would be stretched, and the higher the cumulative mortality.

It is important to highlight that processes responsible for *correlated spatial settlement*, such as synchronous larval transport, are different to the processes determining the *magnitude of the settlement rate*, such as larval supply and the amount of suitable substrate. Consider the hypothetical case of two rocky shores

separated 20 km exposed to the same larval pool abundance, and with similar onshore larval transport regimes, with transport scales larger than the separation distance of the two sites. Consider now that one site has relatively little amount of suitable substrate for settlement because much of the hard substrate is covered by sand. A time series on settlement rate on the two sites would show spatially correlated settlement; peaks would coincide in time. On the other hand, settlement rate magnitude would be very different, with larger rates in the site where there is little substrate available for settlement. Pineda and López (unpub. ms.) present an example that resembles this hypothetical case.

Another characteristic of settlement time-series that may help elucidating transport mechanisms is temporal correlation among different species. If the transporting event transports several larval taxa, one would expect correlation in settlement among species. Pineda (1994) observed that settlement of the barnacles *Chthamalus* and *Pollicipes* were correlated, and suggested that this was consistent with a hypothesis of common transporting events for the two species. Correlated settlement among various species weakens the hypothesis of peaked settlement caused by larval behavior or synchronous egg release, as this would imply adding several additional assumptions to these hypotheses.

Finally, as pointed above under (IV), correlations of settlement magnitude and physical transport (or a proxy variable for physical transport) may be misleading in cases where the larval pool varies, because these analyses assume (a) a linear relationship between settlement and physical transport and (b) little variability in the larval pool. In cases where the larval pool varies and the relationship between settlement and physical transport is non-linear, it may be inappropriate to correlate settlement magnitude and physical transport.

VIII CONCLUDING REMARKS

In summary, this ms. argues that settlement-rate time-series are valuable initial points to formulate larval transport hypotheses. This is not new, as others have implicitly reached this same conclusion. Settlement time-series are valuable provided that one understands that processes other than the rate of larvae arrival influence it, including the amount of suitable substrate for settlement and the sampling interval.

Another point worth underscoring is that in searching for mechanisms responsible for larval transport and dispersal, researchers should try to obtain their own observations instead of invoking published arguments, and that one should measure the scale of the transport mechanism before assuming one. The way the water moves in the nearshore and offshore is very different, and “importing” meso-scale arguments to the nearshore is logically untenable. Measurement of the transport mechanisms is the only way to secure this important knowledge. This is challenging for nearshore oceanographers, and even more for nearshore ecologists with little or no formal training in the geophysical sciences, and yet it appears essential to understand the population and community ecology of nearshore systems.

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