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INTERACTION OF PHYSICAL AND BIOLOGICAL PROCESSES IN THE SETTLEMENT OF PLANKTONIC LARVAE

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ABSTRACT

Planktonic larvae are at the mercy of the currents for their approach to settlement sites. The presence of planktonic larvae at any given location is a random process. Time-series data for phytoplankton suggest that the characteristic time for a plankton patch to be at a given coastal location is about a week. Once at a settlement site, the interaction of physical processes and biological responses determines the spatial pattern of settlement. For example, where larvae settle when they encounter a kelp bed depends on the current speed, vertical larval distribution, and larval behavior. Simple calculations of settling by abalone larvae suggest that their concentrations in the water could be halved within 100 m of entering a kelp bed. The faster currents of a kelp-free area would extend this distance to about a kilometer. This interaction of the physical and the biological is an important aspect of larval ecology.

A benthic animal with a planktonic larval stage is a strange beast. Not only must it survive and prosper in two different realms but it must also successfully make the transitions to the plankton and back to the benthos. In this paper, I consider the role of physical processes in the transition from the planktonic larval stage to the benthic adult.

First, I discuss the length of time that a planktonic organism occurs in a given region. Knowing this time for the larval stage of a benthic organism makes it possible to study variations in recruitment. Knowing this time also makes it possible to sample for planktonic larvae at intervals short enough to give representative values for larval concentrations without oversampling. Second, I discuss the interaction of larval behavior with water movement to determine the small-scale spatial distribution of larval settling in habitat patches.

CHARACTERISTIC PLANKTONIC OCCURRENCE TIMES

The ability to relate benthic organism recruitment to planktonic larval concentrations depends the use of an appropriate sampling interval. Too long a sampling interval may cause measured values to differ from average larval concentrations; too short an interval yields samples with little additional information but a large burden of sample collection and processing. Knowing the temporal distributions of larval concentration makes it possible to plan a better sampling scheme.

An example of such a larval monitoring program was Yoshioka's (1973) daily collection of water samples from the seawater intake system of the Scripps Institution of Oceanography in La Jolla, California. Yoshioka used the water samples to determine concentrations of *Membranipora serrilamella* larvae over a 3-month period. His results showed that larval abundance varied with time. Typical interval for pulses in larval abundance seemed to be about 5-10 days.

To the extent that the same physical processes control planktonic larval abundance as do phytoplankton abundances, statistics calculated from a phytoplankton time series can also tell us about relevant larval time scales. Eppley et al. (1984) have shown that the phytoplankton off the Southern California coast occur in patches that can be 25 km long. Star and Mullin (1981) found characteristic length scales of zooplankton distributions in the same area of about 4 km. Mackas (1984)

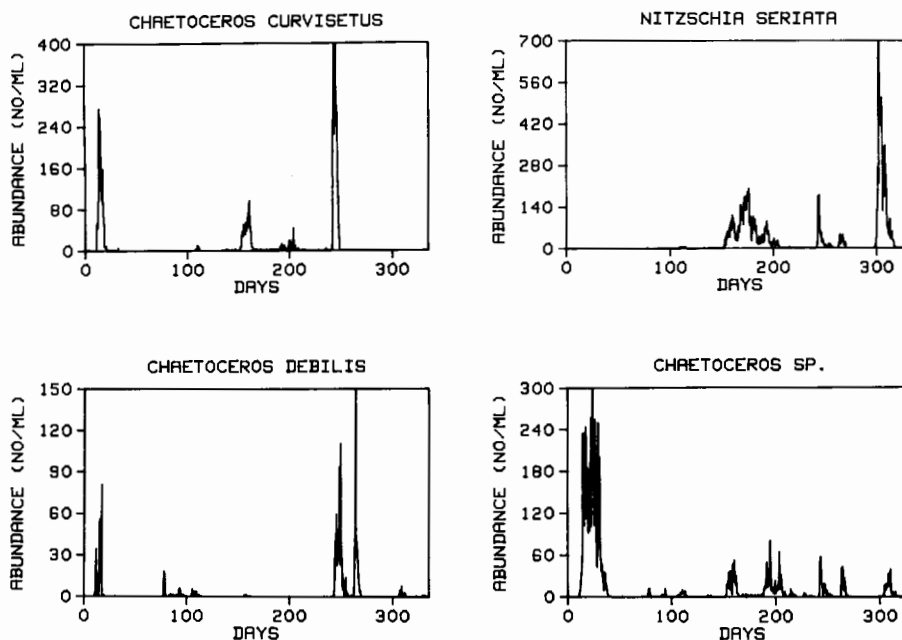


Figure 1. Concentrations through time of the four most abundant diatom species in the Allen record.

studied both zooplankton and phytoplankton patch length scales off British Columbia and found the two slightly different. Different definitions of patch length in the different studies keep these characteristic lengths from being completely comparable. However, these studies suggest that phytoplankton and zooplankton patches can be of the same general size. This allows the use of phytoplankton time-series data to discuss potential time scales for planktonic larval abundances.

For 12 months, from September 1919 to August 1920, Allen twice daily collected phytoplankton samples from the end of the Scripps pier. He used these samples to estimate abundances of diatom and dinoflagellate species. These data offer a long record which can be used to study characteristic time scales for the occurrence of a plankton species at a given location. Enright (1969) has used these data to estimate zooplankton grazing rates off La Jolla.

Diatom abundances do vary, different species having peak abundances at different times for different lengths of time (Fig. 1). Autocorrelations of the time series reflect this (Fig. 2). Autocorrelations decrease with increasing separation intervals or lags. The time interval separating two samples when the correlation coefficient dropped to 0.5 ranged from 1 to 8 days. The two most abundant diatom species had the longest de-correlation times, the fourth most abundant species had the shortest de-correlation time.

The extent to which larval distributions are similar to those of planktonic organisms will depend on the history of the larva. One with a long precompetent period is more likely to have its temporal distribution controlled by the physical processes determining those of the other planktonic organisms than is one with a precompetent period of hours. The fact that planktonic organisms can occur in "blooms" or pulses of only a few days length means that an arbitrarily chosen sampling interval can result in missing a larval pulse and poor estimation of

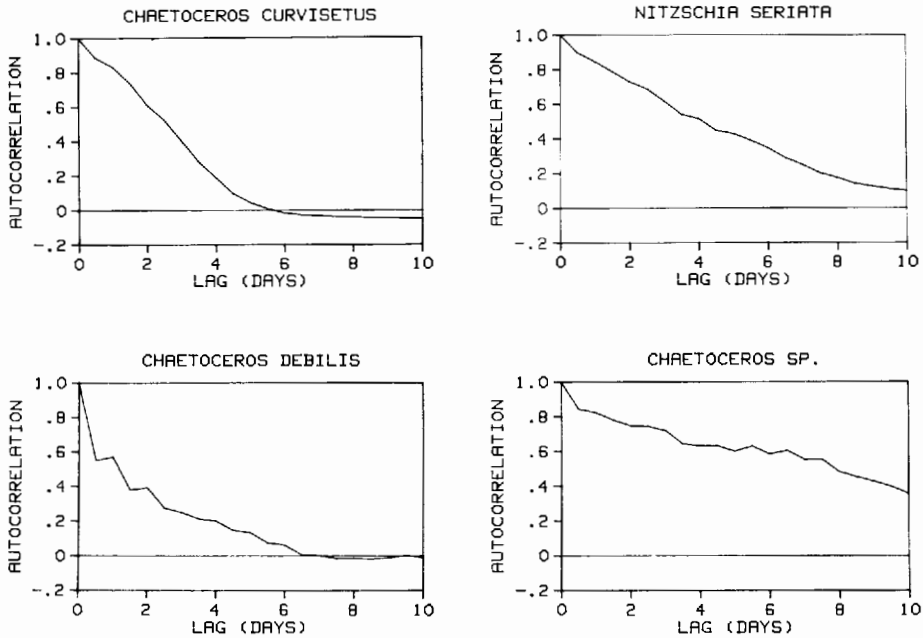


Figure 2. Autocorrelation of diatom time series.

average larval concentrations. The first step in monitoring larval concentrations is the determination of the temporal variability of the larva.

SMALL SCALE SPATIAL PROCESSES

From the moment that a larva is released into the water it is moved by currents and eddies away from the favorable habitat of its parents. After it develops from the precompetent to the competent phase, water currents can determine where it settles. Once a larva has reached a general area suitable for settlement, such as the coastal region, there are additional processes which affect the frequency and abundance of larvae at a particular location. The ocean bottom is not uniform but consists of a range of environments. One area might be mud suitable for a certain polychaete species, another area might have the hard substratum needed for a particular scallop, a third might have the seaweeds needed for a sea urchin larva to settle. When a planktonic larva happens upon its particular environment, it must be prepared to settle. As a water parcel bearing larvae flows over the appropriate area, larvae settle out to become adults. As larvae settle, fewer larvae remain in the water. Virtually all larvae will leave if the water parcel stays a long enough time over suitable substratum. If a benthic habitat is large enough, passage of a water parcel over the habitat will lead to the depletion of larvae before the water reaches the habitat interior region. There would be no recruitment in an otherwise favorable area because no larvae could reach it. It is the interaction of larval settling rate with the rate of water motion that determines the spatial pattern of larval settling within a suitable habitat patch, on a scale smaller than that of precompetent larval dispersal.

In this section I develop models for two current regimes, one constant and the other oscillating, and apply the results for conditions that are characteristic of two

different areas of the San Diego, California coastal environment. I assume that the suitable habitats occur with sharp boundaries as benthic patches having distinct boundaries on the up-current end. Larval concentrations outside such a habitat patch are fixed by external events, those inside a result of larval behavior interacting with water currents.

Currents in a coastal zone are stronger in the longshore direction than in the cross-shore direction (Winant, 1976; Winant and Bratkovich, 1981). Currents in shallower areas (less than 60 m) tend to be slower than those in deeper water. Massive kelp stands further slow water movement. Longshore currents usually consist of a current constant over time scales of days and currents fluctuating at tidal frequencies. Off the Southern California coast the dominant tidal frequency is semi-diurnal. Cross-shore currents are mostly of the oscillating sort. The two types of currents, constant and oscillating, have different effects on larval settling.

Consider first the case of a water parcel in a constant current flowing with a velocity, v , and containing planktonic larvae in concentration, C_0 . Larvae start to settle when the water parcel encounters a suitable habitat patch. If larvae settle at a rate proportional to the number of larvae remaining, the larval concentration in a water parcel at time, t , after encountering the patch is given by

$$dC/dt = -kC \quad (1)$$

$$C = C_0 e^{-kD/v} \quad (2)$$

where k is the settling rate constant, D is the distance to the patch edge, and the relationship $D = vt$ has been used. The concentration used is the concentration averaged over the water column.

The flux of larvae to the bottom, R , equals the rate at which larvae in the total water column z deep settle out, or

$$R = zkC = zkC_0 e^{-kD/v} \quad (3)$$

This is the fairly simple case of exponential decrease in the concentration of larvae with distance into the patch. Decreased values of k lead to increased penetration of larvae into the patch (eq. 2). However, they do not automatically lead to increased settling fluxes because lower values of k also lower R .

As a second case, consider sinusoidal water motion. Examples of this would include cross-shore motions near the coast, tidal currents, and the currents in the Pt. Loma (California) kelp bed. Assume that the current velocities at all locations are given by

$$v = v_0 \sin(\omega t) \quad (4)$$

Water in this case goes nowhere; it just sloshes back and forth. The distance that a water parcel goes into the patch depends on what time in the cycle, t_0 , it enters the patch,

$$D(t) = \int_{t_0}^t v \, d\tau \quad (5)$$

$$= \int_{t_0}^t v_0 \sin(\omega\tau) \, d\tau \quad (6)$$

$$= (v_0/\omega)(\cos \omega t_0 - \cos \omega t) \quad (7)$$

Eq. 7 can be modified to determine t_0 for a water parcel at distance D at time t

$$t_0 = (1/\omega)\arccos[\cos(\omega t) + \omega D/v_0] \quad (8)$$

Larval concentration in the water parcel is an exponential function of the time that the water parcel has been in the patch

$$C = C_0 e^{-(t-t_0)k} \quad (9)$$

$$= C_0 e^{-k(t-(1/\omega)\arccos[\cos(\omega t)+\alpha])} \quad (10)$$

where $\alpha = \omega D/v_0$. Water over the patch when the cycle starts at $t = 0$ is assumed to have no larvae. Only water that has come from outside the patch has larvae. There are larvae over a given location only when water that has passed over the edge is present. The first water parcel to reach a given location is the one that crossed into the patch at $t_0 = 0$. It reaches D at time t_f , given by

$$t_f = (1/\omega)\arccos(1 - \alpha) \quad (11)$$

The last larvae leave a location at time $t_1 = T - t_f$, where $T = 2\pi/\omega$ is the cycle period. This deepest incursion of larvae in the patch occurs right before the flow reverses at $t = T/2$. The deepest penetration corresponds to a distance where $\alpha = 2$ (Fig. 3).

The average concentration, C_{ave} , for any location with α less than or equal to 2 is given by

$$C_{ave}(D) = \frac{1}{T} \int_{t_f}^{t_1} C(D, t) dt \quad (12)$$

$$= \frac{C_0}{T} \int_{t_f}^{t_1} e^{-kt} e^{\beta \arccos[\cos(\omega t)+\alpha]} dt \quad (13)$$

where $\beta = k/\omega$. The average benthic settling flux, R_{ave} , is

$$R_{ave}(D) = \frac{z}{T} \int_{t_f}^{t_1} kC(D, t) dt \quad (14)$$

$$= zkC_{ave} \quad (15)$$

Larval distribution is a function of the settling rate constant incorporated in the dimensionless parameter, $\beta = k/\omega$, as well as α (Fig. 4). For example, the value of α for which the average C decreases to half the external concentration is 1 for the $\beta = 0$ (no settlement), 0.7 for $\beta = 0.1$, and less than 0.1 for $\beta = 1$ or greater. Rapidly settling larvae do not reach far into a benthic patch.

Values for currents off San Diego provide examples of the actual sizes of these relationships. Currents within the Pt. Loma kelp bed are slower than outside because of the high kelp drag (Jackson and Winant, 1983; Jackson, 1983). At one particular location within the kelp the mean current during a late summer deployment was about 0.1 cm sec^{-1} , the root mean square (RMS) current was 2 cm sec^{-1} . The dominant water motion was a semidiurnal longshore current (a period of about 12.4 hours). Offshore from the kelp the mean current was 2.1 cm sec^{-1} and the RMS current was 10 cm sec^{-1} . The effect on larval concentrations and settling rates for these currents and for different values of $k-1/(10 \text{ min})$, $1/(100 \text{ min})$, and $1/(1,000 \text{ min})$ —have been calculated (Figs. 5, 6).

Oscillating flow moves water a maximum of 283 m in the kelp regime and 1,418 m in the sandy regime. Larvae can move deeper into an area only if moved

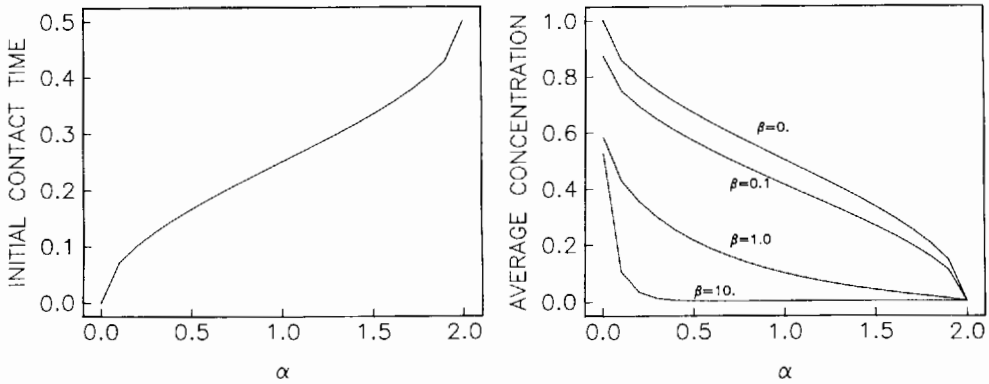


Figure 3. (Left) Initial contact time for larvae as a function of normalized distance from the edge, α , for oscillating flow. The contact time is expressed as a fraction of total period, $2\pi t/\omega$. The normalized distance equals $D\omega/V_0$, where D is the actual distance, ω is the frequency of the motion (in radians per time), and V_0 is the maximum velocity. Notice that the maximum penetration of water from the edge is at normalized time = 0.5, where $\alpha = 2$.

Figure 4. (Right) Average larval concentration within a patch as a function of normalized distance from the edge, α , for oscillating flow. Larval concentrations are relative to the external concentration. The curves for different values of $\beta = k/\omega$ show the effect of differing settling rates. The curve for $\beta = 0$ shows the case when the average concentration of larvae is unaffected by settling but only affected by decreased contact time. Curves for increasing values of β show the effect of increasing larval settlement in decreasing larval concentrations in the interior.

by the constant current. For the two faster settling rate constants ($k = 0.1, 0.01 \text{ min}^{-1}$), oscillating flow allows higher concentrations of settlers than does steady flow. For the slow settling rate constant ($k = 0.001 \text{ min}^{-1}$) higher concentrations result from steady flow. For all settling rates, there is a significant decrease in larval concentrations over distances that are small compared to possible habitat sizes. Larval concentrations were 10% of initial concentrations at 2.7, 27.6, and 276 m from the edge for the three values of k in constant flow and 12, 119, and 220 m from the edge in oscillating flow under kelp bed conditions. The values for the sandy area current conditions were 28, 277, and 2,766 m in constant flow and 60, 596, and 1,395 m in oscillating flow.

Settlement patterns differ from concentration distributions. A larva with a low value of k may have a higher concentration at a given location but a lower settling rate than a species with a higher k value. This is evident in both current regimes (Fig. 6). Settling rates are highest for the fast settling species within the first 26 m in the kelp and 104 m in the sandy area, highest for the intermediate settling rate between 26 and 216 m for the kelp regime and between 104 and 870 m for the sandy area, and greatest further along for the slower settling species. Settling rates in the interior region where the slowly settling larva dominates are slow, less than 1% of the settling rate of the fast settling species at the leading edge.

DISCUSSION

The settling rate constant, k , does not describe a purely biological response but is rather a parameter that incorporates the results of a variety of behavioral and environmental processes. The probability that a larva next to the bottom will settle in a given time interval might depend on the concentration of a chemical

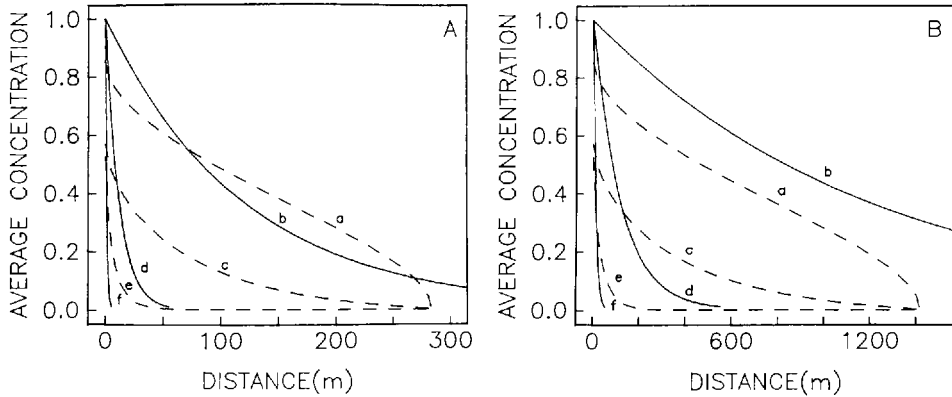


Figure 5. Average larval concentrations within a patch as a function of distance from the edge for typical coastal ocean conditions. A) Conditions typical of the longshore flow in Pt. Loma kelp bed in 14-m deep water (Jackson, 1983). Mean velocity is 0.2 cm sec^{-1} (b, d, f); peak velocity for oscillating flow is 2 cm sec^{-1} (a, c, e). B) Conditions typical of the longshore flow over a sandy bottom off Pt. Loma in 28 m of water (Jackson, 1983). Mean velocity is 2.1 cm sec^{-1} (b, d, f); peak velocity for oscillating flow is 10 cm sec^{-1} (a, c, e). The values of k are 0.1 min^{-1} (c, f), 0.01 min^{-1} (a, b). Dashed lines—oscillating flow; solid lines—constant flow.

cue in the near-bottom water, on the benthic surface roughness, or on the percent cover of a certain alga (Crisp, 1984; Morse et al., 1980). The probability that any given larva will settle out in a time interval depends not only on this probability but also on the probability of the larva being next to the bottom. This latter probability is a function of the distribution of the larvae in the water column and the mechanisms and rates of larval exchange between the bottom and the overlying waters. Such exchange could be caused by purely hydrodynamic processes, such as turbulence or particle sinking, by behavioral responses, such as larval swimming, or by a combination of the two. The parameter k , with units of time^{-1} , incorporates the larval behavior at the benthic surface, the nature of the benthos, and the exchange rate between larvae at the bottom and in the overlying water.

There are several different settling rates of interest. The first is that at which larvae leave a given volume of water and thereby change the larval concentration. This water column settling rate equals the concentration of competent larvae times k and has units of $\text{larvae volume}^{-1} \text{ time}^{-1}$. The second is the rate that the larvae actually settle on the bottom. This benthic larval flux is equal to the number of larvae that have settled out from the overlying water and has units of $\text{larvae area}^{-1} \text{ time}^{-1}$. For the simple model used here, it is equal to the thickness of the larval layer in the water column times the water column settling rate. As long as the larval layer has a constant thickness, as tacitly assumed in this model, the water column settling rate and the benthic larval flux differ only by a constant.

As an example of how to estimate a value of k , consider the abalone, *Haliotis*. When searching for a place to settle, a competent abalone larva swims upward to the surface, then settles to the bottom, both at rates of about 1 m min^{-1} (D. Morse, pers. comm.). If it hits an encrusting coralline alga of the genus *Lithothamnion*, the larva attaches to the bottom and metamorphoses (Morse et al., 1980); if it does not contact the alga it starts to swim up and repeats the cycle. Assume that larvae are distributed uniformly in the water column before coming into a favorable habitat and that 10% of the benthos in that area is covered with

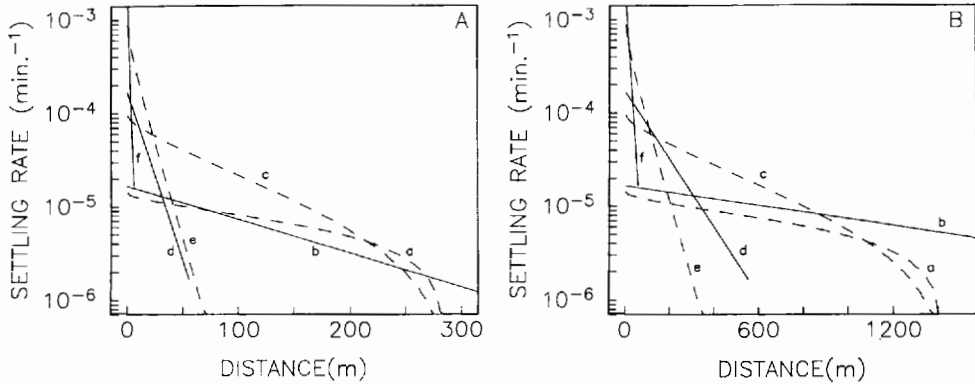


Figure 6. Settlement rate within a patch as a function of distance from the edge for typical coastal ocean conditions (as in Fig. 5). The benthic larval flux equals this settling rate times the initial larval concentration times the water depth. A) Kelp bed. B) Sandy bottom. Oscillating flow—*a, c, e*; constant flow—*b, d, f*; $k = 0.1 \text{ min}^{-1}$ (*e, f*), 0.01 min^{-1} (*c, d*), and 0.001 min^{-1} (*a, b*). Dashed lines—oscillating flow; solid lines—constant flow.

the proper alga. In water 20 m deep, it would take about 40 min for the larvae to make a complete cycle, up and down. During that time, 10% of the larvae would have settled. The estimated value for k is then $0.1/40 \text{ min}$, or 0.0025 min^{-1} . Under the kelp bed conditions (Fig. 5A), larval concentrations would be halved within 100 m of entering the habitat; under the sand bottom conditions (Fig. 5B), larval concentrations would take about 1 km to decrease by half. Shallower water would shorten the distance the larvae move up and down and thereby increase the value of k . In 5 m deep water, k would increase to $0.1/10 \text{ min}$, or 0.01 min^{-1} , and thereby shorten the distance required to halve larval concentrations. Other factors, such as an increase in algal cover and a decrease in current speeds, or a decrease in the larval layer thickness could further decrease the penetration of the abalone larvae into a habitat patch.

What would the larval settling model predict about larval distributions in the kelp bed? The Point Loma kelp bed is about 7 km long (parallel to shore) and about 1 km wide (across shore). Larvae should arrive at any of three edges, the up and down coast edges and the outside edge. Movement into the bed from the up and down coast edges will be as described in Figures 5A and 6A. Of course the longshore movement from a mean current will be from the upstream edge. The semi-diurnal current will move larvae in from these two edges a distance of at most about 300 m. Larvae could be taken further into the bed by the net current but only at low concentrations. There is no net current in the cross-shore direction. Movement across the outer edge will be confined to that driven by semi-diurnal motions. RMS speeds of cross-shore motions decrease going into the kelp bed, being comparable to the longshore values used in Figure 6A at the outer edge and half as fast in the interior. Settling in such a kelp bed would be mostly confined to a band around the perimeter of about 300 m. This band is the result not only of larval depletion but also the result of limited water movement. Larvae carried by a net current penetrate further at lower concentrations and have settling rates significantly less than those of larvae outside.

Similar patterns would occur in a sandy area set in the midst of hard substrata or of reefs in the midst of sand but the scales would be different. Again, steady

motion will move larvae from the upcurrent edge while oscillating motions could move larvae from either edge. In the sandy area, though, net movement is more important in movement of larvae than in the kelp area. The semi-diurnal current moves larvae in by about 1,400 m (Figs. 5B, 6B). Slowly settling larvae ($k = 0.001 \text{ min}^{-1}$) have higher concentrations everywhere under the net current case than under the oscillating case. Despite the scale change, the sandy bottom area would still have large changes in settlement rates over distances on the order of a kilometer.

An environment where a spatial distribution of sessile adults has been observed that is consistent with these models is that provided by *Macrocystis pyrifera*. Bernstein and Jung (1979) sampled the spatial distribution of adult *Membranipora membranacea* in a kelp bed off San Diego. They found a strong edge effect, with high concentrations of encrusting *Membranipora* near the outside edge, low concentrations in the interior, and no *Membranipora* at the inside edge. Bernstein and Jung argued that this was the result of depleted numbers of larvae in the bed interior caused by the larval settling near the exterior. Other species, such as the encrusting bryozoan, *Lichenopora buskiana* did not show this high settlement near the edge. They also found that small kelp beds suffered more from encrusting than did larger ones, presumably because the larvae had settled out in the larger but not in the smaller.

This model shows that where a larva settles depends on the interaction of biological and physical transport rates. Their interaction determines the spatial distribution of the benthic settling flux. As a result, the effectiveness of a species in colonizing a site depends on the patch size and the organism's settling rate. Fast-settling species are very effective colonizers of small patches but cannot reach very far into large substratum patches because they are filtered out; slow-settling species are not effective with small patches because too few settle but can colonize large patches because their larvae penetrate to the interior. For each patch size/physical regime there is an optimal settling behavior for colonizing the whole patch. It is possible that organisms have evolved to settle in habitat patches of different sizes.

Larval settling at different distances from patch edges should have an important effect on benthic ecosystems. If different species with planktonic larvae have a range of settling rates, they will settle differently on different habitat patches. Small patches will have heavy settlement of a few species. Large patches will have a range of settling patterns with gradations of larval fluxes. On a patch's leading edge there will be rapid settling and heavy recruitment. In its interior fewer species will settle at slower rates, implying slower recruitment. This differential settling would be another mechanism for creating different ecological zones in an initially uniform habitat.

This analysis has several implicit assumptions about larval behavior, including that larvae all come from outside the patch, that they are present at the patch boundary at constant concentrations and that current conditions are constant. If currents are as slow as they are in a large kelp bed, some organisms could spend their entire larval phase without leaving the kelp bed. For example, several encrusting organisms, such as *Bugula pacifica* and *Spinrorbis borealis* (listed in Jackson and Strathmann, 1981) have essentially no precompetent period. Larval dynamics in a patch start to resemble island conditions for such species. For other species whose larvae come from outside the bed, there will be changes in the larval concentrations at the patch borders. The discussion in the early part of this paper noted this. The characteristic time for a plankton species to be present, on

the order of a week, is long compared to the 12.4-h period of the semi-diurnal case used for oscillating flow and is presumably longer than any larval settling time constant. As a result, larval transport and settling processes occur faster than changes in larval concentrations. The model provides a reasonable description of these processes. The third implicit assumption, that current conditions are constant, is more problematic. Seasonal changes can cause changes in coastal currents. Longshore "mean" currents in the kelp bed during winter conditions can be as fast as 2 cm sec^{-1} (unpubl. data). Such a current would distribute larvae within the kelp bed in ways more like the conditions for the sandy area portrayed for the mean current speed cases in Figures 5B and 6B. For there to be heavy recruitment during such a relatively rare high speed current would require the co-occurrence of high larval concentrations. If this co-occurrence is rare, then recruitment inside a large patch may be a rare event.

Larval mortality by such means as fish predation can also cause a decrease in larval concentrations over a habitat area. Losses due to mortality can be included in this model with minor changes. If the larval settling constant is k_s and larval mortality rate is given by a mortality constant, k_m , times C then eq. 1 becomes

$$dC/dt = -k_s C - k_m C = -k_t C \quad (16)$$

where $k_t = k_m + k_s$. Concentrations are predicted by eqs. 2, 9, 10, 12, and 13 if the value of k is replaced by k_t ; benthic settling fluxes can be calculated using these concentrations and k_s . Thus, eq. 3 becomes

$$R = zk_s C = zk_s C_0 e^{-k_t D/v} \quad (17)$$

and eq. 15 becomes

$$R_{ave}(D) = zk_s C_{ave} \quad (18)$$

A result of this modification is that larval concentrations and benthic settling fluxes decrease over shorter distances than without mortality. For situations where k_s is less than k_m , the larval mortality controls larval concentration. Species with different values of k_s could have similar concentration distributions, although settling fluxes would differ.

This discussion has emphasized kelp beds because the conditions there are well documented and the currents particularly slow. The same conclusions hold for other patches when length scales are changed to account for different current rates.

CONCLUSION

Planktonic larvae occur in a region at which they can settle in a manner that is patchy in space and time. Phytoplankton records suggest that characteristic times for such occurrences are on the order of a week. Spatial patchiness can result from the interaction of physical and biological processes. The result should be the settling of larvae near the edges of suitable habitats.

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