



Recruitment Dynamics in Complex Life Cycles

Jonathan Roughgarden; Steven Gaines; Hugh Possingham

Science, New Series, Vol. 241, No. 4872 (Sep. 16, 1988), 1460-1466.

Stable URL:

<http://links.jstor.org/sici?sici=0036-8075%2819880916%293%3A241%3A4872%3C1460%3ARDICLC%3E2.0.CO%3B2-Y>

Science is currently published by American Association for the Advancement of Science.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/aaas.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

33. S. D. Tuljapurkar, *Theor. Popul. Biol.* **21**, 141 (1982); R. Lande and S. H. Orzack, *Proc. Natl. Acad. Sci. U.S.A.*, **85**, 7418 (1988).
34. R. B. Harris, L. A. Maguire, M. L. Shaffer, *Conserv. Biol.* **1**, 72 (1987).
35. T. E. Lovejoy et al., in *Conservation Biology, the Science of Scarcity and Diversity*, M. E. Soulé, Ed. (Sinauer, Sunderland, MA, 1986), pp. 257–285; D. S. Wilcove, C. H. McClellan, A. P. Dobson, in *Conservation Biology, the Science of Scarcity and Diversity*, M. E. Soulé, Ed. (Sinauer, Sunderland, MA, 1986), pp. 237–256.
36. A. Okubo, *Diffusion and Ecological Problems: Mathematical Models* (Springer-Verlag, New York, 1980).
37. H. Kierstead and L. B. Slobodkin, *J. Mar. Res.* **12**, 141 (1953).
38. P. H. Leslie, *J. Anim. Ecol.* **25**, 291 (1966).
39. C. M. Pease, R. Lande, J. J. Bull, unpublished results.
40. B. A. Wilcox, in *Conservation Biology, an Evolutionary-Ecological Perspective*, M. E. Soulé and B. A. Wilcox, Eds. (Sinauer, Sunderland, MA, 1980), pp. 95–118.
41. D. H. Janzen, in *Conservation Biology, the Science of Scarcity and Diversity*, M. E. Soulé, Ed. (Sinauer, Sunderland, MA, 1986), pp. 286–303.
42. E. G. Leigh, Jr., A. S. Rand, D. M. Windsor, Eds., *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes* (Smithsonian Institution Press, Washington, DC, 1982).
43. S. T. A. Pickett and P. S. White, Eds., *The Ecology of Natural Disturbance and Patch Dynamics* (Academic Press, New York, 1985).
44. R. Levins, *Bull. Entomol. Soc. Am.* **15**, 237 (1969); *Lect. Math. Life Sci.* **2**, 75 (1970).
45. R. Lande, *Am. Nat.* **130**, 624 (1987).
46. J. L. Brown, *The Evolution of Behavior* (Norton, New York, 1975).
47. M. L. Shaffer, *BioScience* **31**, 131 (1981).
48. W. R. Dawson et al., *Condor* **89**, 205 (1987).
49. R. Lande, *Oecologia* **75**, 601 (1988).
50. "Draft supplement to the environmental impact statement for an amendment to the Pacific Northwest regional guide" (U.S. Forest Service, Portland, OR, 1986), vols. 1–2.
51. J. D. Ligon, P. B. Stacey, R. N. Conner, C. E. Bock, C. S. Adkisson, *Auk* **103**, 848 (1986).
52. R. N. Conner and D. C. Rudolph, "Red-cockaded woodpecker colony status and trends on the Angelina, Davy Crockett, and Sabine National Forests" (U.S. Forest Service, Nacogdoches, TX, 1987).
53. I thank J. J. Bull, S. M. Chambers, D. Jablonski, and C. M. Pease for helpful discussions, and J. A. Coyne, T. D. Price, M. Lynch, M. Slatkin, A. M. Wood, and two anonymous reviewers for criticisms of the manuscript. Supported by U.S. Public Health Service grant GM27120.

Recruitment Dynamics in Complex Life Cycles

JONATHAN ROUGHGARDEN, STEVEN GAINES, HUGH POSSINGHAM

Organisms living in the marine rocky intertidal zone compete for space. This, together with predation, physical disruption, and differing species tolerances to physiological stress, explains the structure of the ecological communities at some sites. At other sites the supply of larvae is limiting, and events in the offshore waters, such as wind-driven upwelling, explain the composition of intertidal communities. Whether the community ecology at a site is governed by adult-adult interactions within the site, or by limitations to the supply of larvae reaching the site, is determined by the regional pattern of circulation in the coastal waters. Models combining larval circulation with adult interactions can potentially forecast population fluctuations. These findings illustrate how processes in different ecological habitats are coupled.

HUMANITY HAS LONG BEEN PERPLEXED BY ERRATIC FLUCTUATIONS in the abundance of commercially exploited marine populations, such as sardines, herring, squid, lobsters, and crabs. One of the first models of theoretical ecology was proposed by Vito Volterra to explain such fluctuations as oscillations resulting from a nonlinear predator-prey interaction (1). Although Volterra's model is still of mathematical interest, fluctuations in marine populations are not regular enough to be considered oscillations (2) and their cause has remained mysterious.

Most biologists assume that marine population fluctuations are somehow caused by events in the offshore waters. The great Danish

marine biologist, Gunnar Thorson, observed that a majority of the marine invertebrate species whose adult phase lives on rocks or burrowed in mud have a two-phase life cycle (3). The conspicuous adult phases of barnacles, starfish, snails, clams, worms, and so forth, are usually preceded by nearly invisible larval phases that live and feed in the coastal waters for a few days to a few months, depending on the species. Most fish also have a two-phase life cycle. The dynamics of a two-phase species can, in principle, be affected at either phase. But Thorson further noted that two-phase species have large fluctuations in abundance when compared to otherwise similar one-phase species. Thus, the larval phase, and not the adult phase, was implicated as the point at which fluctuations affect marine population dynamics. Because most coastal marine populations have

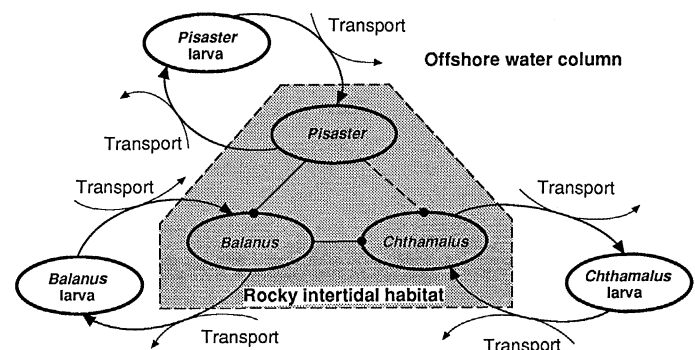


Fig. 1. Schematic of interactions between species in a community of the rocky intertidal zone. Physical contact between adult animals attached to the rocks leads to hierarchical competition for space. As shown with a line terminating in a dot, an individual of *Balanus glandula* overgrows or crushes an individual of *Chthamalus dalli*. Also, mortality from abiotic mechanisms, and from predation by the starfish *Pisaster ochraceus*, affects *B. glandula* more than *C. dalli*. Both species release a larva to the water column that may eventually return to settle on vacant space, as illustrated by the arrow coupling each life cycle to offshore transport mechanisms.

J. Roughgarden is a professor in the Department of Biological Sciences, Stanford University, Stanford, CA 94305, and at the Hopkins Marine Station, Oceanview Boulevard, Pacific Grove, CA 93950. S. Gaines is an assistant professor in the Graduate Program in Ecology and Evolutionary Biology, Brown University, Providence RI 02912. H. Possingham is a postdoctoral research associate in the Department of Biological Sciences, Stanford University.

a two-phase life cycle, the reason why such populations fluctuate is a general question in biology, a question whose answer affects thousands of species many of which have commercial, recreational, or conservation value.

Still, even great fluctuations in the quantity of larvae that return to shore can have little impact on the abundance of adults living along the shore if the shoreline habitat is already saturated with organisms. Thus, processes in the adult habitat that influence whether space or food is available should also be important in some circumstances.

In this article, we review how such factors combine in an explanation of marine population fluctuations, primarily by focusing on a case study involving a common barnacle species of the Pacific coast of North America. Barnacles are abundant in the intertidal zone worldwide, have a representative life cycle, and, for many species, both phases of the life cycle can be identified, located, and censused in the field. No other group of marine organisms presently is as tractable. It will emerge that at some types of sites interactions among adults explain the abundance of populations. At other sites, where the supply of larvae is limiting, currents resulting from wind-driven upwelling along the coast are the primary cause of population fluctuations, although predation by fish on larvae occasionally exerts an important but localized effect.

The work described below exemplifies the progress being made in ecology toward understanding how species with a complex life cycle operate (a complex life cycle contains two or more developmental stages that live in spatially distinct habitats) and how the ecological processes at different places are coupled to one another.

The Ecology of Rocky Shores

Major findings in ecology have come from research in the marine rocky intertidal zone. The intertidal zone is the most accessible of marine habitats, and rocky shores are found along many coastlines. A rocky substrate readily supports small cages for confining an experimental treatment, and the limited mobility and small size of the organisms makes manipulating their numbers feasible. Hence, many field experiments that reveal species interactions have accumulated. The early experiments were carried out on the west coast of Scotland (4) and on the shores of Washington State, and more recently on the coast of New England, New South Wales, Oregon, and California (5–7). The main generalization from the early work is that the species can be ranked with respect to their ability to overgrow one another: the competition for space is hierarchical. If this competition is allowed to go to completion, an area of rock culminates in a near-monoculture of the dominant competitor, which is frequently a mussel. Next in the hierarchy are often medium-sized acorn barnacles that grow to 1 to 2 cm in basal diameter, followed by small acorn barnacles whose basal diameter is 0.5 to 1 cm. The species involved in the hierarchy depend on the coast and type of site. Along most of central California the species are *Mytilus californianus*, *Balanus glandula*, and *Chthamalus dalli* for the mussel, medium-sized barnacle, and small barnacle, respectively.

This competitive hierarchy, together with differing species tolerances for physical conditions, explains much of the composition of intertidal communities where the early work was done. Specifically, the small barnacle is more tolerant of heat stress than the medium-sized barnacle (4, 7–10). Therefore, provided that the mussel is absent, the small barnacle is typically found mostly in the zone above the medium-sized barnacle because the small barnacle is excluded by the medium-sized barnacle in the lower zones where the heat stress is relatively moderate. Similarly, frequent disturbance (any mechanism that opens up vacant space) usually increases species diversity because the dominant competitor is prevented from monopolizing

Fig. 2. Transect lines and stations for the CalCOFI zooplankton samples. These transects were discontinued after 1984.

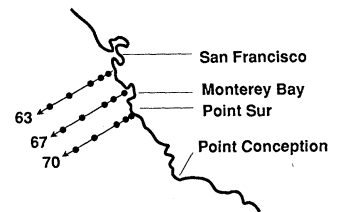


Table 1. Mean annual recruitment rates (averaged from April through July) for *Balanus glandula* on the Pete's Rock site at Hopkins Marine Station, on Monterey Bay in central California ($n = 4$ quadrats), and surface-water transport predicted by mean upwelling indices from mid-January through June (5). A positive index value predicts offshore transport.

Year	Upwelling index (m^3/sec per 100 m of coastline)	Barnacle recruitment (recruits/ cm^2 per week)
1982	46.8 (8.2)*	1.1 (0.1)
1983	-75.3 (7.7)	3.7 (0.3)
1984	52.3 (3.3)	1.4 (0.1)
1985	72.1 (6.0)	0.05 (0.01)
1986	11.6 (8.4)	2.2 (0.6)

*Numbers in parentheses are standard errors.

the space (11). In central California disturbance is caused primarily by the large starfish *Pisaster ochraceus*, a voracious consumer of mussels and barnacles. These relations are illustrated in Fig. 1 within the dotted lines.

Since 1980 the importance of the interactions in Fig. 1 have been increasingly questioned because of observations at newly studied sites. For example, along the central California coastline (7) it is rare to see the classical zonation between barnacles documented in the early studies—at most sites both *Balanus* and *Chthamalus* occur together throughout all heights in rocky intertidal habitat, and substantial vacant space is evident as well. The density of barnacles is simply not high enough for extensive physical contact to develop between adjacent individuals, and the medium-sized barnacle does not exclude the smaller barnacle at heights in the intertidal zone where both are physiologically suited to persist. Similar observations were made earlier in Australia (6).

The classical explanation for this lack of zonation would be that large predators, such as starfish or snails, are sufficiently common to keep the density of barnacles low enough that competition between them ceases (8). But studies at Hopkins Marine Station on Monterey Bay in central California showed that not enough barnacle larvae arrive to occupy all the available space even where large predators such as starfish and snails are rare (7).

Further study showed that spatial variation in the abundance of barnacles on a 10-cm scale at a given height throughout the rocky intertidal habitat was explained by spatial variation in the larval input rates (12). Variation in mortality rates resulting either from predation or physical stress did not contribute to the explanation. The most seaward rocks enjoy a high larval input rate, and a correspondingly high abundance of barnacles, because the water carrying barnacle larvae contacts them first. Once the water reaches the nearshore rocks, the concentration of larvae has become low because most larvae have already settled on the outer rocks. Hence, the nearshore rocks have a lower larval input rate and a correspondingly low abundance of barnacles. Another example of such a “settlement shadow” has been documented for larvae of a bryozoan (13). As these drift into their kelp forest habitat, they settle out on the first blades encountered, contributing to a low density of bryozoans toward the center of the kelp stand.

The importance of the larval input rate (also called the “settlement

rate” and the “recruitment rate”) has now been combined with the factors of hierarchical competition for space, disturbance, and physical stress to produce a new synthetic picture of the ecology of rocky shores (14). Yet new questions are now posed: Is each site idiosyncratic? Is even this new synthesis destined to expand as future studies at more sites reveal still more site-specific phenomenologies and private rules? As will be seen, it now appears that the variation in what happens at different sites can itself be understood and predicted if the regional oceanographic context of the sites is known. Moreover, the distribution of the larvae in the coastal waters can provide clues to reconstructing the circulation pattern in those waters.

Larval Dynamics of Barnacles: A Case Study

Because the settlement rate emerged as a key parameter governing what happens in the rocky intertidal communities of central California, studies were initiated to see what determines the settlement rate. The first factor identified was predation by fish that live in the kelp stands about 100 m wide that lie immediately offshore of the intertidal habitat (15). During the spring, juvenile rockfish (*Sebastes* spp.) living in these kelps prey on the barnacle larvae during two periods—when they are first released (as stage II nauplii) and 2 to 3 weeks later when they return (as stage VI nauplii and cyprids). The quantitative effect of this factor in any year depends on the number of juvenile rockfish and size of the kelp forest that year and may be very large.

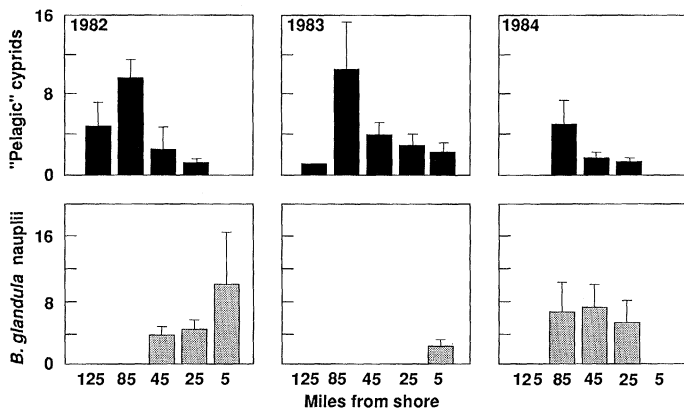
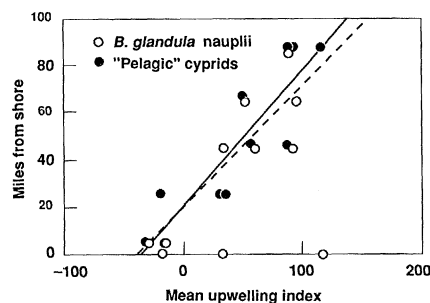


Fig. 3. Distributions of *B. glandula* stage VI nauplii and pelagic barnacle cyprids from CalCOFI plankton samples. Samples from each of the three transects are treated as replicates for the central California region. Values are means with standard errors shown from the three samples at each distance from shore. The dates for the samples are 25 to 30 April 1982, 1 to 6 April 1983, and 19 to 24 May 1984.

Fig. 4. Distributional limits for *B. glandula* stage VI nauplii (22) (offshore margins) and pelagic barnacle cyprids (inshore margins) relative to the mean upwelling index (20) for the 3-week period before the collection. Data are from 11 years between 1969 and 1984. Least-squares regression lines are plotted for each. The three sample dates without *B. glandula* nauplii were excluded from the regression calculation (*B. glandula* nauplii, $y = 20.8 + 0.51x$; pelagic cyprids, $y = 19.5 + 0.55x$; y , miles from shore; x , m^3/sec per 100 m of coastline).



Although many examples are known of offshore predators eating the larvae of adults living on rocks or burrowing in mud (3, 13, 16), the significance of such predation to larval recruitment rates is not clear. Most examples do not establish whether offshore predators are consuming larvae that would otherwise return to shore. Predators consuming larvae that are not destined to enter the adult stock anyway are, in effect, scavengers, and do not affect the population dynamics of their prey.

To ascertain whether larvae are bound to return to their adult habitat requires analyzing the circulation pattern in the offshore water column. Water motion on a daily to monthly time scale may be decomposed into geostrophic flow, caused by pressure differences within the ocean combined with the Coriolis force, and Ekman flow (17), caused by wind blowing on the water's surface together with the Coriolis force (18).

Consider now the Ekman component in more detail (19). Below the ocean's waves is a layer, nominally between 10 and 40 m deep, that is affected by the wind. The integral of the flow over this so-called Ekman layer is a simple expression predicting the total volume of water transported per unit time per unit of coastline

$$T = \tau / [\rho 2 \omega \sin(\phi)]$$

where τ is the force of the wind on the water's surface (the wind stress), ϕ the latitude of the location (positive to the north of the equator), ρ the density of the seawater, and ω the angular velocity of the earth's rotation. This formula indicates that Ekman transport increases both as the wind increases and as the Coriolis force increases. The Ekman transport for a given wind stress increases from the poles to the equator. Moreover, in the Northern Hemisphere the Ekman transport is directed 90° to the right of the wind so that winds blowing from north to south along the Pacific coast of North America cause water to move away from the coast.

The main difficulty with applying this theory is that the depth of the Ekman layer is not well specified and, therefore, neither is the speed of the water flow. A given total volume of transport can be achieved by either a thin layer moving rapidly or a thick layer moving slowly.

Ekman transport in the open ocean leads to water motion near the water's surface. But Ekman transport perpendicular to a coastline produces upwelling near the coast, typically bringing cold nutrient-rich salty water to the surface. Thereafter, this water moves offshore and becomes progressively warmer.

Because of the possible significance of upwelling to production in commercial fisheries, the National Marine Fisheries Service (20) developed an index to predict the extent of upwelling in various places throughout the world. This index embodies two components—the formula above for total Ekman transport together with an estimate of the wind stress. The wind stress computation begins with data on pressure gradients within the atmosphere; these are used to predict wind speeds. For large spatial scales (≥ 900 km) these predicted winds are close to winds measured over the ocean (although accuracy can be improved with relatively small systematic corrections) (21). The wind stress, τ , is then proportional to the square of the predicted wind speed (18).

A season's recruitment to the population of *Balanus glandula* at Hopkins Marine Station has been found to be negatively correlated with the upwelling index averaged through that season (Table 1; $r = -0.96$; $n = 5$ years). Larvae of *B. glandula* live for 2 to 3 weeks in the water column; they die if they do not settle within the final week of this larval life span (22). Therefore, we hypothesized that during upwelling events, offshore moving waters in the Ekman layer were carrying barnacle larvae far enough away from the adult habitat to prevent their returning within 3 weeks, resulting in low recruitment to the adult stocks. We now present data to support this.

If strong upwelling conditions do cause larval loss because larvae are transported away from shore, then barnacle larvae should be found farther out to sea in years with strong upwelling than in years with weak upwelling. To test this prediction we tested zooplankton samples from the California Cooperative Oceanic Fisheries Investigation (CalCOFI) archived at Scripps Institution of Oceanography for the years corresponding to the data on barnacle recruitment at Hopkins Marine Station. Specifically, samples from transects 63, 67, and 70 (Fig. 2) were analyzed for 1982 to 1984 and, to obtain a longer record, transect 67 was also analyzed back to 1969. Each zooplankton sample comes from a single oblique tow with 0.505-mm mesh nets. Because of this large mesh size only the last nauplius

stage was reliably collected. (Stage V was sporadically collected and other stages were omitted altogether.)

As Fig. 3 illustrates, in 1982 larvae of *B. glandula* extended out 45 nautical miles from shore, in 1983 the distance dropped to 5, then it reached 85 miles in 1984. These observations coincide with the Ekman transport indices for those years and are opposite to the recruitment in the intertidal zone in those years (Table 1).

Furthermore, larvae from a pelagic group of barnacles were discovered to be abundant near the seaward margin of the *B. glandula* larval distribution. These pelagic barnacles are species whose adult phase lives on whales, turtles, and driftwood, but cannot be identified more specifically.

Fig. 5. Distribution of phytoplankton in the California Current system as revealed by the Coastal Zone Color Scanner (CZCS) aboard the Nimbus-7 polar orbiting satellite (29). Images are colored from red, through yellow to green, ending in blue, to indicate a progression from high (~3 mg of chlorophyll per cubic meter) to low chlorophyll concentrations (30). Dates of photographs are 19 April 1982, 3 April 1983, and 6 April 1984. Notice that in 1982, there was a high concentration of phytoplankton offshore and a relatively low concentration adjacent to the coast; also the current system is wider in the south than in the north. In 1983, during the El Niño, productivity in the California Current appeared to drop and then to return nearly to previous levels in 1984.

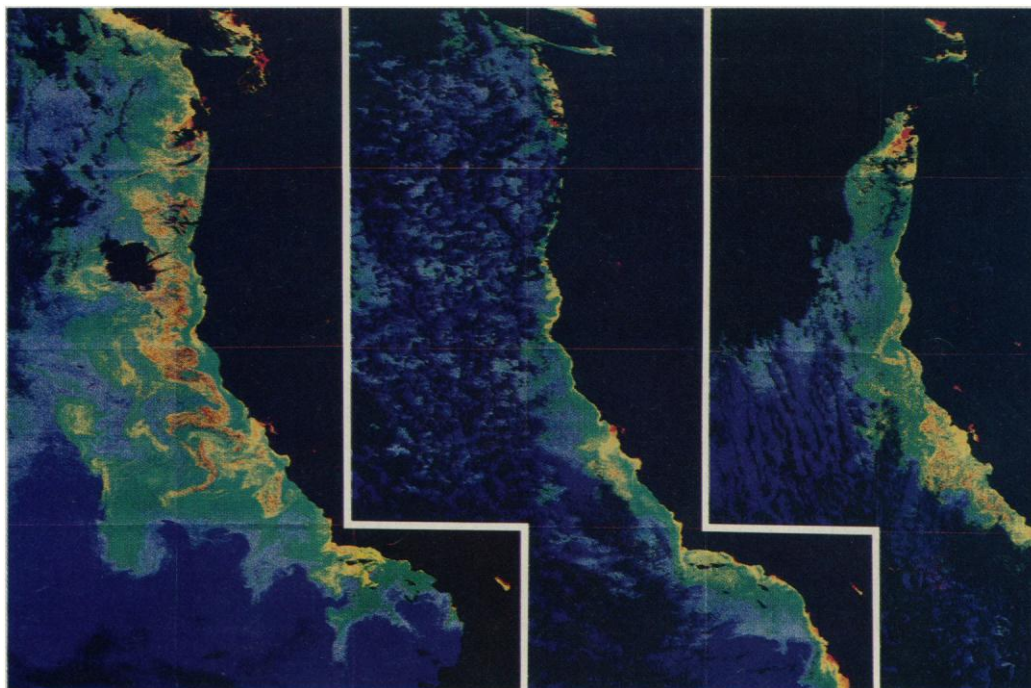
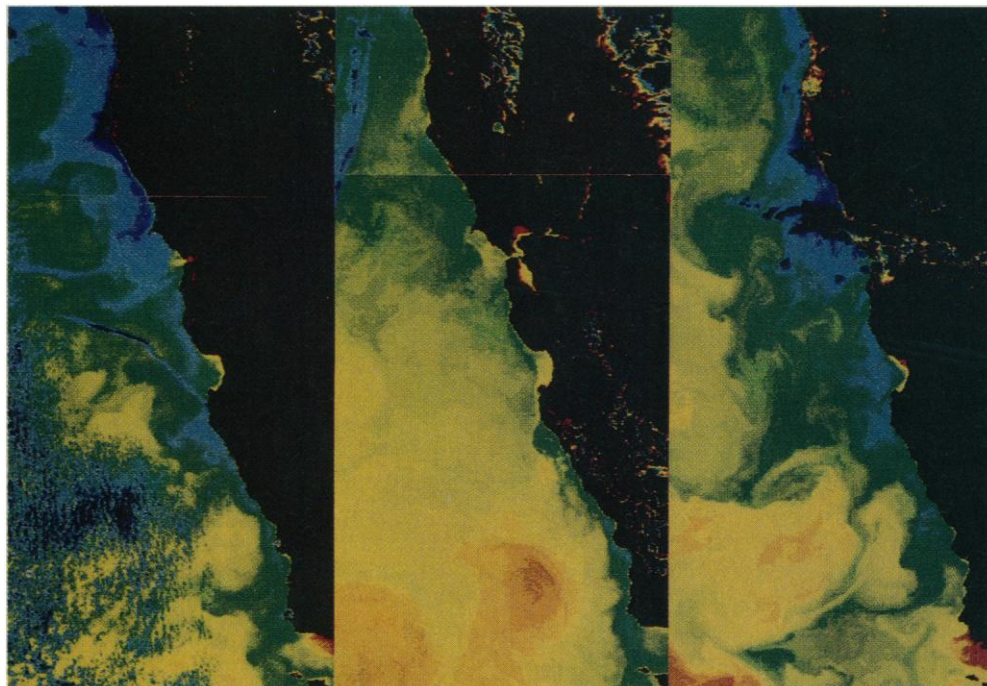


Fig. 6. Sea-surface temperature adjacent to the central California coast revealed by the Advanced Very High Resolution Radiometer (AVHRR) aboard the TIROS-N and NOAA series satellites (31). Images are colored from dark blue (~5°C), through light blue to green to yellow, ending in red (~15°C), to indicate a progression from cold to warm water (30). Dates of photographs are 18 May 1982, 6 April 1983, and 21 May 1984. Notice the upwelling of cold water at points along the shore in 1982 and 1984 and the relative absence of upwelling in 1983.



To examine further the distance from shore where *B. glandula* ends and where the pelagic barnacles begin, samples from transect 67 were analyzed back to 1969. The sample month ranged from February to June, and 7 of the 11 samples were taken in April. Figure 4 shows the location of the margins of these distributions as a function of the upwelling index during the 3 weeks preceding each cruise. On average, the seaward margin of the *B. glandula* distribution coincides with the shoreward margin of the pelagic barnacles, although some overlap occurs in any year.

These data suggest that, on average, a frontal boundary exists between two water masses, one of which communicates with rocky intertidal habitat and another that resides offshore. This boundary is far from shore following a strong upwelling period and close to shore when upwelling conditions have been weak. The average distance of the boundary from shore is about 50 miles.

Related Studies in the California Current

The average distance from shore of hake larvae (*Merluccius productus*) is governed by upwelling conditions (23) in a manner nearly identical to *B. glandula*. Recruitment in the widow rockfish (24) (*Sebastes entomelas*) is also correlated with weak upwelling conditions.

Off the Oregon coast (25), barnacle larvae have been observed only within 10 miles from shore. Moreover, a frontal boundary defined by the distribution of copepod species was observed—it too typically lies about 10 miles offshore. These data were taken as support for a “two-cell” model for the circulation off the Oregon coast (26), with the front marking the boundary between two circulation cells. This front may be continuous with the front indicated by barnacle larvae offshore of central California, although the front is farther from shore off California than off Oregon. The front appears to delimit the upwelled water.

A latitudinal gradient in the amount of upwelling (more upwelling off California than Oregon) may explain in part why upwelled water is farther from shore off central California than off Oregon. The strength of the Coriolis effect varies with latitude and a factor of about 1.2 in the gradient is explained in this way [$\sin(45^\circ)/\sin(35^\circ) \approx 1.2$]. More importantly, the wind speed tends to vary latitudinally, with stronger and less variable along-shore winds off California than farther north (20, 21). The combination of these factors causes a latitudinal gradient in the upwelling index, and evidently in the actual degree of upwelling as well.

Beyond the upwelled water near the coast, which is generally cold and saline, are the waters of the California Current. CalCOFI zooplankton data analyzed to species groups (27), together with physical oceanographic studies, indicate that the California Current typically consists of southward flowing waters that are cold and relatively low in salt (28). From about central California north to Washington, the California Current contains zooplankton with a northern affinity that have presumably been advected southward by geostrophic flow. The satellite imagery shown in Fig. 5 illustrates the California Current system. Notice that in 1982, for example, there is a narrow band of water adjacent to the coast with relatively little phytoplankton, whereas the waters farther offshore are rich with phytoplankton. Moreover, the whole system tends to widen out toward the south.

Further clues are revealed from the El Niño year of 1983 (32). As noted in Table 1, the upwelling index was low in 1983, indicating stationary or onshore moving coastal waters; it was also the year of the highest barnacle recruitment and of the closest proximity to shore of the barnacle-larvae frontal boundary. And as Fig. 6 shows, sea-surface temperature data from satellite imagery tend to confirm

that 1983 was a year of less upwelling than 1982 or 1984, as already reported in a comparison of 1982 with 1983 (30). Thus, the distribution of barnacle larvae together with these large-scale physical data support the hypothesis that the El Niño year of 1983 was a time of greatly reduced coastal upwelling along California and a time when the California Current moved closer to shore than usual (33).

Finally, satellite imagery invariably reveals mesoscale structures in the coastal waters that were not anticipated by Ekman's theoretical treatment. Rather narrow streams of cold water at the water's surface are observed leading away from the coast; this contrasts with the expectation of a relatively uniform sheet of water moving away from the coastline. Figure 6 illustrates several such streams in light blue.

A Synthetic Hypothesis

In 1983 Sverdrup (34) outlined a cross section of the vertical circulation during an upwelling event in the California Current system based on physical-oceanographic data. He noted a frontal boundary between upwelled water and California Current water, although some mixing of upwelled water into the California Current was explicitly indicated. Some mixing is also suggested biologically by the statistically significant relations between zooplankton abundance in all species groups in the California Current and Ekman

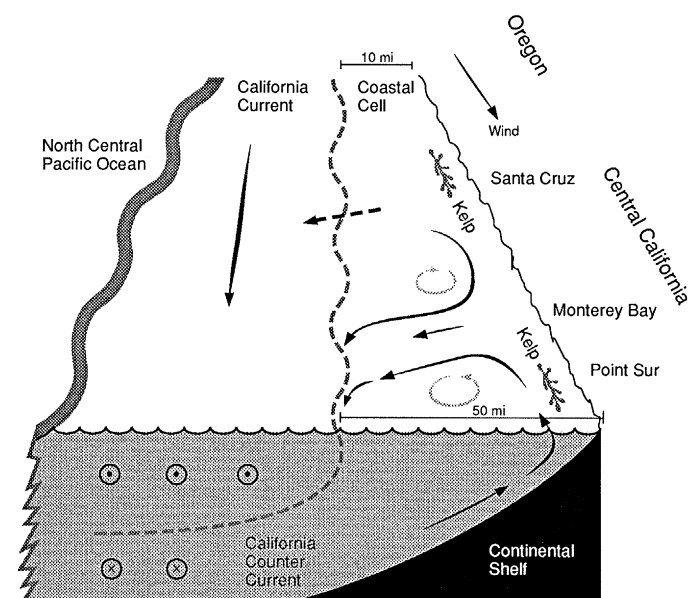


Fig. 7. Schematic of proposed California Current system adjacent to central California during the spring. The California Current lies offshore of a coastal cell; its flow is southerly. Below it is the California Counter Current with a northerly flow. Wind-driven upwelling brings cold saline water to the surface. When in contact with the coast this water accumulates the larvae of intertidal barnacles; it then moves offshore and tends to drop below the warmer and less saline water of the California Current, producing a “coastal cell.” Some of the upwelled water is postulated to mix into the California Current, however. The shoreward margin of the California Current is a meander that buds off eddies. These eddies may focus the upwelled water into narrow streams of cold water that can last for several days. In the absence of upwelling, as in the spring of 1983, the coastal cell shrinks, the margin of the California Current comes closer to shore, and coastal species whose larvae occur in the surface Ekman layer suffer less larval wastage and enjoy a higher recruitment rate. The current system off central California is visualized as an extension of that off Oregon, except that, on average, the greater upwelling off California is hypothesized to lead to a wider coastal cell; the California Current is wider off California as well.

transport indices (27), even though advection from the north (28) also strongly affects the California Current. A frontal boundary delimiting the upwelled water is also described in the Benguela Current of the South Atlantic (35) and may occur in most upwelling currents (18, 36). Although a frontal boundary cannot be taken as established for the California Current system (37), the distribution of barnacle larvae off central California and copepods off Oregon, as described above, support Sverdrup's interpretation of a frontal boundary between the upwelled water adjacent to the coast and the water of the California Current.

Sverdrup (34) also observed an eddy derived from the meandering California Current. Such features can focus the upwelled water into "streams." Figure 7 presents a schematic of what appears to be happening in waters adjacent to central California.

The circulation pattern proposed in Fig. 7, and the key role of the average Ekman transport, potentially accounts for the systematic differences found in the community ecology of the rocky intertidal zone along the Pacific coast of North America. In this scheme, the sites to the north receive, on average, a higher larval return rate than those to the south because there is usually less Ekman flow away from shore in the north to produce larval wastage there. Consequently, communities in the rocky intertidal zone of the north regularly receive higher larval settlement, and are therefore more dominated by post-settlement interactions among adults than rocky intertidal communities of central California. In central California the settlement rate is generally lower, and hence intertidal communities there tend to mirror processes, such as upwelling events, located in the offshore current system.

Linking Offshore Circulation with Population Dynamics

The biological value of knowing the circulation of offshore waters

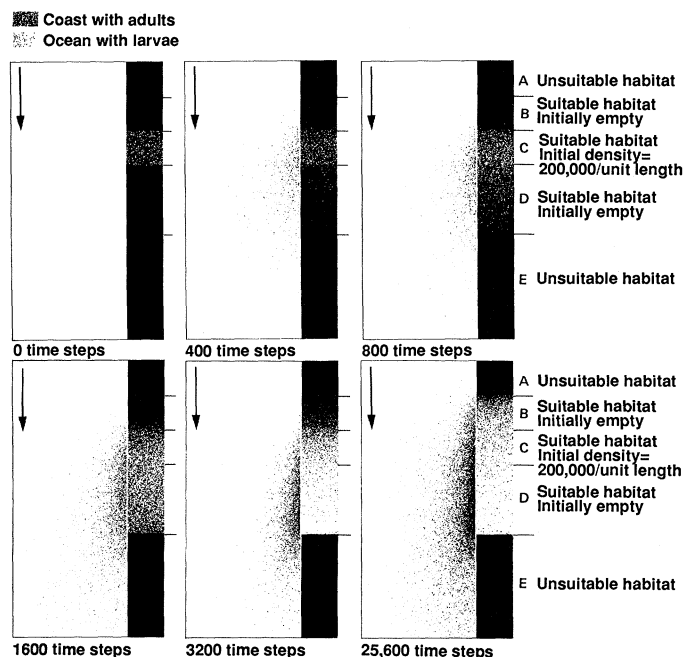


Fig. 8. Population dynamics in time and space of a model species with sessile adult and pelagic larval phases. The density of larvae in the offshore waters is indicated by black dots on a white background and the density of adults on the rocky shoreline in reverse. The following nondimensional model parameters were used: $u = 0$, $v = 40$, $K = 360$, $\lambda = 0.4$, $\mu = 0.1$, $c = 0.02$, $m = 2.4$, $A = 100$, and $a = 10^{-4}$.

is that a predictive model for population dynamics can be developed that combines both ecological and physical-oceanographic information. To illustrate, consider a straight coast aligned with the y axis, and focus on the water's surface. Let the coast be the line $(0, y)$, and the ocean the half plain $(x < 0, y)$. Then the dynamics of a model barnacle population may be formed that combines both adult and larval phases of the life cycle. The rate of change of adult barnacles $B(y, t)$, at location y and time t , is

$$dB(y, t)/dt = c(y)F(y, t)L(0, y, t) - \mu(y)B(y, t)$$

where $F(y, t)$ is the vacant space at location y , and $L(0, y, t)$ is the density of larvae in the adjacent water column. The $c(y)$ is a rate constant indicating the settlement rate at the site per unit vacant space there and per unit larval density in the adjacent waters; the entire first term represents the larval input rate to the coastal site. The second term is the adult mortality rate at the site, with $\mu(y)$ being the per capita death rate of barnacles at site y . For simplicity, age is not included here, and the model parameters are obtained from age-specific data by averaging over the age distribution. The vacant space is obtained from the constraint that the total area of the site is conserved

$$A(y) \equiv F(y, t) + a(y)B(y, t)$$

where $a(y)$ is the average basal area of a barnacle, and $A(y)$ is the available space at location y . The larval half of the life cycle is governed by the transport equation

$$\begin{aligned} \partial L(x, y, t)/\partial t + u(x, y, t)\partial L(x, y, t)/\partial x + v(x, y, t)\partial L(x, y, t)/\partial y \\ = K[\partial^2 L(x, y, t)/\partial x^2 + \partial^2 L(x, y, t)/\partial y^2] - \lambda(x, y, t)L(x, y, t) \end{aligned}$$

where u is the velocity of water in the x direction, v the velocity in the y direction, K is the diffusivity of larvae, and λ is the mortality rate of larvae in the water column. The u and v pertain to the flow of larvae brought about by the pattern of circulation, and the term with K refers to diffusive mixing of larvae within the water. The net production of the larvae is specified by a coastal boundary condition for the larval pool

$$K[\partial L(x, y, t)/\partial x | x = 0] = -c(y)F(y, t)L(0, y, t) + m(y)B(y, t)$$

where the first term on the right-hand side represents the loss of larvae to settlement, and the second term the production of larvae; $m(y)$ is the reproductive rate per barnacle at location y . Finally, the spatial extent of the region is specified with still more boundary conditions.

A simple prediction from this model appears in Fig. 8. The coast is divided into five sections. A and E are unsuitable for barnacles, whereas B, C, and D are suitable. The barnacles are initially introduced to C, and their eventual spread into B and D can be predicted with the use of finite difference techniques to solve the transport equation. Moreover, the larval pool is assumed to be flowing to the south ($v < 0$) with no net offshore transport. Figure 8 illustrates the buildup of larvae adjacent to the coast where the barnacles are originally introduced, and the gradual spread of the population downstream. The population eventually equilibrates with a distribution resulting from the interaction of the larval flow field with the distribution of suitable habitat along the coast.

Any type of flow pattern can, in principle, be represented by u and v , and thus we can envision being able to forecast how events in the water column affect coastal populations. Moreover, the extent to which populations at different sites are coupled to one another by sharing a common larval pool or isolated from one another by a feature in the offshore circulation system can eventually be understood. Models of this genre have already been used to study theoretically the forces that may have caused the evolution of

complex life cycles and the conditions for coexistence between species that compete for space as adults and which have a complex life cycle (38).

The model described above is more realistic than the “stock-recruitment” approach to marine population dynamics (39), where in the larval input rate is regressed against the stock size with a second-degree polynomial. The polynomial’s coefficients are interpreted in terms of density-dependent mechanisms affecting fecundity, growth, and mortality. Such an approach would seem appropriate only if the larvae are confined to some small neighborhood of the adult habitat.

Implications for Ecology

Ecological theory in population and community ecology today is weighted in favor of organisms with a simple life cycle, where juveniles are born into nearly the same habitat as their parents. Although this life cycle is true for humans, mammals, birds, and perhaps plants, most animals have a complex life cycle with at least two stages—frogs, salamanders, and fish among vertebrates; holometabolous insects; and most marine organisms. The dynamics of these populations involve processes in different habitats that are coupled by some transport mechanism. In some cases, animals simply migrate by their own means from their juvenile habitat to the adult habitat; in others, as discussed here, physical transport mechanisms are responsible for the mobility. In every case, studies at only one of the habitats tell no more than half the story. Study of both habitats involved in a two-phase life cycle is feasible both theoretically and in the field.

Many propose that the most fundamental question in ecology today is to understand scale and coupling among spatially separated sites; and that the crux lies at the mesoscale. This is the scale between the processes operating within a local study site that can be studied through the now-conventional methods of field experimentation and the biogeographic and ecosystem scale. Progress at the mesoscale requires fusing the “reconstructional logic” of the earth sciences with the field experimentation of the last decade in community ecology. Small-scale field manipulation, by itself, is misleading when larger scales are considered. This is exemplified by the inability to “scale up” the early rocky intertidal zone experiments discussed above and by the inability of small-scale removal experiments to predict the ecological impact on coral reef communities of the epidemic that has just decimated *Diadema* sea urchin populations throughout the Caribbean (40). Yet the mesoscale is quite tractable, provided mesoscale processes are taken into account as part of the research program. Thus it appears a new category of discoveries concerning scale and coupling among scales will be emerging in ecology during the next few years.

REFERENCES AND NOTES

1. V. Volterra, *Leçons sur la Théorie de la Lutte pour la Vie* (Gauthier-Villars, Paris, 1931); F. Scudo and J. Ziegler, *The Golden Age of Theoretical Ecology, Lecture Notes in Biomathematics* (Springer-Verlag, Heidelberg, 1978).
2. U. D’Ancona, *Bibl. Biotheoretica* **6**, 1 (1954).
3. G. Thorson, *Biol. Rev.* **25**, 1 (1950).
4. J. Connell, *Ecology* **42**, 710 (1961); P. Dayton, *Ecol. Monogr.* **41**, 351 (1971).
5. B. Menge, *ibid.* **46**, 355 (1976).
6. A. Underwood, E. Denley, M. Moran, *Oecologia* **56**, 202 (1983).
7. S. Gaines and J. Roughgarden, *Proc. Natl. Acad. Sci. U.S.A.* **82**, 3707 (1985).
8. J. Connell, *Ecol. Monogr.* **40**, 49 (1970).
9. A. Hines, in *Reproductive Ecology of Marine Invertebrates*, S. Stancyk, Ed. (Univ. of South Carolina Press, Columbia, SC, 1979), p. 213.
10. J. Roughgarden and S. Gaines, unpublished observations at Hopkins Marine Station; see also R. Paine, *Paleobiology* **7**, 553 (1981).
11. R. Paine and R. Vadas, *Limnol. Oceanogr.* **14**, 710 (1969); J. Lubchenco, *Am. Nat.* **112**, 23 (1978); W. Sousa, *Ecol. Monogr.* **49**, 227 (1979).
12. S. Gaines, S. Brown, J. Roughgarden, *Oecologia* **67**, 267 (1985).
13. B. Bernstein and N. Jung, *Ecol. Monogr.* **49**, 335 (1979).
14. See B. Menge and J. Sutherland [*Am. Nat.* **130**, 730 (1987)] for details.
15. S. Gaines and J. Roughgarden, *Science* **235**, 397 (1987).
16. R. Bray, *Fish. Bull. (Dublin)* **78**, 829 (1980); C. Young and F. Chia, *Reprod. Mar. Invertebr.* **9**, 385 (1987).
17. V. Ekman, *Ark. Mat. Astron. Fys.* **2**, 52 (1905).
18. K. Bowden, *Physical Oceanography of Coastal Waters* (Halstead Press, Chichester, 1983).
19. J. Price, R. Weller, R. Schudlich, *Science* **238**, 1534 (1987).
20. A. Bakun, *Tech. Rep. NMFS SSRF-671* (1973); *Tech. Rep. NMFS SSRF-693* (1975); J. Mason and A. Bakun, *NOAA Tech. Memor. NMFS SWFC-67* (1986).
21. G. Halliwell, Jr., and J. Allen, *J. Geophys. Res.* **92**, 1861; P. Strub, J. Allen, A. Huyer, R. Smith, R. Beardsley, *ibid.*, p. 1507.
22. S. Brown and J. Roughgarden, *J. Crust. Biol.* **5**, 574 (1985); E. Branscomb and K. Vedder, *Crustaceana* **42**, 83 (1982).
23. K. Bailey, *Mar. Ecol. Prog. Ser.* **6**, 1 (1981).
24. J. Norton, *Alaska Sea Grant Rep.* **87**, 73 (1987).
25. W. Peterson and C. Miller, *Sea Grant Publ. ORESU-T-76-002* (1976).
26. ———, A. Hutchinson, *Deep-Sea Res.* **26A**, 467 (1979).
27. J. Colebrook, *Fish. Bull.* **75**, 357 (1977).
28. J. Reid, Jr., G. Roden, J. Wyllie, *CalCOFI Prog. Rep.* (1 July 1956 to 1 Jan. 1958) (1958), p. 27; D. Chelton, P. Bernal, J. McGowan, *J. Mar. Res.* **40**, 1095 (1982).
29. Digital images courtesy of the NASA Ocean Data System, Jet Propulsion Laboratory, Pasadena, CA.
30. P. Fiedler, *Science* **224**, 1251 (1984).
31. Digital images archived at Scripps Satellite Oceanography Facility, La Jolla, CA.
32. R. Barber and F. Chavez, *Nature* **319**, 279 (1986).
33. J. Simpson, *Geophys. Res. Lett.* **11**, 241 (1984).
34. H. Sverdrup, *J. Mar. Res.* **1**, 155 (1938).
35. T. Hart and R. Currie, *Discovery Rep.* **31**, 123 (1960).
36. R. Smith, *Oceanogr. Mar. Biol. Annu. Rev.* **6**, 11 (1968).
37. D. Halpern, *Deep-Sea Res.* **23**, 495 (1976).
38. J. Roughgarden, Y. Iwasa, C. Baxter, *Ecology* **66**, 54 (1985); J. Roughgarden and Y. Iwasa, *Theor. Popul. Biol.* **29**, 235 (1986); Y. Iwasa and J. Roughgarden, *IMA J. Math. Appl. Med. Biol.* **2**, 93 (1985); *Theor. Popul. Biol.* **30**, 194 (1986); J. Roughgarden, *Mathematical Evolutionary Theory*, M. Feldman, Ed. (Princeton Univ. Press, Princeton, 1988), chap. 12.
39. B. Rothschild, *Dynamics of Marine Fish Populations* (Harvard Univ. Press, 1986).
40. H. Lassius, *Annu. Rev. Ecol. Syst.*, in press.
41. We thank D. Bracher for Herculean efforts at coordinating the satellite data, A. Bakun for consultation throughout the study, T. Farrell and E. Rykiel for improvements to the manuscript, W. Newman for help with the barnacle identifications, G. Snyder for assistance with the CalCOFI samples, the NODS task group for the CZCS images, M. Ciandro for the AVHRR images, and Image Understanding Systems for image analysis software. Primary research support from the Ecological Research Division, Department of Energy (DE-FG03-85ER60362), with supplemental funding from NASA-Ames Research Center (Joint Research Interchange NCA2-258), is gratefully acknowledged.