Dynamics of the rocky intertidal zone with remarks on generalization in ecology

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SUMMARY

Ecological systems at both population and community scales are recognized increasingly as being more open than previously thought. In coastal marine systems, physical oceanographic processes affecting larval stages are as, or more important than, biological interactions affecting adults. In terrestrial systems, the membership in ecological communities is controlled by geologic transport processes as much as by species interactions. Hence ecological science has become increasingly an earth science, and less a biological science. The differences between marine and terrestrial ecosystems imply that terrestrial systems are more localized functionally than marine systems; more likely to suffer extinction from habitat loss; and less likely to recover upon removal of stress. In addition, damage to a marine system is more likely to be felt further from the source of stress than it would in a terrestrial system. Finally, harvesting strategies at sea should react to continuous environmental monitoring whereas on land, demographically based strategies of harvest can suffice.

1. INTRODUCTION

Perhaps more than ever before, because of policy decisions affecting habitat use and climate change, ecologists need to offer consensus about how ecological systems work. Consensus might take the form of agreed-upon generalizations about how all ecosystems function or are structured. Are there such generalizations or might consensus take some other form?

Terrestrial community ecology is witnessing a renewed recognition of slow processes with timescales of 10^4 to 10^7 years, such as the sea-level changes and plate tectonics. Since the 1950s, ecology has been viewed as one of the levels of organization of biology. Population dynamics and species interactions were supposed to be fast enough to erase the initial condition established by geology, as though the ecological play were independent of the contractor who constructed the theatre. In fact, the ecological play is taking place as the theatre is being built and the species occasionally join in the carpentry. Indeed, a growing view amoung community ecologists is that ecology is not a part of biology after all, but is an organic earth science.

Marine community ecology has also been transformed in the last decade. According to ecological research early in this century, each kind of organism was found wherever it was physiologically qualified to live. In the 1960s the emphasis shifted to species interactions. Each kind of organism was found wherever it was not eaten, smothered by a competitor, or crushed by logs or ice. On either of these views a tidepool is a mostly closed system. Recently, recogni-tion that the life cycles of the organisms in coastal ecosystems pass through an oceanic phase where the controlling ecological processes are often located has lead to a system conceptualization containing equally important benthic and oceanic components. This newer conceptualization has discredited the food webs of coastal ecosystems prepared during the 1960s and 1970s that express a closed-system picture. Today, marine ecology is as much the physical oceanography of currents and winds as it is the biology of eating and mating.

If both terrestrial and marine community ecology have escaped from biological control, what form shall generalizations in ecology shall take, including genera-lizations across terrestrial and marine ecosystems? In biology, generalizations rely on common mechanisms (e.g. DNA). In elementary physical sciences, generali-zations are theoretical laws. But what of the earth sciences, including ecology? No one mechanism makes volcanos, and no ideal river underlies all real rivers. Instead, generalization, or at least consensus, consists of finding a small collection of big particulars. There are only seven continents, four large ocean gyres, two hemispheres, and one Earth. The finiteness of the earth itself limits the number of particulars, provided the particulars are sufficiently big.

Thus, a route to generalization in ecology, or at least to consensus, is to exhibit how particular, but large, ecosystems work. Here then we present how an oceanographic mechanism controls the dynamics of coastal populations along California. This coast is comparable to the world's three other major upwell-ing systems off Peru, Portugal and northwest Africa,
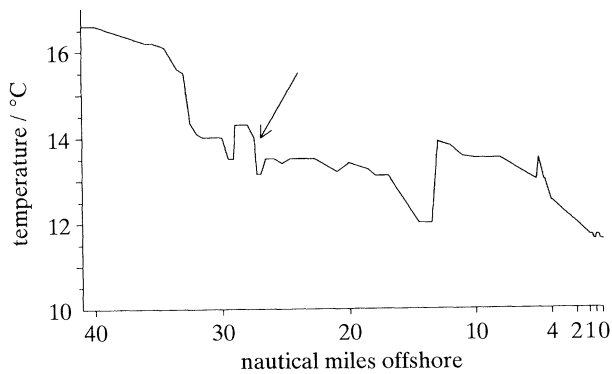
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Figure 1. Sea surface temperature along a transect due magnetic west into the Pacific Ocean from a location (36° 25.9′N, 121°55.0′W) on the central California coast on July 25 1990 (Julian day 206).

and southwest Africa. Specifically, we offer new data on how the movement of offshore fronts affects the population dynamics of barnacles in California, and on how this mechanism can be incorporated into models for the dynamics of coastal populations.

2. OCEANOGRAPHY OF LARVAE FROM INTERTIDAL ADULTS

Coastal marine populations exhibit large fluctuations in abundance. In 1931 Vito Volterra proposed one of the first models of theoretical ecology, a model for the predator–prey interaction, to explain the fluctuations evident in the fish markets of Trieste. It turned out that the fluctuations are not regular enough to be an oscillation as predicted by Volterra's model and the cause of marine population fluctuations has remained mysterious.

Along the California coast the cause of population fluctuation lies somewhere in the ocean and not on the coast itself. With intertidal barnacles, for example, adults attached to the rocks steadily release larvae into the sea during the spring and summer. Yet the mature larvae arrive back to the intertidal zone in episodic pulses that bring about large fluctuations in abundance. Determining the cause of episodic recuitment of larvae into the adult stock has come to be known as the 'recruitment problem' in marine ecology. Solving this problem involves two sub-problems: finding the mechanism that concentrates the larvae into discrete aggregates or 'patches', and finding the mechanism that determines when the patches of larvae arrive at the shore causing a recruitment pulse.

Although understanding recruitment has long been of interest in relation to explaining population fluctuations, the level of recruitment also determines qualitatively what processes take place in benthic communities. During the 1970s the rocky intertidal zone was the source of three generalizations: (i) species occupying space such as barnacles and mussels are ordered in a linear competitive hierarchy; (ii) an intermediate degree of disturbance prevents the dominant competitor from excluding other species; and (iii) a predator that prefers to feed on the dominant competitor also may prevent it from excluding other

species. Our earlier studies in the rocky intertidal zone showed that these generalizations depended on the recruitment of the dominant competitor being sufficiently high (Gaines & Roughgarden 1985). If the recruitment to the rocky intertidal zone is relatively low, as it is in much of California, then the dominance hierarchy does not develop, and both the intermediate disturbance principle and keystone predator concepts are not applicable. Thus, the recruitment level determines qualitatively what processes take place within the rocky intertidal zone.

Our studies in recent years have concerned a specific hypothesis that may solve the recruitment problem for intertidal barnacle populations along the California coast (Roughgarden *et al.* 1991). As the cold and saline water upwelled adjacent to the coast moves away toward the open ocean it intersects the relatively warm and fresh water of the southward flowing California Current, forming a frontal boundary. This frontal boundary is a convergence zone, and it is hypothesized that planktonic organisms, including barnacle larvae, accumulate there. The location of the front moves according to the winds that control the strength of upwelling. When the winds are strong, the front is pushed far from shore and transport of upwelled water at the surface carries intertidal larvae away from shore. As the winds weaken, the strength of cross-shelf transport weakens and the front moves closer to shore. If wind relaxation occurs for an extended time the front apparently can collide with the coast and deposit its accumulated larvae producing a recruitment event. This hypothesis potentially explains both the timing of recruitment at the coast and why it occurs in discrete pulses.

Until now, evidence for this hypothesis has come primarily from two sources. First, the ocean off California contains larvae of many species of barnacles, and of these several types come from adults that live in the intertidal zone, and several other types come from adults that live attached to driftwood and other surfaces in the California Current. Plankton samples from CalCOFI cruises showed the existence of a front separating the offshore pelagic barnacle larvae from the inshore intertidal barnacle larvae. Moreover, this front moved away from shore when the winds were strong and back toward shore when the winds were weak (Roughgarden *et al.* 1988). Second, recruitment pulses along the California coast were observed to coincide with the arrival at the shore of the warm low-salinity water typical of the California Current; this replaced the cold high-salinity water normally found adjacent to the coast (Farrell *et al.* 1991).

Here we note a third form of evidence: direct data that larvae are concentrated at an upwelling front and that the collision of a front with the intertidal zone caused a pulse of larval settlement. Six short cruises to sample plankton on both sides of upwelling fronts were taken off the central coast of California with a small 14.6 m boat based in Santa Cruz, the R/V *Shana Rae*, during the summers of 1989 and 1990. From these cruises, the dates of July 25–26 1990 (Julian Day 206–207) are particularly interesting because, by chance, upwelling was very strong on the day the
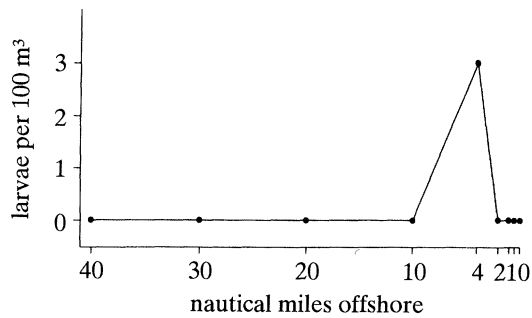
Figure 2. Abundance of cyprids of intertidal barnacles at fixed stations along the transect depicted in figure 1.

Figure 4. Sea surface temperature at 13 stations from 10 mi to shore along the transect one day later (Julian day 207) than in figure 1.

cruise began and by the end of the second day the wind died and a large relaxation had set in.

Figure 1 illustrates the sea surface temperature along a transect that began at shore adjacent to the Granite Canyon Marine Laboratory (36°25.9′N, 121° 55.0′W) on the open coast between Point Sur and Point Lobos, and proceeded 40 nautical miles (mi) due magnetic west. From 0–2 mi the water is freshly upwelled, and is adjacent to the relatively warm water found from 4–14 mi. Cold water that upwells at a point north of Monterey Bay usually flows southwest, across the mouth of Monterey Bay and may be found about 15 nautical miles offshore of the Granite Canyon Laboratory. Thus, the relatively cold water from 14–27 mi offshore is interpreted as another band of upwelled water, although not as recently upwelled as that immediately adjacent to the shore. From 27–32 mi is the zone where upwelled water meets the California Current, and from 32 mi out to 40 mi the water is the true California Current.

On July 25 1990, the experiment consisted of taking samples at the stations noted on the horizontal axis of figure 1, and at the sharp front between upwelled water and oceanic water at 27 mi noted with the arrow in figure 1. On July 26 1990, the experiment was to detail how the situation had changed following the wind relaxation. The results are noted in figures 2–6.

For July 25 1990, figure 2 shows that some cyprid larvae (the final larval stage of barnacles) of intertidal adults were found at the 4 mi station and not
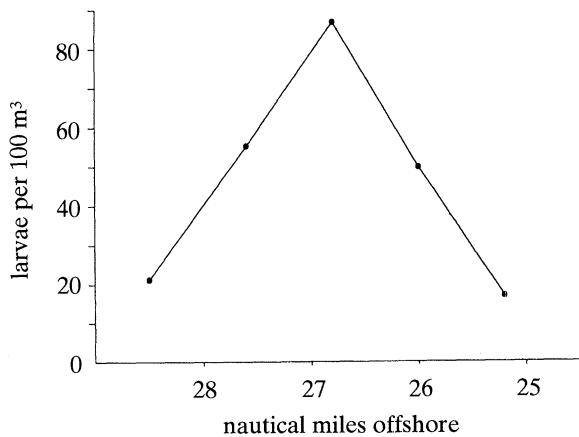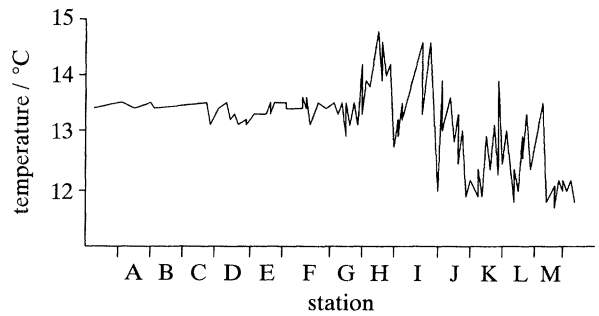
elsewhere. The 4 mi station is in the frontal zone between recently upwelled water and warmer more oceanic water. However, note the low abundance: only 3 per 100 m³ at the 4 mi station. Figure 3 pertains to the sharp front at 27 mi. Five stations spanning 3 mi across the front were taken and figure 3 presents the number of intertidal cyprids at these stations. About 20 times as many larvae were found at this feature than at the 4 mi front. Meanwhile no larvae were found at the stations between the fronts.

The next day the original cruise plan was to return to 10 miles from shore and to do fine-scale sampling across the 4 mi front. Figures 4 and 5 illustrate the results. It happened that on July 26 1990 (Julian day 207) the winds relaxed, the sea became calm, and drift algae that had been noticed at the fronts had moved close to shore. Station A is 10 mi from shore, whereas station M is at the edge of the kelp stand about 100 m from shore. The water temperature is about 1°C hotter than the previous day. From station H in toward shore, this hotter surface water is shallow. The erratic temperature trace in figure 4 from station H inwards represents the boat's rolling, resulting in the thermistor being dipped to about 4 m and then being raised to the surface. Figure 5 shows that the abundance of barnacle larvae has increased about 400-fold since the day before. This astonishing appearance of a huge abundance of larvae where there had been almost none the day before is mirrored by the settlement record taken as Asilomar Beach, about 10 mi to the north. On July 27 1990 (Julian day 208)

Figure 3. Abundance of cyprids of intertidal barnacles at the five stations across the front at 27 mi noted with an arrow in figure 1.
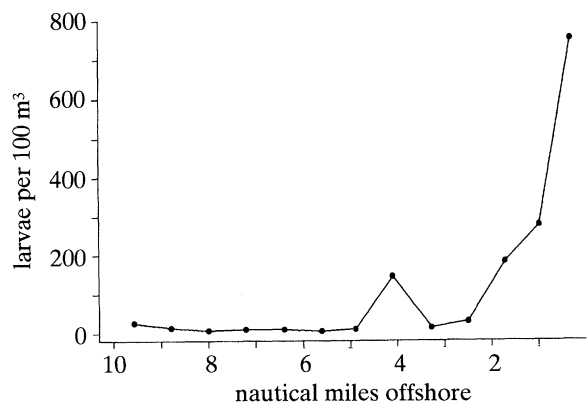

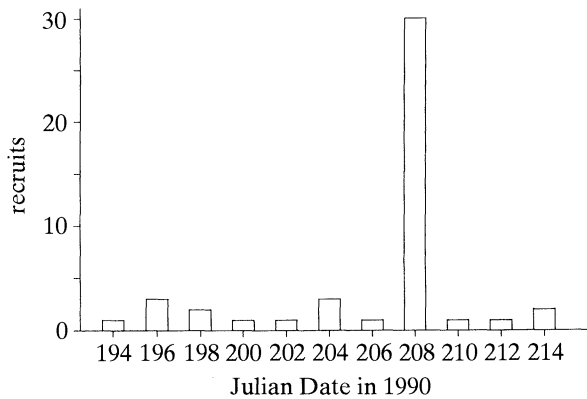Figure 5. Abundance of cyprids from 10 mi to shore one day later (Julian day 207) than in figure 2.

Figure 6. Recruitment of barnacles to small settling plates (50 cm², made of safety walk tape 3M Co product 7740 on fibreglass) at Asilomar Beach about 10 mi from the shoreward point on the transect.

a huge settlement pulse was recorded, as illustrated in figure 6.

We now turn to the kind of model needed to predict the population dynamics of intertidal barnacles taking into account both ecological and physical–oceanographic processes.

3. POPULATION DYNAMIC MODEL WITH OCEANIC AND BENTHIC COMPONENTS

The model extends earlier work on population dynamics with benthic and pelagic stages (Possingham & Roughgarden 1990). The new feature is to represent the upwelling front as a reflecting boundary located at x_f. First the adult dynamics are described followed by the larval dynamics. The example is for one dimension.

The adult population is situated at a point, the

are advected offshore at a rate U, and diffuse along the positive x-axis at a rate set by the eddy-diffusion coefficient, K. The larval death rate is v. The equation describing larval population dynamics is

$$\frac{\partial L(x,t)}{\partial t} = - U \frac{\partial L(x,t)}{\partial x} + K \frac{\partial^2 L(x,t)}{\partial x^2} - vL(x,t). \qquad (3)$$

The two boundary conditions also include an advective component. The boundary condition at the coast, where larvae are produced by the adults at rate m and settle on free space at the coast, is

$$UL(0,t) - K \frac{\partial L(x,t)}{\partial x}\bigg|_{x=0} = mB(t) - cF(t) L(0,t), \qquad (4)$$

The boundary condition at the offshore front is

$$UL(x_f,t) - K \frac{\partial L(x_f,t)}{\partial x}\bigg|_{x=x_f} = 0. \qquad (5)$$

This model can be solved analytically to some extent using an approximation based on a different time scaling for larvae and adults. The adult population, $B(t)$, may be viewed as more or less constant in time relative to changes in $L(x,t)$ because barnacle adults grow much more slowly than the water column processes operate. The entire larval life cycle is approximately 4 weeks long, compared with an average adult life cycle of more than one year. With this assumption, the equation for $L(x,t)$ may be solved for equilibrium with a fixed B and then the equation for $dB(t)/dt$ may be stepped forward in time. Thus the idea is to let the larval population 'track' the dynamics of the adult population. In this way, an equation for the adult population is derived that combines both oceanographic and benthic parameters:

$$\frac{dB}{dt} = \left(\frac{mc(A - aB)(\beta_2 - \beta_1)}{(U - K\alpha_1 + c\,(A - aB))\beta_2 - (U - K\alpha_2 + c\,(A - aB))\beta_1} - \mu \right) B, \qquad (6)$$

origin. Larvae are released from the adult population at this point and are diffused laterally, along the x-axis, by turbulence in the ocean. The rate of change of the number of adult barnacles at the coast at time t, $B(t)$ is

$$dB(t)/dt = c\,F(t)\,L(0,t) - \mu\,B(t), \qquad (1)$$

where F is the amount of free space available, $L(0,t)$ is the larval concentration at the coast at time t, c is the proportionality constant for the rate of larval settlement, and μ is the death rate of the adult barnacles. The total amount of space, A, is equal at all times to the amount of free space, $F(t)$, plus the amount of occupied space, $aB(t)$, where a is the average basal area of an adult

$$A \equiv F(t) + a\,B(t). \qquad (2)$$

The larval population is situated on an interval of the x-axis between the origin and a point, x_f, which is the location of an offshore reflecting boundary. Larvae

where

$$\alpha_1 = (1/(2K))(U + \sqrt{(U^2 + 4vK)}), \qquad (7)$$

$$\alpha_2 = (1/(2K))(U - \sqrt{(U^2 + 4vK)}), \qquad (8)$$

$$\beta_1 = (U - K\alpha_1)\exp(\alpha_1 x_f), \qquad (9)$$

$$\beta_2 = (U - K\alpha_2)\exp(\alpha_2 x_f), \qquad (10)$$

The first term in the parenthesis can be thought of as the per capita recruitment rate to the benthic site, and the second term is the per capita mortality rate in the benthic site. When recruitment comes into balance with mortality, a steady state population size, $\hat{B}$, is attained. Moreover, the condition for $\hat{B} > 0$ coincides with the condition for increase when rare

$$\left(\frac{dB}{dt}\bigg|_{B=0} > 0 \right).$$

If the water column parameters of cross-shelf advection U and front location x_f change slowly relative to
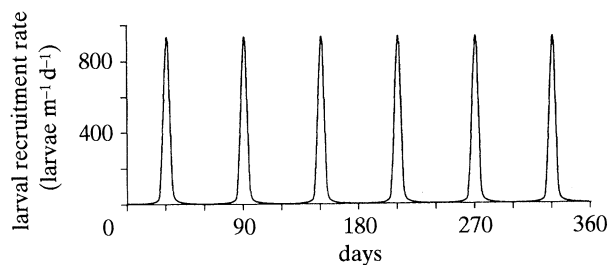
Figure 7. Larval recruitment rate in larvae $m^{-1} d^{-1}$ as a function of time in d sampled every 3 h. Parameter values are typical of the barnacle, *Balanus glandula*: the eddy diffusion coefficient, K, is 10 m s^{-1}; the larval mortality rate, v, is $5.6 \times 10^{-7} \text{ s}^{-1}$; the larval settlement coefficient, c, is $5.6 \times 10^{-6} \text{ s}^{-1}$; the benthic mortality rate, μ, is $2.8 \times 10^{-7} \text{ s}^{-1}$; the total area, A, is 1 m^2; and the area covered by a barnacle is 10^{-4} m^2. The time step in the iteration of equation (6) was 3 h, and the parameters expressing rates in s were multiplied by the number of seconds in 3 h, before being used.

the speed at which the larval population comes to equilibrium, one can take $U = U(t)$ and $x_f = x_f(t)$ as time-dependent parameters, and directly force the model by assuming a temporal pattern for these parameters. We consider therefore a hypothetical scenario in which the location of the front, x_f, moves sinusoidally between 1 and 25 km offshore with a period of 60 d, together with a similar sinusoidal pattern for the strength of advection, U, which varies from 0.2 m s^{-1} at maximum upwelling to 0 m s^{-1} at maximum relaxation. Figure 7 illustrates recruitment pulses to the intertidal zone that occur in this physical scenario. This model thus offers an idealized picture of how the dynamics of the California Current control the dynamics of the ecosytem in the rocky intertidal zone along the coast.

In the future, this model can be further developed by extending it to two dimensions: the larval pool lies in a finite area adjacent to the y-axis in the left half-plane, and the benthic site is a finite interval of the y-axis. Then the implications for coastal populations of mesoscale features such as meanders, squirts and jets in the California Current can be investigated. Furthermore, data on the position of offshore fronts and on the vector field of advection in the surface mixed layer of the ocean can be obtained from remote sensing technology. The AVHRR sensor in the NOAA satellites yields images of sea surface temperature, and fronts are located in the images as locations of high gradients in surface temperature. The technology of CODAR yields a map of current vectors for an semicircle of with a radius of about 50 km from the station. These data can be assimilated every 3 h, say, and used to forcast the time series of recruitment and population dynamics of coastal populations.

4. DISCUSSION

As for generalization across marine and terrestrial systems, what can be ventured? Both marine and terrestrial communities are increasingly viewed as open systems. Sometimes the organisms transport

themselves across the system boundaries, as if acting as their own agents. More often, the transport is brought about by, or permitted by, physical processes taking place in the habitat or its vicinity.

In marine ecosystems the transports involve currents, and more specifically, the motion of fronts at which organisms have been concentrated. These transport mechanisms enter in models at the population scale, and then are propagated to the community scale and higher.

Terrestrial ecosystems are more closed than marine ecosystems because water is a habitat whereas air is not. Animals and plants live while suspended in the water, whereas air is visited only for brief periods. Hence, by increasing the perimeter of a terrestrial site's boundary, the site becomes increasingly closed, whereas marine sites quite large by terrestrial standards are still open systems because of the longevity of the dispersive phase. As a result, an ordinary differential equation of a kind familiar in the traditional ecological literature may be satisfactory for a terrestrial population, provided the site is taken to be sufficiently large. (A caveat is that if the site is taken to be too large, it is internally heterogeneous, requiring treatment as a metapopulation of interconnected sites.) In contrast, at the community scale, transport mechanisms such as wind for spores and bacteria, land bridges for mammals, and plate tectonics for reptiles must be explicitly considered for community patterns. Ecological interactions simply do not explain much about community structure unless the cast of characters is known, and the casting is carried out by these physical transport processes.

These generalizations suggest six policy implications. First, terrestrial systems are functionally more localized than marine systems, and extinctions more likely to result from habitat development. Second, a widespread terrestrial biome, such as a forest, is not functioning as a large single system but as many instances of the same system that happen to be contiguous, whereas the similarly widespread rocky intertidal zone is functioning more as single ecosystem because of the large spatial scale of the larval transports across it. Third, damage to a marine ecosystem is likely to be discerned farther away from the spot of the stress than in a terrestrial ecosystem. Logging in streams affects fishing stocks hundreds of miles away where different industries and political constituencies are involved. Damage to a terrestrial ecosystem is more likely to be discerned near where the damage occured: soil runoff impacts the very neighborhoods where the clear cutting has taken place. Fourth, recovery of marine ecosystems is faster and more possible when stress is removed because recolonization of the stressed area is faster and components are less likely to be lost permanently. In a terrestrial ecosystem full recovery is impossible if extinctions have occured. Fifth, precious ancient life forms and species combinations are more common and more endangered on land than at sea. Sixth, management of renewable marine resouces is different on land and at sea, requiring adaptive harvesting strategies at sea that are tied to continuous environmental monitoring,

whereas on land a harvesting strategy based on demographic theory is more likely to be sufficient.

REFERENCES

Farrell, T., Bracher, D. & Roughgarden, J. 1991 Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnol. Oceanogr.* **36**, 279–288.

Gaines, S. & Roughgarden, J. 1985 Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc. natn. Acad. Sci. U.S.A.* **82**, 3707–3711.

Possingham, H. & Roughgarden, J. 1990 Spatial population dynamics of a marine organism with a complex life cycle. *Ecology* **71**, 973–985.

Roughgarden, J., Gaines, S. & Possingham, H. 1988 Recruitment dynamics in complex life cycles. *Science, Wash.* **241**, 1460–1466.

Roughgarden, J., Pennington, J., Stoner, D., Alexander, S. & Miller, K. 1991 Collisions of upwelling fronts with the intertidal zone: the cause of recruitment pulses in barnacle populations in central California. *Acta Oecologia* **12**, 1–17.

Discussion

C. CLARK (*Department of Mathematics, University of British Columbia, Vancouver, Canada*). I was disappointed that Professor Roughgarden seems to be saying that eventually we will need to develop a global 'atlas' of models for a vast number of separate systems. What would be the point of such an exercise? Surely the message of his paper is that it has now become routinely possible to study ecological processes by a judicious combination of intelligent empirical studies and modelling. Hypotheses can be formulated and tested by using an interactive development in which theory and observation mutually support each other. Wherever one wishes to study a particular system or phenomenon, this approach can be used, to great effect, as the authors' paper so brilliantly demonstrates. However, the idea of building a catalogue of models which could be lifted off the shelf as needed seems misguided.

J. ROUGHGARDEN. I sympathize with Professor's Clark's sense of disappointment at the seeming absence of generalizations in ecology, and with his fear that our study may become little more than the stamp collecting of particularities, including particular models. But I ask him to consider further the following points:

1. Ecologists do not need to provide generalizations to policy makers and others needing to apply ecological knowledge, but we do need to supply consensus on how particular ecological systems work. For example, as Professor Powell's talk illustrates, we need to determine what is going on in the Georges Bank ecosystem to guide the recovery of cod and other commercial stocks that have become depleted. We need to get it right about this particular system; for purposes of application we do not need to know if Georges Bank is a case of some generalization. One professional responsibility is met with the successful analysis of the particular, and we should not confuse the need of ecologists to pull together and to speak with one voice with a demand that we sign on to generalizations we do not accept.

2. An 'atlas' of models may be a perfectly natural way to classify ecological models, rather than by, say, their mathematical or computational structure, by the ecological processes represented in them, or by the kinds of predictions they make. Ecology may be inherently a geographical subject, and atlases are extraordinarily useful methods of representing geographical information.

3. The absence of generalizations in ecology is usually interpreted in two ways, either poor generalizations have been proposed, or ecologists are indisposed to generalization and prefer quarrelling and microarguments instead. But we now have a 70 year track record of failed generalizations, ranging from the incorrect organism concept of an ecosystem, through irrelevant thermodynamic concepts of ecosystems, to partially correct claims such as those involving competition and niche theory, the intermediate disturbance principle and keystone predator, the turnover theory of island biogeography, optimal foraging theory, life history theory, food web patterns and theory, and on and on. For every general claim, anyone with empirical experience can cite counter examples. The life cycle of general claims in ecology is to survive only in highly qualified form, if at all. Well, perhaps the life cycle of generalizations in ecology is not the fault of ecologists, but actually reflects the deep structure of our material. If so, we should develop classifications of our knowledge that take this natural variation on the earth into account.

4. Finally, I hope it is true that successful research on ecological processes by combining empirical studies with field work has become 'routinely possible'.

M. MANGEL (*Section of Education and Ecology, University of California, Davis, California, U.S.A.*). The argument presented in this paper about the formation of communities is a powerful one, especially since so much of the historical record concerning animals and plants is lost relative to the physical geological record. In such a case, I wonder if instead of asking how communities are formed (i.e. the historical question), we would be better off focusing on how communities are maintained?

J. ROUGHGARDEN. I am far more optimistic about reconstructing historical processes that determine the initial condition of a community than previously. For terrestrial systems, the plate tectonic revolution in the earth sciences has provided us with causal processes to reconstruct historical conditions with scientific methods. History to us now becomes merely the scientific study of slow processes, instead of a domain beyond science as previously thought. Still, I agree that the study of what maintains the configuration of an ecological community is more amenable to study, and also is usually the information most relevant to policy concerns.

J. S. GRAY (*Section of Maine Zoology and Marine Chemistry, Department of Biology, University of Oslo, Norway*). How general does Professor Roughgarden believe his model is? Does it, for example, apply to the whole range of the barnacle species studied and to its predator? Is it, in his opinion, likely that we will need different models for each species in a community?

J. ROUGHGARDEN. I suspect the model, considered as the starting point for a more comprehensive treatment including a two-dimensional larval pool and more species, is fairly general for rocky intertidal barnacles. For rocky intertidal

habitats not adjacent to upwelling areas the offshore 'reflecting boundary' is a front made by some other water-column processes, such as tidal fronts. In addition, a moving sequence of partially reflecting boundaries could be used for locations where larval transport by internal waves is important. The key points to the model here are that it uses a phenomenological representation of oceanographic features so that the model has an even balance of detail in both the physical and biological parts, and that the density dependence comes from exploitative competition for space. To use it with other kinds of species, such as a starfish that preys on barnacles, the benthic part too would have to be changed to account for food rather than space as a limiting resource. So certainly, we do need different models for each species, but not radically different models for each, simply variants on a common theme. In my geological metaphor, no two river deltas are the same, and therefore identical bridges cannot be built over them, but still a common knowledge can be brought to bear.

A. GRANT (*School of Environmental Sciences, University of East Anglia, U.K.*). Professor Roughgarden has shown a graph of the temporal variation of barnacle settlement at a single site. Over what spatial scales do these temporal fluctuations show coherence?

J. ROUGHGARDEN. Empirically, settlement from the north of Monterey Bay at Santa Cruz to near the entrance to San Francisco Bay at the Golden Gate Bridge is quite coherent, and the stretch of coast from the Monterey Peninsula to Point Sur is as well. Both these intervals are about 50 nautical miles (mi), so, once allowance is made for local features such as points and outcroppings with special upwelling or other currents, the coherence scale is about 50 mi. The settlement is consistently about 10–20 times higher in the interval north of Monterey Bay compared with the stretch of coast to the south of the bay. I attribute this difference in total settlement rate to a consistently closer position of the California Current in the north relative to the south, caused by the persistent location of the California Current meander in this region. The lower bound to the coherence scale for settlement is probably determined by some counterpart of the KiSS patch length, where eddy diffusion matches larval production rate from a point on the coast.

J. H. STEELE (*Woods Hole Oceanographic Institution, Massachusetts, U.S.A.*). In the model for a barnacle population, where is the population regulation, in the benthic site or in the water column?

J. ROUGHGARDEN. The density dependence is the benthic site, where space is the limiting resource. So the population cannot tend, mathematically, to infinity because of space limitation in benthic part of the model. Concerning the other equilibrium point, extinction, the condition for increase when rare is that the front be sufficiently close to shore or that the offshore advection be sufficiently weak. Therefore, the water-column part of the model determines whether the species can exist. Thus, the essence of supply-side ecology as I see it is that both benthic and oceanic parts must be considered equally important to the total picture.