

HISTORY AND CURRENT DEVELOPMENT OF A PARADIGM OF PREDATION IN ROCKY INTERTIDAL COMMUNITIES

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Abstract. A paradigm is a set of mutually supportive hypotheses that provides a frame of reference within a field. In 1962, Kuhn proposed that paradigms form within the dual contexts of empirical evidence and intellectual history. Facts potentially contradictory to a paradigm may not be recognized until they are observed repeatedly and incorporated as supportive evidence into a new theory.

Support for this interpretation can be found in the history of a paradigm of predation in rocky intertidal communities. Hypotheses were developed in the contexts of innovative field experiments and historical arguments of competition theory. The resulting paradigm proposed that predators restrict populations of competitively dominant prey to refuges. Different types of refuge, or no refuge, prevail in different areas of the intertidal zone, accounting for patterns of prey distribution, the coexistence of natural enemies, and the local maintenance of diversity. An ensuing period of criticism made reference to potential contradictions. Rather than by predation alone, prey abundances are determined largely by an interplay of varying rates of predation and prey production. Furthermore, prey refuges are neither necessary nor sufficient to explain all observed instances of local coexistence of predators and prey.

We present a model in which intertidal boundaries of prey are set by equilibria between predation and prey production. Predation and prey productivity vary with environmental gradients and with explicit spatial configurations of the prey. This synthesis relies on insights of the original paradigm, incorporates the contradictory observations, and depends on novel capabilities afforded by spatially explicit computer simulations. The resulting synthesis provides explanations for distinctive aspects of zonation, including abrupt prey boundaries in continuous gradients of predation, and converging upper and lower prey boundaries in gradients of decreasing wave exposure.

Key words: *competition; diversity; Mytilus; niche; paradigm; Pisaster; predation; refuge; regulation; rocky intertidal communities; zonation.*

INTRODUCTION

This essay follows one thread through the tapestry of ecological thought. It traces the historical development of a paradigm of predation in rocky intertidal communities. Simply stated, the paradigm holds that horizontal bands or zones of adult prey form in refuges from dominant “keystone” predators. The theory takes on much wider significance than merely an explanation for zonation. It is seen as an exemplary mechanism simultaneously accounting for patterns of distribution and abundance, the coexistence of natural enemies, and the maintenance of local diversity. Therefore, we trace an effort to solve some fundamental problems in ecology.

Our narrative begins with a brief overview of early works that played a role in the development of the paradigm. We suggest that the paradigm was a response to innovative field experiments and prevailing theories of the time, most notably niche theory. We describe an

ensuing period of criticism and continuing research that brought forth contradictions and eventually revisions to the paradigm. We then draw upon new theoretical approaches from other fields of ecology to propose a synthesis that resolves remaining contradictions and promises continuing advances in predation theory. Finally, we ask whether the original concepts of intertidal predation are indeed a paradigm as conceived by Kuhn (1962). We conclude that the theory appears to meet the criteria of a paradigm in all respects except one. Changes have not proceeded as revolutionary paradigm shifts. Rather, crucial insights of earlier studies are preserved, and theory changes gradually (Graham and Dayton 2002, Paine 2002).

However one may regard paradigms, the purpose of this essay is to explore the influence of prior thinking on current ecological theory, and to use this understanding to develop more general explanations of ecological phenomena.

HISTORICAL CONTEXT

In the first half of the 20th century, benthic ecology was predominantly an observational science. The proposition that patterns of distribution are shaped directly

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by physical gradients at the margins of the oceans seemed self-evident. Ubiquitous intertidal zonation was the subject of various classification schemes which all relied on varying degrees of wave action and tidal exposure to catalog the diverse patterns (e.g., Colman 1933, Stephenson and Stephenson 1949, 1972, Lewis 1964). Assigning cause to correlations, the concept of critical tidal factors maintained that species were distributed over the gradient of tidal exposure according to their tolerance to desiccation or flow (e.g., Colman 1933, Doty 1946; see Wolcott [1973] and Underwood [1978] for discussion). The advent of controlled field experiments in this environment at first strengthened the case for direct physical causes of zonation. Hatton (1938) reduced desiccation stress in the upper shore levels using runoff from artificial pools, and thus improved survivorship or raised upper vertical limits of certain species high on the shore (later examples in Castenholz [1961], Frank [1965], Dayton [1971]). However, beginning in the second half of the 20th century, field experimentation was expanded to include population manipulations that tested the effects of biotic factors.

The first population manipulations removed consumers from rocky shores of the British Isles. Smashing limpets and other herbivores in a vertical swath through the zones on a rocky shore of the Isle of Man produced a uniform sward of green algae, and thus demolished the concept of critical tidal levels (Jones 1948, Burrows and Lodge 1950, 1951). Experiments involving invertebrate predators soon followed. Kitching et al. (Kitching et al. 1959, Ebling et al. 1964, Kitching and Ebling 1967) transplanted mussels from wave-swept sites to more quiet shores and observed their consumption by crabs and snails. In support of the experimental results were the observations that the mussels formed beds in certain back-bay areas from which predators appeared to be intermittently removed by episodes of extremely high biological oxygen demand (Kitching et al. 1976), or on wave-beaten points where hydrodynamic stress appeared to hinder predator foraging. In these instances, physical factors appeared to influence patterns of zonation indirectly, by moderating the intensity of biotic factors. These findings also suggested that physical stress may create prey refuges from predation.

The concept of prey refuges had an historical antecedent in early laboratory experiments. The predatory ciliate *Didinium* was cultured with *Paramecium* prey (Gause 1934) and the predatory mite *Eotetranychus* was placed with orange mites *Typhlodromus* (Huffaker 1958). Rapid extinctions were the consistent outcome in the simpler systems, as predators invariably starved after driving the prey to extinction or to numbers too small to sustain predator populations. Adding a substratum of decaying oats provided a refuge for *Paramecium* from *Didinium* and prolonged coexistence. Periodic inoculations of the cultures with predators and prey also prolonged coexistence. Predator-prey inter-

actions seemed prone to instability. Coexistence appeared to require either prey refuges or a prey population divided into subunits continually undergoing extinction and recolonization. Thus, the concepts of refuge and metapopulation dynamics, central to later thinking about intertidal communities, surfaced in early experimental work with nonmarine species (see Taylor [1984] and Taylor [1990] for further history of laboratory experiments and discussion of stability via refuges or metapopulation dynamics).

The concept of refuges was set within a much wider discussion of mechanisms allowing the coexistence of competing species, as well as predators and prey. The earliest ecological theory emphasized that the potential for geometric increase of populations must be opposed by features of a finite environment. A struggle for existence is the inevitable result (Malthus 1798, Darwin 1859; review in Hixon et al. [2002]). Darwin's (1859) assertion that the struggle should be keenest among the most similar beings focused attention on competition. Gause's (1934) laboratory experiments, the first controlled tests of species interactions as limiting factors, repeatedly confirmed that competition could decide the outcome of the struggle (see Crombie [1945], Park [1948], [1954], and Birch [1953] for later examples). Prompt extinction of one competitor occurred in most experimental contests, but in some cases competitive exclusion was circumvented by competitors using different resources. Gause (1934) concluded "as a result of competition, two similar species scarcely ever occupy similar niches. . . ."

By the mid-20th century, competition was widely viewed as the principal organizing force in communities, and the niche was the fundamental unit of that organization (e.g., Vandermeer 1972; discussion in Connell [1975]). MacArthur's studies of woodland warblers (MacArthur 1958, MacArthur and Levins 1967) became the archetypal example of niche theory: a depiction of a community at equilibrium, finely organized through competitive interactions. That such an organization followed from a vision of populations inexorably expanding to the depletion of their resources has been termed by Strong (1984) the Neo-Malthusian Perspective.

Experiments on intertidal zonation at first reinforced the idea of a central organizing role for competition. In an early work that remains largely unknown, Sarah Baker (1909, 1910) used the simplest of laboratory apparatus to indirectly investigate zonation of brown seaweeds, *Fucus* spp. She suggested that species are arrayed over the tidal gradient as the result of adaptive trade-offs between tolerance to desiccation and competitive ability, foreshadowing much later explanations (e.g., Connell 1975, Lubchenco 1980). In the first and perhaps most influential field experiments to investigate competition, Connell (1961a, b) reduced densities of the barnacle *Semibalanus* (then *Balanus*) *balanoides* and observed improved survivorship of a smaller bar-

nacle *Chthamalus stellatus*. Adult *Chthamalus* were observed to form dense aggregations only above the vertical distribution of *Semibalanus*, a limit evidently set by desiccation. In the decade succeeding Connell's work, a number of other experimental field studies confirmed the existence of competitive effects (e.g., Stimson 1970, 1973, Dayton 1971, Menge 1972, Haven 1973). Several of these (e.g., Kohn 1971, Harger 1972) interpreted the findings in light of niche theory, providing a marine analog to MacArthur's warblers.

However, the strands of intertidal and terrestrial theories diverged at this point. Niche theory was not widely applied to intertidal systems. As the number of intertidal field experiments grew, the process of competitive exclusion often seemed checked by predation, an idea that can be traced to Linnaeus (1760) and Darwin (1859) among others (reviewed in Egerton [1973]). The predation paradigm developed in the context of the Neo-Malthusian perspective, and it addressed the central concerns of that perspective differently than did niche theory.

THE PREDATION PARADIGM

Seminal field studies

Paine's manipulations of seastar densities (1966, 1974) provided a central body of evidence in the formative period of the predation paradigm. Plucking *Pisaster ochraceus* from a rocky shore on Tatoosh Island precipitated the downward extension of an upper intertidal bed of the mussels, *Mytilus californianus*. The mussels overgrew algae and invertebrates which otherwise comprised the dominant cover of lower shore levels. No such changes developed in an unaltered control site nearby. Paine (1974) also observed that the lower boundaries of natural mussel beds were remarkably constant from year to year. Evidently, physical stress set the upper limits of predation, which in turn set the lower boundary to a spatial refuge. Below the spatial refuge, one occasionally found very large mussels, in clumps, coexisting indefinitely with the seastars. This fact and the observation that *Pisaster* consumed mussels smaller than the maximum available suggested that sometimes mussels may reach a size invulnerable to predation, a size refuge (Paine 1976). Parallel results were found in studies of predation by whelks on barnacles and mussels at several Pacific Northwest locations (Connell 1970, Dayton 1971).

Predators such as *Pisaster* play a special role in maintaining the structure of their communities. Analogous to the keystone of a medieval cathedral arch, remove such predators, and the community architecture crumbles (Paine 1969; see Castilla and Duran [1985] and Paine et al. [1985] for examples outside North America). Removal of *Pisaster* allowed the downward expansion of competitively dominant mussels, threatening the loss of competitive subordinates, and potentially affecting still more distant trophic links. In one

scenario, removal of predators allowed increases in their herbivorous prey, which in turn suppressed primary producers, a sequence termed trophic cascade (sensu Paine 1980; reviews and discussion in Kerfoot [1987], Power [1992], Strong [1992], and Polis [1994]). Control of the community was top down, the changing conditions at higher trophic levels affecting the lower trophic levels. Thus, the predation paradigm wove together the concepts of refuge, keystone predation, top-down control of communities, and trophic cascades.

Historical role of the paradigm

The influence of the predation paradigm stemmed from (1) the experimental character of its evidence and (2) its power to answer in a simple way fundamental questions arising in the formative period of ecology. The series of controlled population manipulations from the 1940s through the early 1970s defined a watershed period for benthic ecology. They were among the first controlled field manipulations, and set ecology on an equal footing with other experimental sciences. The simple population manipulations revealed otherwise hidden biotic interactions (competition and predation) proffering that such manipulations could resolve ambiguities in the interpretation of observations alone (Connell 1974, Paine 1977, 1980).

Equally important, the experiments gave compelling answers to several fundamental questions. Perhaps the most basic question asked which factors control the distribution and abundance of organisms (Andrewartha and Birch 1954). The accumulation of experimental evidence indicated that the lower limits to rocky intertidal zones are set by biotic factors, whereas upper limits are set by physical stresses (Connell 1972). In shore populations controlled by predation, these limits were the bounds of prey refuges. Another question, inspired by the vision of the struggle for existence, asked what mechanisms allow the coexistence of natural enemies. Adult prey in refuges produce a continuous supply of juveniles that both support predators and replenish their own stocks. Prey population stability and coexistence with predators seemed assured in the local, constituent populations. Hypothetical mechanisms affecting coexistence on the metapopulation level of organization assumed less importance, although this possibility eventually received theoretical treatment as well (e.g., Reeve 1990, Hanski 1999).

The same mechanisms explained the coexistence of potential competitors. In the *Mytilus-Pisaster* interaction, beds of *M. californianus* were depicted as competitively dominant monocultures expanding glacially downward, and whose otherwise devastating advance was checked at the upper limit to seastar foraging. Similarly, physical disturbances were shown to remove mussels and other competitors, clearing space on the rock surface, apparently the limiting resource for competitively subordinate species. In the context of com-

petitive exclusion, physical catastrophes and predation were seen as functionally analogous (e.g., Dayton 1971, Connell 1978, Sousa 1979, 1984, Paine 1980, Paine and Levin 1981, Petraitis et al. 1989), and predation that freed space was sometimes referred to as biotic disturbance.

The view that disturbance and predation perpetually deflected trajectories of population growth from competitively set equilibria lent impetus to an important shift in thinking. It encouraged doubts as to whether competition is the primary factor, or even a significant influence, structuring many communities (e.g., Connell 1975). Niche theory did not receive broad application in marine communities, and the counterexamples drawn from the benthic environment were among the factors that lead to the downfall of niche theory as the putative unifying principle in ecology (Weins 1977, 1983, Connell 1983, Strong 1983; review in McIntosh [1987]).

REVISIONS OF THE PARADIGM

We consider revisions of two implications of the original predation paradigm: (1) that top-down dynamics alone determine intertidal community structure, and (2) that refuges are the essential mechanisms of coexistence of predator and prey species.

Revision of top-down dynamics: varying prey production incurs feedback

Over the last 25 yr, the original paradigm changed in one important aspect: top-down dynamics were replaced with a view emphasizing the interaction of predation with variable prey production. (In this essay, we consider production to be recruitment to the local benthic population and growth of the members of that population, excluding reproductive products released into the plankton.)

The characterization of predation as a thwart to otherwise unremitting competition presupposed that prey recruitment was consistently above the threshold that would incur severe competition in the absence of predation. The implication that variation in recruitment could be safely ignored was challenged in cautionary reviews of intertidal community research (Dayton 1979, Dayton and Oliver 1980, Underwood and Denley 1984) and in studies of coral-reef fish populations (Doherty 1983, Victor 1983). A series of articles (Roughgarden et al. 1984, 1985, 1987, 1988, 1991, Gaines and Roughgarden 1985, 1987, Gaines et al. 1985, Roughgarden 1986, Roughgarden and Iwasa 1986) argued that recruitment variation was a leading determinant of intertidal population structure, influencing adult abundances, their degree of crowding, and consequently the intensity of competition. Models established the theoretical possibility that below a threshold rate, variation in recruitment rates, not competition, explained most of the variation in the adult populations, and that at higher recruitment rates, the settling of initial recruits could preempt the successful settling of later individ-

uals. Thus, competition was not unremitting, and recruitment variation could generate feedback affecting the intensity of competition. The emerging synthesis was dubbed supply-side ecology (Lewin 1986). From this point onward, perhaps no other topic garnered more attention from benthic ecologists, and the number of empirical studies of recruitment exploded (compare reviews by Connell [1985] and Caley et al. [1996]).

Supply-side considerations bore implications for the keystone predator hypothesis. Underwood and Denley (1984) argued that rates of productivity often vary along environmental gradients, so that effects of changing productivity are confounded with predation. For example, settlement of some species may decrease towards low shore levels, in which case the lower limit of the prey zone may be attributed as much to diminished recruitment as to predation. Recognizing variation in prey recruitment also resolved inconsistencies in the experimental evidence for the keystone predator effect. Removals of a predator that produced marked increases in the competitively dominant prey in one experiment sometimes produced no effects in a second experiment (e.g., Dayton 1971, Paine et al. 1985). Seastar removals did indeed produce significant results in a diverse array of rocky shore communities, provided they were done in years when the mussel recruits were abundant (Paine et al. 1985). Varying prey recruitment also explained marked differences in experimental outcomes across small spatial scales in the interaction between intertidal mussels and predatory spiny lobsters in southern California (Robles 1997).

In the preceding cases, recruitment variation determined whether effects of keystone predation were observed, which posed a modification, but not a substantial revision of the paradigm. However, varying prey recruitment implied differing amounts of the prey supporting the predator populations, and hence, the possibility of feedback effects. For example, the lower limit of zones of *Mytilus californianus* appears to remain relatively constant from year to year, and the shore below the mussel beds is kept continually free of significant numbers of prey by seastars, occasional escapes of a few mussels in size refuges notwithstanding. But since predation is size limited, extreme prey recruitment variation, if met with an insufficient predator response, would lead to formation of dominant year classes of prey, and changing zonation patterns (discussion in Underwood and Denley [1984]). Therefore, interannual variation in mussel recruitment must either remain below that which could be controlled by a static predator population, or the predator population must respond sufficiently to keep the prey in check. Under the paradigm, the latter possibility was expressly discounted (e.g., Valiela 1984, Murdoch and Bence 1987; discussion in Robles et al. [1995]).

Subsequent findings (Robles et al. 1995) revealed that *Pisaster* moves along the shore, responding quickly to differences in recruitment of *Mytilus* spp. Local

densities of *Pisaster* changed many-fold within days in response to natural or experimental additions and losses of mussel recruits. From year to year, within and among separate local populations, natural seastar densities were positively correlated with an index of recruitment of the mussels. These findings demonstrated a possible mechanism for the maintenance of the prey-free zone despite extreme interannual recruitment variation. Top-down dynamics appeared to be but half of an interaction loop affecting prey populations (Menge et al. 1994).

The preceding supply-side phenomena involved the interactions between pairs of species. However, these populations are enmeshed in a larger food web, and therefore, effects of varying productivity may have ramifications through a complex network of interactions (see Holt [1977], Paine [1980], Abrams [1987], Kerfoot [1987], Power [1992], Wootton [1994], and Menge [1995] for examples from the extensive literature on indirect effects). One aspect of food-web dynamics stands out as the multispecies elaboration of supply-side effects. Variation in production at lower trophic levels impacts higher trophic levels, producing bottom-up effects. Bottom-up effects include variation in inorganic resources supporting primary producers, variation in the primary producers affecting growth rates or reproductive outputs of primary consumers, variation in recruitment of primary consumers affecting their predators' populations, and so forth. For example, Bosman and Hockey (1986, 1988*a, b*) proposed that the structures of intertidal limpet populations were affected by both the top-down effect of predation by birds and the bottom-up effect of guano enhancing the production of algal forage of the limpets.

Menge et al. (Menge 1992, 2000, Menge et al. 1994, 1997*a, b*) proposed that from location to location along the Oregon coast, nearshore waters show large differences in nutrients and planktonic larval supply. These differences affected the recruitment and growth of suspension feeders and algae, which occupy the base of the intertidal food web. The relative abundance of various higher level consumers varied greatly from shore to shore, depending on which basal species were favored by the oceanic conditions. On shores supporting the rapid recruitment and growth of suspension feeders, seastar densities, biomass, and consequently predation rates were higher than on less productive shores.

Acceptance of supply-side and bottom-up dynamics was, de facto, a major revision of the original predation paradigm. The primacy of top-down interactions was replaced by a view emphasizing interaction between predation and varying recruitment, including functionally significant feedback (see discussions in Power [1992] for terrestrial counterparts of this argument). Such feedback dynamics may be especially important in regulating populations with dispersing larvae, because they potentially counteract or accentuate effects of external forcing factors. Even though local mussel

populations may be affected by extreme variation in recruitment from planktonic larval stocks, local mechanisms appear to dampen, to varying degrees, resulting variation in the adult populations (e.g., McGroarty and Goss-Custard 1993; discussion in Caley et al. [1996]). Theoretical studies are just beginning to explore how local feedback interacts with metapopulation dynamics to produce patterns of distribution and population stability (discussion in Reeve [1990], Murdoch [1994], and Hanski [1999]).

*Revision of refuges: variable risk,
spatially conditioned*

We focus on three propositions of the refuge hypothesis: (1) that physical stresses set the lower boundary of the spatial refuge at a shore level that the predators cannot invade (Connell 1975), (2) that spatial and size refuges are different types of escapes from predation which occur on separate shore levels, and (3) that refuges must exist for dense concentrations of adult prey to persist.

Early discussions referred to two different types of refuges on separate shore levels. For example, Paine (1974) states, "The mussel band clearly can be considered a refuge (from predation). . . . Individuals below the band's lower limit are often large; they have escaped their major predator, *Pisaster*, by growing too large to be eaten. . . . They thus form an alternative stable solution to the predator-prey interaction. . . ." Subsequent discussion of the zonation of tropical shores accepted the original typology of refuges and added three-dimensional spatial refuges (crevices in the rock surface: Menge and Lubchenco 1981). Relatively recent reviews of intertidal community dynamics reiterate the two types of prey refuges, with the lower bounds of the spatial refuge set by a vertical limit to predator foraging imposed by desiccation stress alone (e.g., Hughes 1990, Seed and Suchanek 1992, Chapman 1995).

Connell (1975) proposed a specific mechanism for the spatial refuge: "The highest levels on the shore provide a refuge where the predators cannot drill and consume a barnacle during the short period of a high tide." But prey-handling times are positively related to prey size (Emlen 1968, Penny and Griffiths 1984, McClintock and Robnett 1986). Consequently, an adult prey of a size too large to be handled at a given shore level could be vulnerable in the longer submergence times of lower shore levels. Juvenile prey or adults of smaller species, which require only brief handling, could be vulnerable even to the highest reach of the tide, provided that as the predators advance with the rising tides they are not allayed by prey at lower shore levels. That the risk of an individual prey depends on the frequencies of other prey on surrounding shore levels was suggested by findings of Emlen (1968) and J. Menge (1974). Therefore, the proposed mechanism does not necessarily imply an inviolable spatial refuge

zone with a separate size refuge below that zone (the first two propositions above). Rather, at any location within the range of the tides, a prey's risk of predation would depend simultaneously on the densities of predators, the prey's size and shore level, and its position within the spatial configuration of the prey population. Both the density of predators and the configuration of prey can change with prey production, as explained in the section on supply-side effects. Furthermore, acknowledging supply-side effects raises the possibility that sufficiently high production could sustain concentrations of adult prey without recourse to refuges of either type, contrary to the third proposition.

Verbal and graphic models of the refuge hypothesis do incorporate multifactor interactions. For example, Connell (1975) presents a graphic model in which mortality from predators and physical stress vary over gradients of prey size and environmental harshness. It depicts absolute spatial refuges (Fig. 4 in Connell 1975) and size refuges (Fig. 5 in Connell 1975) bounded by contours of probability of mortality from the two factors. This is an important step towards developing a spatially explicit dynamic model. The graphic model is, however, essentially static, ignoring the effects of both varying prey productivity and changing spatial configurations of prey over the intertidal landscape.

The speculations about spatially explicit dynamics would be superfluous if the refuge hypothesis explained all relevant interactions of predators and prey. However, a growing number of observations appear to contradict the hypothesis. Shortly after the appearance of the original experimental works, Paine (1976) published observations of subtidal sea mounts (pinnacles of rock that do not break the surface at low tide) just offshore from his intertidal sites at Tatoosh Island. The sea mounts supported massive beds of large mussels coexisting with large seastars, even though there was no tidal emergence to impose constraints on foraging, and the largest of the seastars were capable of consuming the largest mussels. Reusch and Chapman (1997) modeled such dynamics in the interaction of the European mussel *Mytilus edulis* and the seastar *Asterias rubens*. The vast majority of mussels in a bed are in some degree vulnerable, but their losses to *Asterias* are offset by recruitment and the growth of surviving mussels. The productivity is high enough to sustain both high predation and high prey abundance. Griffiths and Hockey (1987) describe an interplay of prey production, size-dependent predation, and competition for space to explain the variable structure mussel beds in South Africa.

The intertidal zone also presents exceptional cases. In the California Channel Islands, spiny lobsters (*Panulirus interruptus*) enter the intertidal zone on nocturnal high tides and feed on mussels (*Mytilus californianus*; Robles 1987, Robles and Robb 1993). Lobsters sometimes forage within mussel beds, and reach above the upper boundary of the mussel beds as well (Robles et

al. 2001). Laboratory studies, direct observations by divers, and collection of shells bearing characteristic damage marks, confirmed that the lobsters can and do kill some of the largest mussels within the beds (Robles et al. 1990). However, they prefer to consume small mussels, and an enclosure experiment demonstrated that they reduced the frequency of small mussels in a mussel bed (Robles et al. 2001). Surveys of mussel settlement rates show that the input of mussels is greater on sites supporting the mussel beds than elsewhere (Robles 1997, Robles et al. 2001). Therefore, predation rates may be size dependent, but absolute spatial or size refuges are not a prerequisite for adult mussel populations (Robles et al. 1990).

Observations of the *Mytilus-Pisaster* interaction in the intertidal zone also suggest an exception. Desiccation is confined to higher shore levels on wave-exposed sites because wave wash reaches higher in these areas. If desiccation stress from tidal emergence sets the upper limit to seastar foraging, then one would expect to observe the upper extent of seastar foraging to ascend as one surveyed from sheltered to wave exposed shores. In fact, just the opposite is observed (Robles et al. 1995). Observations by divers revealed that the seastars move with the ebb and flow of the tides, and if their retreat on the receding tide is fast enough they avoid desiccation stress. The high tide forays of seastars reach progressively higher levels on progressively more sheltered sites (Fig. 1A), and the lower limits to the mussel beds ascend towards more sheltered sites (Fig. 1B). On any given high tide, seastars could be observed foraging above the lower boundaries of the mussel beds. Evidently lower boundaries are not simply set by desiccation, and they are invaded by the seastars.

A hypothesis based on physical stresses alone might still seem viable, if effects of hydrodynamic stresses on seastar foraging at high tide were added to those of desiccation stress at low tide. Limited data for seastars and other predators (Menge 1978a, b, 1983, Robles et al. 2001) suggest that hydrodynamic stresses at wave-exposed sites probably do hinder the upward advance of aquatic predators at high tide. One would expect mussel distributions to extend to lower shore levels before effective predation is encountered. However, the settlement rates and growth rates of mussels are positively related to wave exposure (Menge 1992, Dahlhoff and Menge 1996, Robles 1997; C. D. Robles, K. Johnson, A. L. Martel, and W. B. Chesney, *unpublished manuscript*). The greater downward extension of mussels on wave-exposed sites appears, therefore, to result from a combination of hindered foraging and increased prey production. Seastars on sheltered shores were observed (C. D. Robles, *unpublished data*) to forage to the extreme upper reaches of the tides (above 3.0 m Normal Lower Low Water [NLLW]; Fig. 1A), where they exploited the sparse numbers of small prey, barnacles and juvenile mussels. This observation is con-

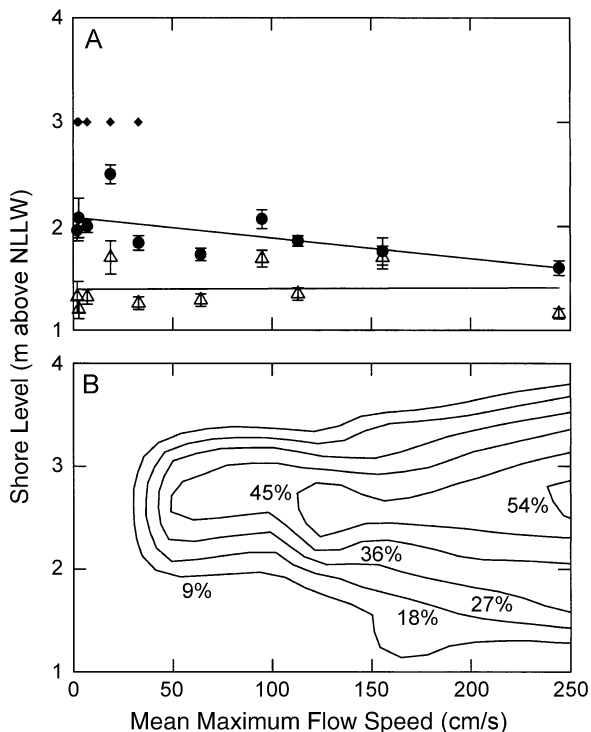


FIG. 1. (A) Relationship between seastar foraging height and wave exposure within the Barkley Sound Region of British Columbia, Canada. For each of 10 survey sites, the mean height ± 1 SE of *Pisaster ochraceus* foraging at high tide (solid circles) is plotted as a function of mean maximum bottom flow speed, both estimated by divers in the intertidal zone at high tide. Mean height above Normal Lower Low Water (NLLW) ± 1 SE of seastars at rest at low tide (open triangles) is also plotted. Lines are least-squares linear fits. Regression of seastar height at high tide vs. flow speed is significantly negative ($F = 14.90$; $df = 1, 170$; $P < 0.001$). Diamonds indicate sites on which the highest seastars reached ≥ 3.0 m NLLW at high tide. Descriptions of sites and survey methods are in Robles et al. (1989, 1995). (B) Contour lines represent varying mussel abundances over tidal and wave exposure gradients. Percent covers of *Mytilus californianus* in 2040 quadrats (each 400 cm²) parceled among stratified random quadrat arrays on each of the 10 sites were fitted to a distance weighted least-squares surface, and the resulting contour lines plotted (description of survey given in Robles et al. [1995]; software SYSTAT [SPSS 1996]). On average, high abundances span increasingly wider vertical ranges toward greater wave exposures. Similar trends can be observed in one continuous mussel bed spanning a range of wave exposures.

sistent with the prediction of spatially explicit dynamics that small, quickly handled prey are potentially vulnerable even at high tidal levels.

The operation of intertidal refuges is still more uncertain if we acknowledge the possible effects of avian predators, which can kill comparatively large prey and have ready access to upper shore populations (Hartwick 1978, Morrel et al. 1979, Griffiths and Hockey 1987; C. Garza, *personal communication*).

Taken in sum, recent empirical findings provide exceptions to the original refuge hypothesis. An exami-

nation of mechanisms, both real and hypothetical, calls for a synthesis that is sufficiently general to reproduce both the classical and exceptional cases of predator-prey interactions.

SPATIALLY EXPLICIT POPULATION MODEL

The model is a type of Spatially Explicit Population Model (SEPM) known as stochastic cellular automata (Ermentrout and Edelstein-Keshet 1993). These models provide an apt format to analyze the dynamics of sedentary populations. They keep track of individuals, and express biological processes, such as their growth and mortality, as functions of each individual's attributes, including their location and proximity to others within the landscape. Thus, population structure emerges from expressions of the biology of individuals. We propose a SEPM in which mussel recruitment, growth, and predation vary over the intertidal landscape according to environmental gradients, and the mussel's size, location, and proximity to others. The model reproduces details of mussel zonation by incorporating variation in recruitment and feedback mechanisms at local spatial scales, but without assuming prey refuges.

SEPMs have been applied widely to terrestrial systems (reviews in Turner 1989, Hastings 1990, Dunning et al. 1995, Tilman and Kareiva 1997). We know of four spatial models for intertidal communities (Paine and Levin 1981, Wilson et al. 1996, Burrows and Hawkins 1998, Wootton 2001). Three are phenomenological, predicting features of distribution patterns from observed rates of their change rather than from expressions for the underlying biological mechanisms. None of the previous models explicitly deals with predator-prey dynamics that form the crux of the paradigm examined here.

Model expressions

We envision an intertidal rock surface overlaid by a rectangular lattice of grid cells. The gradient of tidal exposure spans the columns; the gradient of wave exposure spans the rows. Each cell represents a potential site for occupation by sedentary prey (mussels) within the littoral arena (Fig. 2). A cell is denoted by its x and

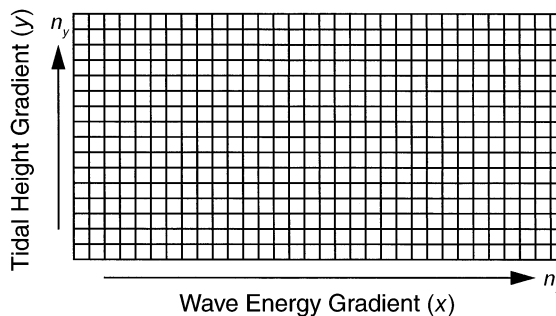


FIG. 2. Graphical depiction of the spatially explicit population model. Each cell represents a potential site for occupation by a mussel.

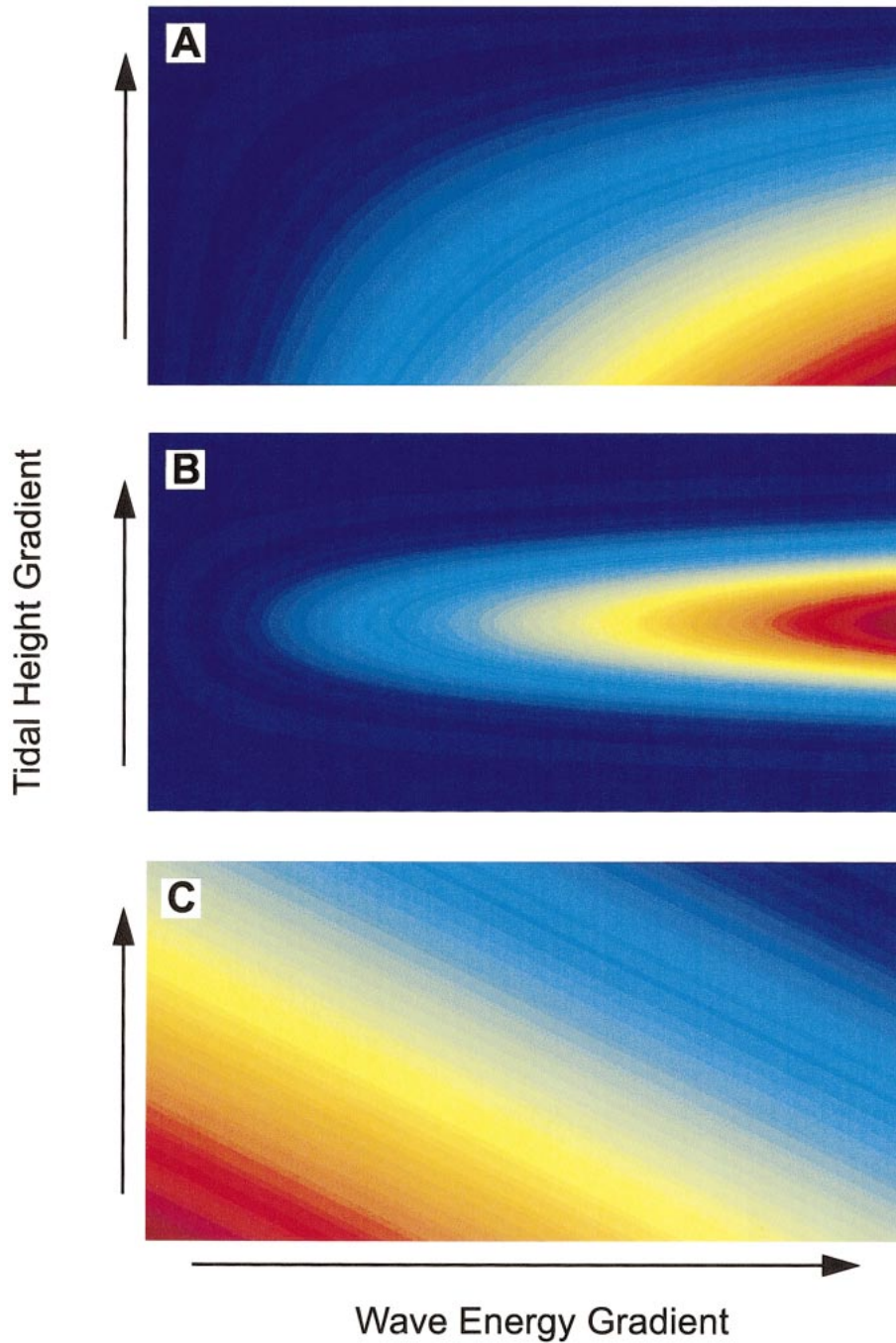


FIG. 3. Contour plots of the surfaces for (A) growth, (B) recruitment, and (C) vulnerability to predation used in the spatially explicit population model. Probabilities are color coded from red for large through blue for small.

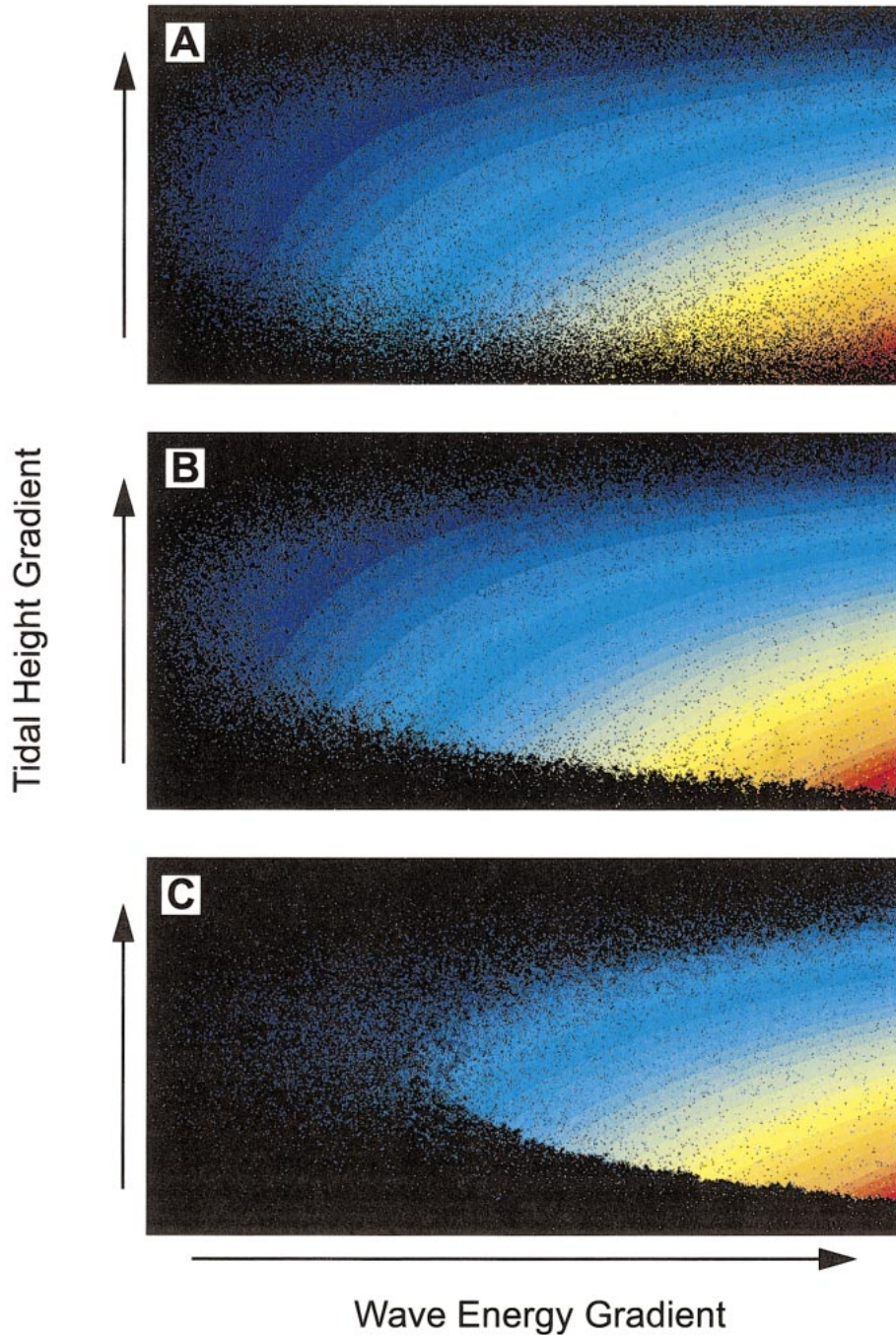
y coordinates. The state variable for the cell in column x and row y at time t is $s_{xy}(t)$. The entire arena is specified by an $(n_x + 1) \times (n_y + 1)$ matrix:

$$\mathbf{S}(t) = \{s_{xy}(t)\} \quad 0 \leq x \leq n_x \quad 0 \leq y \leq n_y. \quad (1)$$

The value of the state variable, $s_{xy}(t)$, represents the size of the mussels in each cell. Size classes are denoted by the integers $0, 1, 2, \dots, m$, where 0 is an empty

site and m is the maximum attainable size. Thus, the distribution and sizes of mussels over the entire arena at any time t is represented by the matrix $\mathbf{S}(t)$. An additional global variable, $P(t)$, represents the number of predators.

Temporal change of prey in the arena is expressed by a separate transition probability matrix for each cell. We denote these transition matrices by:



SPECIAL FEATURE

FIG. 4. Output from the spatially explicit population model with (A) spatial gradients but no neighborhood effects, (B) spatial gradients and neighborhood effects, and (C) spatial gradients, neighborhood effects, and a tenfold increase in the immigration rate of predators. Mussel size is color coded from red for large through blue for small.

$$\begin{aligned}
 \mathbf{Q}_{xy}(t) &= \{q_{xy,ij}(t)\} \\
 0 \leq x \leq n_x \quad 0 \leq y \leq n_y \quad 0 \leq i, j \leq m \quad (2)
 \end{aligned}$$

where $q_{xy,ij}(t) = \Pr\{s_{xy}(t) = j \mid s_{xy}(t - 1) = i\}$. In other words, $q_{xy,ij}(t)$ is the probability that cell x,y goes from state i at time $t - 1$ to state j at time t , and $\mathbf{Q}_{xy}(t)$ are these probabilities arranged in an $(m + 1) \times (m + 1)$

matrix. The transition probabilities represent the likelihood of recruitment, growth, or death in each cell. For example, growth represents the transition $i \rightarrow j$ for $i < j$; that is, mussels go from a smaller to a larger size. Different growth rates are set by adjusting these probabilities so that transitions to larger sizes are more probable when conditions favor rapid growth (Caswell

1989). The transition $i \rightarrow 0$ for $i > 0$ represents the loss of prey due to predation and nonpredatory natural mortality. These probabilities are adjusted to represent the effects on predation of prey size, tidal exposure, and hydrodynamic stress. Recruitment into unoccupied cells is represented by the transition $0 \rightarrow 1$. We assume open recruitment, that is, the size of the local population does not affect the potential recruitment it receives, exclusive of neighborhood effects.

Predator dynamics are represented as a stochastic process of immigration and emigration. At every time step, a discrete number of predators enter the arena and each predator present in the previous time step is assigned a probability to remain or exit the arena. The number of immigrants is represented as a Poisson random variable with a constant mean value, and the number of emigrating predators is determined using a binomial distribution with probability $e(S)$. We assume that the emigration probabilities are inversely proportional the overall per capita rate at which predators consume prey. The reproduction and mortality of the predator population is not considered. The number of predators $P(t)$ is used to determine the cell transition probabilities of predation.

In formulating the transition probability matrices for each cell, we combined insights of the original predation paradigm with the more recent findings. Physical stresses do constrain, but not prevent, predator foraging, therefore we set the vulnerability of prey so that, for a given number of predators, the probability of predation diminishes with increasing tidal height (lower to higher cells within a column) and with increasing wave exposure (left to right within a row). Predation is size dependent: lower nonzero states (smaller mussels) have a higher probability of mortality than higher states. To these top-down effects are added supply-side considerations. Through migration, predator numbers vary with prey availability (Robles et al. 1995). The likelihood of prey recruitment reaches a peak at middle shore levels of wave-exposed sites, and diminishes towards other shore levels and lesser wave exposures. This pattern was found in repeated spatial surveys of mussel recruits similar to those reported in Robles (1997). Mussel growth rates and terminal sizes increase towards lower shore levels and higher wave exposures (Kanter 1977, Kopp 1979, Leigh et al. 1987, Dahlhoff and Menge 1996). Fig. 3 shows hypothetical surfaces for the probabilities of recruitment, growth, and predation based on empirical evidence.

The transition probabilities change gradually over the environmental gradients, but they are also modified locally by neighborhood effects. The probability of predation increases as a mussel becomes surrounded by smaller, preferred sizes, or decreases as the mussel is increasingly surrounded by larger mussels, representing size-dependent predation and the aggregation response (Paine 1976, McClintock and Robnett 1986, Robles et al. 1995, 2001). Large mussels in neighboring

cells make recruitment more likely; the probability of recruitment in a given cell is weighted by the sum of the states in the surrounding cells. This feature addresses the observation that settling mussel larvae are attracted to the byssus of the adults, and overstories of adults may harbor greater densities of recruits than bare rock or other sedentary species outside the mussel beds (Petersen 1984a, b, Paine et al. 1985, Iwasaki 1994; see Pawlick [1992] for a review of aggregative settlement in benthic organisms). Thus, feedbacks are expressed in the model as functions of the spatial arrangements of individuals.

Most importantly, there are no absolute refuges. Probabilities of predation are positive at all locations.

Model results

Fig. 4 presents the output for each of three successive versions of the model. Each simulation was started with an empty arena and iterated until it reached a steady state. In the first version, spatial gradients in recruitment, growth, and predation were imposed, but no local feedback. A diffuse mussel zone is apparent (Fig. 4A). In the second version, both gradients and neighborhood effects were imposed (Fig. 4B). This version reproduces details of mussel zonation. Viewing from exposed to sheltered portions of the gradient of wave action (right to left in the figure), upper boundaries descend and lower boundaries ascend; at the sheltered extreme, no zone of adult mussels exists. Within the mussel bed at any given wave exposure (up any column) mussel sizes decrease towards higher shore levels. The lower boundary is abrupt. Mussels occur below the main mass, but then as one or a clump of large individuals. The same trends are commonly observed for *Mytilus californianus* beds on a topographically uniform shore laying along a gradient of wave exposure, or as differences in mean measures of the demographic characteristics of mussel beds arrayed across regions of varying wave exposures (Fig. 1B; Stephenson and Stephenson 1949, Lewis 1964, Kanter 1977, Kopp 1979, Leigh et al. 1987; C. D. Robles, unpublished data).

The third version is the same as in Fig. 4B, except that the rate of predator immigration was increased tenfold (Fig. 4C). The mussel bed contracts to only the most wave-exposed regions and the lower boundary of the mussel retreats to a higher shore level. The shifts of the lower boundary in the wave-exposed portion of the arena imitate experimental findings (Paine 1974). Seastar removals suppressed seastar densities on the treatment site and the mussel bed extended downwards. Once removals ceased, seastar abundances increased with net immigration. The lower boundary of the mussel bed receded upward. The model captures a suggestion of the empirical findings that the lower boundaries of prey at any point along shore are determined by a dynamic balance of predation and prey production

conditioned by the size and spatial distribution of the prey.

*Biological interpretation of the model:
the adjusted equilibria hypothesis*

Under the original predation paradigm, the persistence of prey concentrations was attributed to different types of refuge on different shore levels. In the new model, the probability of mortality of an individual depends simultaneously on its location, size, and the spatial arrangement of other prey. There are no absolute refuges. Low probabilities of predation develop, but these are an emergent property of the continuous, spatially conditioned population process. The few large mussels low in the intertidal zone and extensive aggregations of smaller individuals on higher shore levels result from a unified underlying process.

The model expands upon the premise that lower boundaries are the product of complex adjustments between the antagonistic populations forced by differing physical conditions. At any one location along the shore, mussel beds extend down into increasingly greater risk of predation until a crucial level is reached at which mechanisms dependent upon the corresponding mussel productivity cannot sustain prey numbers. From the sheltered to the wave-exposed locations, the crucial level shifts progressively downward as increasing wave action hinders predator foraging and elevates prey growth rate and, along any given shore level, prey recruitment. In essence, effects of increasing accessibility to predators compensate for effects of increasing prey productivity, causing prey population boundaries to shift regularly over the landscape. We call this interpretation the adjusted equilibria hypothesis.

One might expect that continuous, gradual change over the arena in the probability of predation would produce clines of density, that is, fuzzy boundaries. This pattern was not produced by the model. In addition to changing over environmental gradients, probabilities were modified by neighborhood effects. For example, the otherwise high probability of predation of small mussels low on the shore was reduced by a surrounding group of large mussels. Gregarious settlement and a phalanx of larger mussels covering more vulnerable recruits are conspicuous features of the natural history of mussel beds. The simulation results suggest that neighborhood processes in nature might produce abrupt lower boundaries and a few large mussels below the main mass of the bed. The upper boundaries of the mussel beds are often more diffuse, both in nature and the simulations. In the model, boundaries are less pronounced at the upper levels because mussel growth and recruitment together are curtailed, and consequently neighborhood effects are diminished, relative to other parts of the arena.

We focused on predatory mortality and prey production. This heuristic version of the model does not include all the factors possibly affecting mussel pop-

ulations. For example, we have not modeled direct effects of battering by high waves and logs (Dayton 1971), which could introduce patchiness into the size structure of the mussel bed (Paine and Levin 1981, Wootton 2001). Nonetheless, the model does express the central elements of the hypothesis: probabilistic processes of prey production and loss apposed over environmental gradients, and modified by spatial configurations.

IS THE ORIGINAL THEORY OF PREDATION A
KUHNIAN PARADIGM?

We compare the original theory to six criteria that we abstract from Kuhn (1962). First, paradigms arise in response to both the intellectual history and empirical knowledge of the discipline. Second, they provide a comprehensive frame of reference within the field, uniting mutually supportive hypotheses to explain diverse phenomena. Third, paradigms resist change in part because contradictions are not initially recognized as such. Fourth, as contradictions eventually mount, older theory gives way to new syntheses. Fifth, the formation of new syntheses is often associated with technological innovations that allow new approaches or supply new evidence. And sixth, new syntheses lead to a revolutionary paradigm shift, after which the new corpus of theory bears little relationship with the old.

The theory of intertidal predation meets most of these criteria. It arose in response to historical concerns about the mechanisms of coexistence, and it provided an alternative to niche theory. It united and reinforced the working hypotheses of its field. Refuges, size-limited predation, keystone predation, effects of physical stresses, and the competitive exclusion principle were woven into a coherent overview of the field.

Kuhn's controversial proposition that paradigms resist change (Kuhn 1962; see Barber [1961] for a precursor) requires explanation. Once a paradigm is accepted, observations posing contradictions are sometimes discounted as erroneous, dismissed as anomalous, or simply accorded little significance. Alternatively, if the observations are accepted, then definitions within the paradigm may be stretched to allow its coexistence with the new findings. At some point, the expanding definitions may give way to new conceptualizations. In essence, potential contradictions require reinforcement, and sometimes, the formulation of an alternative synthesis with which they are consistent, before they take their place as evidence against the original paradigm. In this regard too the original predation hypothesis displays the attributes of a paradigm.

The study of recruitment antedated the supply-side synthesis by many years (reviews by Young [1987], Underwood and Fairweather [1989], Grosberg and Levitan [1992], and Olafsson et al. [1994]). Indeed, concern about the effects of recruitment variation can be seen in early speculations about the causes of seastar

size–density relationships (Paine 1976) and the possible swamping of predator control in episodes of massive prey recruitment (Dayton 1971). Yet within the formative period of the theory, recruitment variation remained a side issue (discussion in Dayton [1979]).

Why was the significance of recruitment variation not immediately recognized? Several factors seem relevant. The recruits of benthic species are minute and difficult to census. Initial evidence for recruitment effects was largely observational, sometimes consisting merely of anecdotes. The most compelling evidence for the predation paradigm was drawn from field experiments, which manipulated only large conspicuous consumers, further focusing attention on top-down dynamics. However, the factor most relevant to the present context is the impetus of intellectual history. The Neo-Malthusian view opens with the premise that chronically high reproduction routinely causes intense competition. For local benthic populations, the functional analog of reproduction is recruitment. We suggest that weak or highly variable recruitment was not consonant with the central premise of the prevailing view. Recruitment variation held little place in formative discussions of intertidal predation theory not merely because the data were incomplete, but also because the discussions were held against the background of the competitive exclusion principle and related arguments. The recent explosion of research into recruitment effects coincided with the formulation of supply-side dynamics, theory delineating a pivotal role for recruitment variation (discussion in Grosberg and Levitan [1992]). This coincidence supports the proposition that full recognition of contradictory evidence sometimes awaits formulation of new theory with which that evidence is consistent.

In Kuhn's (1962) analysis, the recognition of contradictions may also be delayed while definitions within the paradigm enlarge to accommodate them. The concept of refuge remains in the contemporary literature, but its definition has gradually expanded to cover a broad range of circumstances. Beginning with Gause's (1934) definition of refuge as a part of the habitat inaccessible to the predators, the concept has been expanded to include instances where prey are accessible but too large to be killed (e.g., Connell 1970, Paine 1976); accessible and vulnerable, but residing in a subpopulation not yet discovered and eliminated by predators (e.g., Connell 1975); and, discovered by predators, vulnerable, but among a group of sufficient number and rates of recruitment and growth that concentrations of adults persist (e.g., Reusch and Chapman 1997). Called a relative refuge, the latter circumstances sustain high rates of predation and seem a refuge in name only. Terminology notwithstanding, the original view is giving way to theory that reconciles effects of size-dependent predation and varying prey production.

Our case history of intertidal predation theory is consistent with the paradigm criteria in one other regard:

theoretical developments sometimes depend upon, and consequently are delimited by, specific technological innovations. The advent of removal experiments was a historically significant addition to the complement of tools available to challenge hypotheses. However, the technique lent itself most easily to the removal of the most conspicuous competitors or predators. Thus, it is perhaps not surprising that the early predation experiments emphasized top-down dynamics. Multifactorial experiments (discussion in Bender et al. [1984]), including ones that manipulate rates of production as well as consumption, although more difficult to arrange, are becoming increasingly common (e.g., Morin 1983, Rosemond et al. 1993, Naeem et al. 1994, Hixon and Carr 1997, Cottingham 1999). These have supported the formulation and testing of correspondingly sophisticated hypotheses. Similarly, the advent of Spatially Explicit Population Models depended upon the development of computers and simulation software. The latter provide the technical capability for a landscape approach in which complex factor interactions occur as spatially conditioned population processes. This approach originated in terrestrial plant ecology and is being applied to an increasingly broad range of problems (reviews in Tilman and Kareiva [1997] and Levin [1999]).

One aspect of the theory of intertidal predation does not match the criteria of a paradigm. The progression from the original statement of the paradigm, to the revelations of supply-side effects, to the spatially explicit model does not fit the notion of a Kuhnian revolution (Wade 1977). The historical development of theory did not ensue from a clean sweep of older premises in favor of the new (Wade 1977, Graham and Dayton 2002, Paine 2002). The earlier synthesis emphasized key factors expressed as verbal hypotheses. The new synthesis emphasizes emergent properties of multifactor, spatially conditioned processes, which are expressed quantitatively. Thus, the aggregate of methodologies and hypotheses has changed, and our perspective has shifted appreciably. Yet there remains a crucial role for predation, constrained by spatially varying physical conditions and prey defenses. The two depictions of intertidal community process, therefore, are not alternative theories in the narrow sense. The second relies upon the enduring insights of the first.

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