

Species Diversity: Prey Refuges Modify the Interactive Effects of Predation and Competition

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We explore the effects of interactive variation in predation, interspecific competition, and the availability of absolute, spatial prey refuges on the local diversity of a sessile prey assemblage potentially competing for space. Prey diversity responds to increasing predation intensity in a characteristic pattern, called a "prey-diversity response." Previous theoretical and empirical studies have demonstrated three prey-diversity responses: negative, unimodal, and bimodal. Using simple simulations involving two to five prey species, we examine four scenarios: (1) Given a negative response in a simple habitat, such that diversity only decreases as predation intensity increases, increasing the proportion of the habitat that is safe from predation should result in a gradual flattening of the negatively sloped diversity-response curve. (2) Given a unimodal prey-diversity response where the dominant competitor persists over most predation intensities, such that diversity initially increases and subsequently decreases as predation increases from zero, the effects of refuges are more complex. As the proportion of prey-refuge space increases at low predation intensities, prey diversity should decrease monotonically. However, at high predation intensities, prey diversity should initially increase and subsequently decrease as refuge space increases. Consequently, the shape of the prey diversity-response curve should change progressively from a unimodal function, with the peak shifting to the right, to a monotonically increasing function which gradually flattens. (3) Given a system where the dominant is extirpated at low predation intensity, but a unimodal prey-diversity response occurs nonetheless, increasing refuge space should result in diversity initially increasing and subsequently decreasing at most predation intensities. In this case, the position of the peak of the unimodal curve should not shift along the abscissa. (4) Combining the previous two patterns, prey refuges can transform a bimodal response into a unimodal response. Although no explicit tests if these models are currently available, data from three published experimental studies of sessile marine benthos are consistent with some of these predictions. © 1991 Academic Press, Inc.

1. INTRODUCTION

During the 1980s, a general consensus emerged among ecologists that complex interactions among factors underlie the structure of communities. Hypotheses that communities were structured primarily by a single process, such as competition, have been replaced by more pluralistic hypotheses incorporating a variety of biotic and abiotic factors (e.g., Connell, 1975, 1983; Menge and Sutherland, 1976, 1987; Tilman, 1982; Schoener, 1983, 1986; Strong *et al.*, 1984; Diamond and Case, 1986; Yodzis, 1986). One of the major parameters characterizing community structure is local species diversity, a measure of the number of species coexisting in a habitat (richness) and the equitability of their relative abundances (evenness).

1.1. *Predation, Competition, and Local Diversity*

Interactions between predation and competition have long been known to affect the local diversity of prey species (reviews by Harper, 1969; Connell, 1975; Lubchenco and Gaines, 1981; Sih *et al.*, 1985; Hixon, 1986). Correspondingly, theoretical studies have explored the mechanisms by which these processes manifest their combined effects, especially the conditions under which predation may promote the coexistence of competing prey (e.g., Slobodkin, 1961; Parrish and Sella, 1970; Cramer and May, 1972; Slatkin, 1974; Van Valen, 1974; Roughgarden and Feldman, 1975; Yodzis, 1976, 1977, 1978; Abrams, 1977; Holt, 1977, 1984, 1985; Caswell, 1978; Vance, 1978; Hastings, 1978, 1980; Crowley, 1979; Levin, 1981).

We define "predation intensity" as a measure of the extent to which susceptible prey populations are reduced by predators (cf. McNair, 1986; Sih, 1987). As predation intensity increases from zero to very high levels, the local diversity of a prey assemblage may change in a characteristic pattern, which we call the *prey-diversity response*. Theoretically, interactions between predation and interspecific competition can produce a variety of prey-diversity responses, including bimodal patterns (Sebens, 1987; P. Abrams, personal communication). Empirically, field studies have documented only two patterns: a unimodal response, in which prey diversity initially increases and subsequently decreases as predation intensity increases; and a negative response, in which diversity only decreases. We review the causes of these patterns below.

1.2. *Habitat Complexity and Local Diversity*

Structural complexity of the habitat can also affect diversity, by providing competitive refuges and/or prey refuges. Typically, field observations have indicated that local diversity increases with habitat complexity (e.g., MacArthur and MacArthur, 1961; Rosenzweig and Winakur, 1966; Kohn, 1967; Pianka, 1967; Murdoch *et al.*, 1972). The generally accepted

mechanism underlying this pattern is that increased complexity provides new microhabitats or competitive refuges, allowing more species to coexist through spatial partitioning of limiting resources (e.g., Klopfer and MacArthur, 1960; MacArthur and Levins, 1964).

More recently, the role of habitat complexity providing refuges from predation has received considerable empirical attention (reviews by Murdoch and Oaten, 1975; Taylor, 1984) and theoretical interest (reviews by Murdoch and Oaten, 1975; McMurtrie, 1978; Stenseth, 1980; Crowley, 1981; Taylor, 1984). Most theoretical studies have focused on "absolute refuges," where the prey are completely invulnerable to predation. The major thrust has been to examine how such refuges affect the stability of one predator-one prey systems (e.g., Leslie and Gower, 1960; Bailey *et al.*, 1962; Rosenzweig and MacArthur, 1963; Maynard Smith, 1974; MacNair, 1986; Sih, 1987).

1.3. *Combined Effects of Predation, Competition, and Habitat Complexity*

To our knowledge, only Holt (1987) has explored the effects of prey refuges on the coexistence of prey species, considering the consequences of predators forcing prey to compete for absolute refuges. His models indicated that prey coexistence in this circumstance can occur under several conditions: if each prey has an exclusive refuge, if the competitively dominant prey suffers strong intraspecific interference, if there are trade-offs among the prey between competitive ability for refuges and for other resources, or if the prey that is subordinate in competition for refuges can better withstand predation.

Thus, unlike models examining the effects of two factors on local diversity, there is little theory concerning the response of prey diversity to interactive and simultaneous variation in three factors: predation, interspecific competition, and the abundance of prey refuges. Holt's (1987) models assumed that the prey were mobile, such that interactions occurred between refuge and nonrefuge subpopulations. Here, we consider sessile prey in open systems, where refuge and nonrefuge subpopulations do not interact.

We examine the question: Given a particular prey-diversity response occurring in a structurally simple and homogeneous habitat, what are the effects of increasing the proportion of the habitat that is safe from predation? We consider three types of prey-diversity response: negative, unimodal, and bimodal. Testing the predictions of our models requires factorial experiments involving at least three levels each of both predation intensity and refuge availability. Especially necessary are multiple levels of predation intensity so that the initial shape of the prey-diversity response can be determined (Hixon, 1986). We are aware of only three studies which

approach these criteria, one involving a negative prey-diversity response and two involving unimodal responses. Bimodal responses have yet to be documented in the field.

2. ASSUMPTIONS

As a first step in approaching multifactorial effects on local diversity, we have structured the assumptions of our models so that the resulting predictions can be evaluated by the only relevant data sets we could find: field experiments on marine hard substrata.

2.1. *Prey Population*

The prey assemblage consists of sessile species which recruit from an open pool of propagules such that local reproductive output is largely unrelated to subsequent recruitment, a common feature among marine systems (Connell, 1985). We assume further that recruitment limitation is not operating; the local system is always potentially open to colonization by all prey species. A major consequence of these conditions is that prey occupying refuges do not interact with prey in nonrefuge areas. Prey potentially compete for primary space in both subhabitats, but the outcome of interactions in one area does not affect the other. Local species diversity is entirely a function of local processes. Thus, our predictions are amenable to tests by field experiments, both being relevant at local spatial scales.

2.2. *Prey Refuges*

We assume that only two kinds of subhabitats exist: nonrefuge space, which is exposed to predation, and absolute refuge space, which is safe from predation. Thus, the overall diversity of the prey assemblage is a weighted combination of the diversities in refuge and nonrefuge areas. Although prey may compete for refuges (see Holt, 1984, 1987), there is no inherent cost of occupying a refuge (see Sih, 1987). For sessile marine systems, absolute refuges are simply holes and crevices in hard substrata which are inaccessible to predators, whereas exposed flat surfaces constitute nonrefuge space.

We assume further that increasing the abundance of prey refuges does not also provide competitive refuges or new microhabitats per se. This implicitly assumes that both recruitment processes and mortality factors other than predation are the same inside and outside of refuges. Consequently, the prey assemblage occurring within refuge space is always the same as that occupying nonrefuge areas where predators have been removed. Note that this condition is essential to ensure that the effects of *quantitatively* adding prey refuges are not confounded by habitat com-

plexity *qualitatively* adding competitive refuges. This is perhaps our most unrealistic assumption, but it is easy to determine whether a real system violates this condition: if the relative abundances of prey species change (especially if richness increases) following the addition of refuge space to areas where predators have been removed, then new microhabitats or competitive refuges have also been added. We examine this possibility in our empirical examples.

2.3. *Predator Behavior*

We assume that predator behavior and population dynamics do not change as the proportion of refuge space increases. Whatever the effects of a particular predation intensity may be in nonrefuge space, these effects are the same per unit area whether 100% or less than 1% of the habitat is exposed to predation. This assumption is necessary for our predictions to be testable in the field. Field manipulations alter refuge space over limited areas, typically far less than the home ranges of predators. Thus, for example, if an experimental construct somehow created a patch of 100% refuge space, the predators would move to another "habitat" rather than go extinct.

3. MODELS

Our models explore how the shapes of prey diversity–response curves in homogeneous habitats lacking prey refuges should change as the proportion of prey-refuge space progressively increases. We consider three different prey-diversity responses: negative, unimodal, and bimodal. We partially evaluate our predictions for the first two responses with available field data. The predictions for the negative response are intuitively simple, whereas those for the unimodal and bimodal responses are surprisingly complex.

3.1. *Negative Prey-Diversity Response*

A negative prey-diversity response will occur in a habitat patch under either of two circumstances, regardless of the particular role of competition (reviews by Yodzis, 1986, 1989): (1) when predation disproportionately decreases the abundances of the rarer prey species in an assemblage, thus decreasing evenness and perhaps richness; or (2) when predation is equivalently nonselective on all species or even slightly disproportional on the more common species, eventually extirpating rare species and thus decreasing richness. In either case, predation does not moderate competition between prey species, unlike the unimodal responses described below. Negative responses have been documented in freshwater (e.g., Addicott,

1974), marine (e.g., Lubchenco, 1978), and terrestrial systems (e.g., Waser and Price, 1981).

Given that the prey assemblage occupying refuge space should be the same as that occupying nonrefuge space in the absence of predators (see above), increasing the proportion of refuge space will simply increase the similarity of the overall prey assemblage to that which occurs at zero predation (Fig. 1A). In other words, if predation acts only to eliminate species, then increasing the proportion of refuge space should decrease the extent to which species are locally extirpated, especially at higher predation intensities. At 100% refuge space, predation would obviously have no effect and prey diversity would be constant (uppermost curve in Fig. 1A).

Thus, this model predicts that, given a negative prey-diversity response in a homogeneous habitat lacking refuges, increasing the proportion of the habitat that is safe from predation will progressively flatten the negatively sloped curve. That is, prey diversity overall will increase at all nonzero predation intensities, yet more so at higher intensities.

A study in Hawaii of parrotfish grazing on differentially accessible substrata provides a relevant example of a negative prey-diversity response (Brock, 1979). Brock compared benthic assemblages which developed over 36 days in outdoor microcosms containing both a range of zero to eight juvenile parrotfish (*Scarus taeniurus*) and a range of four substratum complexities. The substratum treatments were exposed, flat terra-cotta tiles and tiles overlaid with fine, medium, or coarse plastic mesh. Coarser mesh sizes provided surfaces with deeper holes, which were progressively less susceptible to fish grazing. The patterns of benthic species richness in this experiment (evenness and overall diversity were not reported) indicate that, first, the basic outcome was a negative prey-diversity response, and, second, the effect of increasing refuge space was similar to that predicted by the model (Fig. 1).

Note, however, that more species occurred in the zero-fish treatment on substrata overlaid with plastic mesh than on exposed substrata (Fig. 1B). This outcome suggests that the mesh altered the local substratum environment in such a way that new microhabitats, and thus new species, were introduced. Thus, habitat complexity appeared to provide mostly prey refuges, but also competitive refuges, in this system.

3.2. Unimodal Prey-Diversity Response

Many mechanisms may underlie a unimodal prey-diversity response, depending on a variety of factors (reviews by Tilman, 1982; Hixon, 1986; Yodzis, 1986, 1989). The best documented unimodal responses occur when a competitive hierarchy exists among the prey species, such that dominant competitors locally exclude most other species in the absence of predation (e.g., Paine, 1966; Neill, 1975; Lynch, 1979; Lubchenco, 1978). Typically, a

trade-off exists where the dominant competitors are differentially susceptible to predation and the subordinates are intrinsically predation resistant, or at least not preferred by the predators (e.g., Paine and Vadas, 1969; Carpenter, 1981; Hixon and Brostoff, 1983; Menge *et al.*, 1985). Thus, in homogeneous habitats, predation that disproportionately reduces the dominants initially increases diversity by releasing the subordinate species

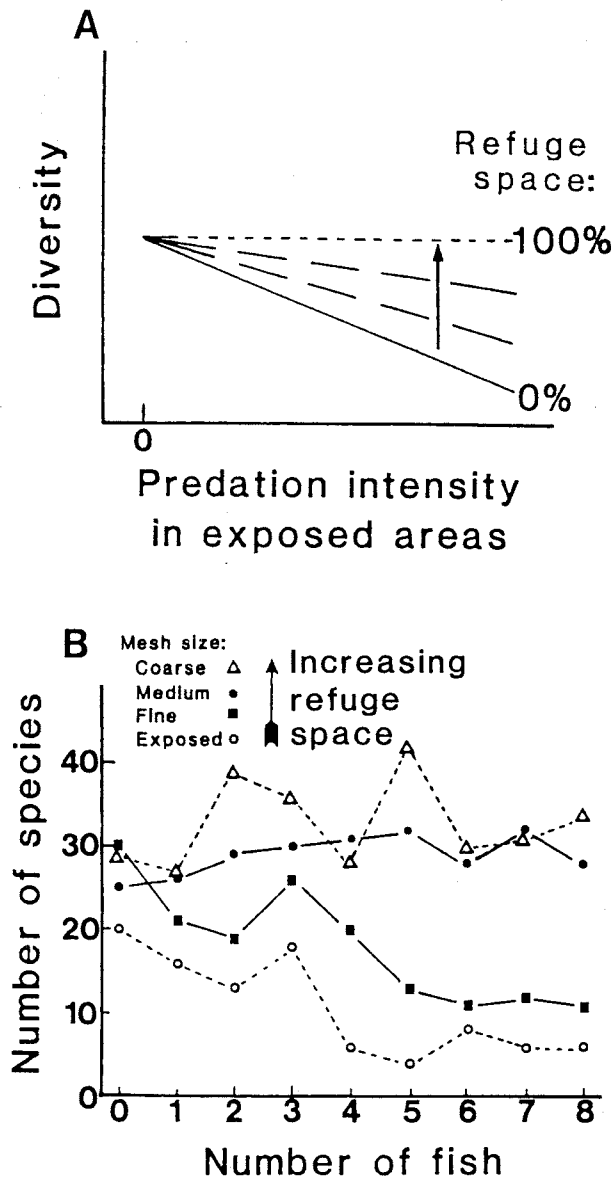


FIG. 1. (A) Predicted effect of increased prey-refuge space on a negative prey-diversity response. The original pattern in a homogeneous habitat (0% refuge space, solid curve) progressively flattens (dashed curves) toward the ultimate limit of the entire habitat being a prey refuge (100% refuge space, dotted curve). (B) Sessile benthic species richness as a function of increasing parrotfish density (= predation intensity) and mesh size overlying flat substrata (= prey-refuge space) within microcosm tanks. Redrawn from Brock (1979).

from competitive suppression or exclusion, increasing prey evenness and perhaps richness. At higher predation intensities, the dominants and perhaps some subordinates become rare or locally extirpated, and prey diversity subsequently decreases. Note that, due to changes in evenness, unimodal responses may occur whether or not local species composition or richness changes with predation intensity.

How will a unimodal prey-diversity response change as the proportion of absolute refuge space increases? In refuge space, competitive dominants will exclude all other species regardless of predation intensity outside the refuges, and prey diversity should always be low (as occurs in nonrefuge space in the absence of predation). In nonrefuge space, prey diversity should always respond unimodally to variation in predation intensity. Therefore, when refuge and nonrefuge space are combined along a gradient of increasing refuge space, overall diversity becomes increasingly dependent on diversity in the refuges.

3.2.1. *Two prey species.* Consider the simplest case of a predation-susceptible competitive dominant (D) interacting with a predation-resistant subordinate (S). If not predators occur in the habitat, increasing the proportion of refuge space obviously has no effect on prey diversity since the dominant will occupy both refuge and nonrefuge space (Fig. 2, left column). At moderate predation intensities, where diversity peaks in nonrefuge areas, increasing refuge space can only decrease overall diversity because the consequent increase in the relative abundance of the dominant decreases evenness (Fig. 2, center column). In other words, diversity is decreased by combining the dominants in refuges with the more even mixture of dominants and subordinates in nonrefuges. Finally, at high predation intensities, where the dominant is extirpated in nonrefuge areas, increasing refuge space first increases and then decreases diversity (Fig. 2, right column). This occurs because adding refuge space increases the representation of the competitive dominant in a circumstance where only the predation-resistant subordinate species occupies nonrefuge space. Thus, increasing the abundance of the dominant initially increases overall evenness (Fig. 2, right column, top and middle illustrations). With further increases in refuge space, however, diversity decreases as the relative abundance of the refuging dominant exceeds that of the subordinate occupying the now rare nonrefuge space (Fig. 2, right column, middle and bottom illustrations).

Changes in the shape of a unimodal diversity-response curve resulting from these interacting factors can be illustrated by simple simulations. Assume that the entire substratum is covered by sessile prey, and that there is a linear replacement of the dominant by the subordinate as predation intensity increases from zero to some high value. Thus, the dominant

decreases in proportional abundance from 1.0 to 0.0 as the subordinate increases from 0.0 to 1.0. Plotting a diversity index (H'), these conditions result in a typical unimodal curve in the absence of prey refuges (Fig. 3A, 0% refuge space). (We are aware of the differential biases among the various diversity indices [Peet, 1974], but have found that H' provides results qualitatively similar to other indices in our simulations.)

What happens to this curve if refuge space is introduced? If the percentage of refuge space is increased to, say, 10% of the habitat, then at least 10% of the substratum will be covered by the dominant regardless of predation intensity in nonrefuge areas. At each predation intensity, calculating diversity would involve a weighted combination of the relative abundances of the two prey along the original unimodal curve (nonrefuge

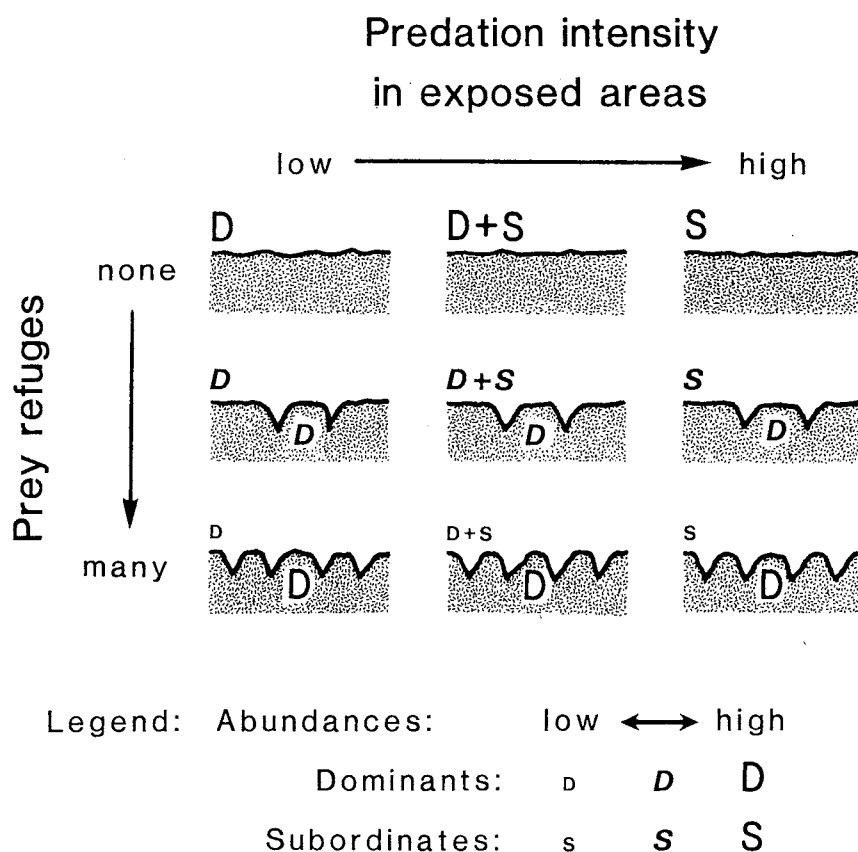


FIG. 2. Diagrammatic summary of the effects of prey refuges on a unimodal prey-diversity response in a two-prey system. The drawings illustrate cross sections of a hard substratum with different percentages of surface space protected from predation (crevices) relative to space exposed to predation (flat surfaces), each experiencing different levels of predation on the exposed surfaces. "D" and "S," respectively, represent competitively dominant (predation-susceptible) and subordinate (predation-resistant) sessile prey species. The size (and position) of each letter indicates the relative abundance (and location) of each species (top, on exposed surfaces; bottom, in crevice refuges) at each combination of predation intensity and refuge space. See text for further explanation.

space) and the constant abundance of dominants occupying the 10% of the habitat that was a refuge (Fig. 3A, 10% refuge space). Quite simply, if r is the proportion of the habitat that is refuge space, then the total proportional abundance of the dominant is

$$D = D_r + D_n = r + (1 - r) d_p,$$

where D_r and D_n are the proportional abundances of the dominant in refuge and nonrefuge areas, respectively, and d_p is the proportional abundance of the dominant in nonrefuge areas at a given predation intensity. Iterative calculations of the diversity index following incremental

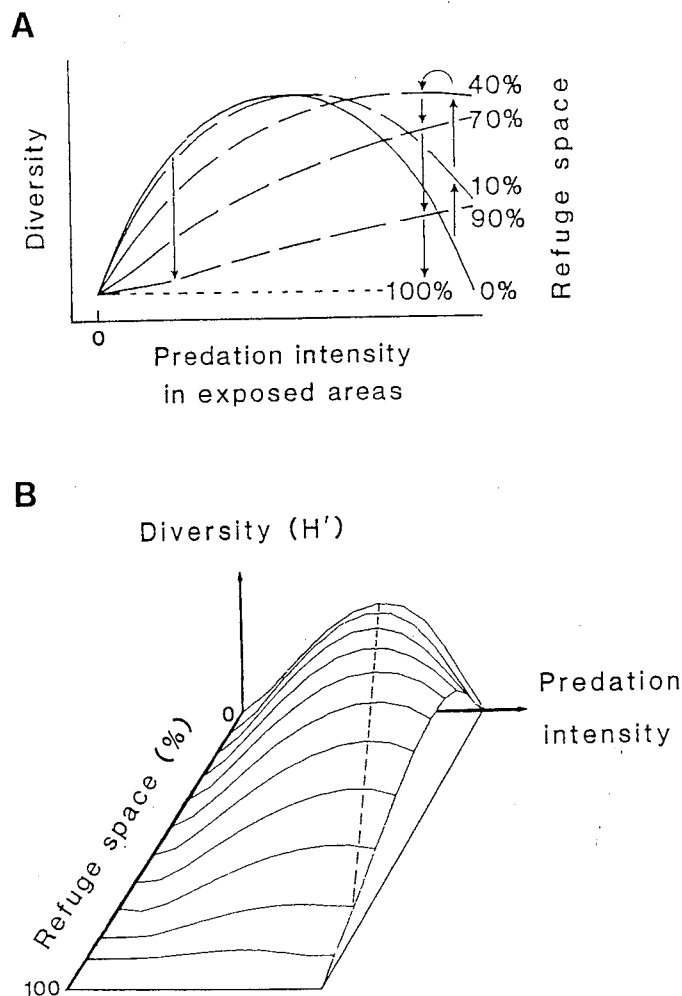


FIG. 3. (A) Predicted effect of increased prey-refuge space on a unimodal prey-diversity response. The peak of the original pattern in a homogeneous habitat (0% refuge space, solid curve) gradually shifts to the right (10 and 40%), becomes a monotonically increasing curve (70 and 90%), and then flattens toward the ultimate limit of the entire habitat being a prey refuge (100% refuge space, dotted curve). (B) Three-dimensional projection of (A) showing that increasing prey-refuge space initially increases and then decreases diversity at high predation intensities. The dashed line follows the peaks of successive diversity-response curves.

alterations of both predation intensity in nonrefuge areas and the proportion of the habitat that is a refuge result in the curves shown in Fig. 3.

Note that with increasing refuge space, the peak of the original unimodal curve initially shifts to the right (Fig. 3A, 0 to 40% refuge space). Eventually, the shape of the curve shifts from a unimodal to a monotonically increasing function, which flattens gradually as the habitat approaches 100% refuge space (Fig. 3A, 40 to 100% refuge space). In a three-dimensional perspective, prey diversity at high predation intensities first increases and then decreases as the proportion of refuge spaces increases, producing a unimodal curve parallel to the refuge-space axis (Fig. 3B; cf. Fig. 2, right column).

In summary, this model predicts that, given a unimodal prey-diversity response in a homogeneous habitat lacking refuges, progressively increasing the proportion of the habitat that is safe from predation will: (1) only decrease overall prey diversity at low predation intensities; and (2) initially increase and subsequently decrease prey diversity at high predation intensities. Overall, adding refuges progressively causes the peak of the unimodal curve to shift to the right, then causes the curve to become monotonic and gradually flatten.

3.2.2. *Three or more prey species.* We have run similar simulations involving three to five prey species. These simulations result in the same predictions as long as one criterion is met: in the original system (0% refuge space), the competitive dominant persists at the predation intensity where the unimodal curve peaks. In this condition, as in two-prey systems, the peak of the unimodal curve occurs where the most even possible mixture of prey species exists, including the competitive dominant. Clearly, adding refuge space (and thus dominants) to such an assemblage decreases evenness and thus overall diversity (cf. Fig. 2, middle column). As before, the dominant will be rare in nonrefuge areas at high predation intensities, so adding refuges will cause the same pattern as in two-prey systems (cf. Fig. 2, right column).

For example, consider a five-prey system meeting the above criterion, such that the dominant species is not extirpated from nonrefuge areas until very high predation intensities (Fig. 4A) and the prey-diversity response in the absence of refuges is unimodal (Fig. 4B, 0% refuge space). Following the same iterative procedures described above for two-prey systems, we see that progressively adding refuge space qualitatively produces the same outcome as before: diversity only decreases at low predation intensities, and initially increases and subsequently decreases at high predation intensities (Fig. 4B; cf. Fig. 3). We predict that this is the most common scenario in nature because very high predation intensities appear to be required to extirpate competitive dominants in real systems (reviews by Harper, 1969;

Paine, 1980; Hixon, 1986). In any case, this assumption can be tested by observation.

Suppose, however, that the dominant is very susceptible to predation and is extirpated at low predation intensity in the absence of prey refuges. If new prey species colonize as a result of the dominant disappearing, then a unimodal response can still result. In this system, adding refuge space will initially increase diversity at all but the lowest predation intensities because the dominant is reestablished at predation intensities where it was previously extirpated (i.e., richness increases). As before, with further increases in the proportion of refuge space (and thus in the relative abundance of the dominant), evenness and thus overall diversity will eventually decrease.

Another five-prey system exemplifies how these conditions affect the shape of the prey diversity–response curve. Here, the dominant is extirpated at low predation intensity (Fig. 5A), and is replaced by a series of subordinates resulting in a unimodal prey-diversity response (Fig. 5B, 0% refuge space). Only below the predation intensity where the dominant prey maximally contributes to diversity does increasing refuge space decrease diversity. At all other predation intensities, including that where the original unimodal curve peaks, increasing refuge space initially increases

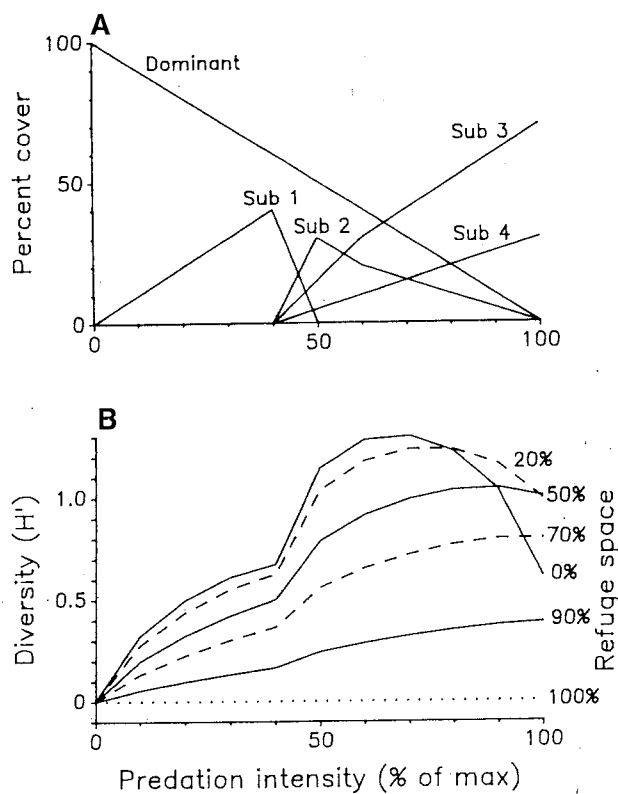


FIG. 4. (A) A five-prey system (competitive dominant plus four subordinates, "Sub 1" to "Sub 4") in the absence of prey refuges. The dominant persists until the very highest predation intensity. (B) Predicted effect of increased prey-refuge space on prey diversity in this system (cf. Fig. 3).

and subsequently decreases diversity (Fig. 5B). Thus, virtually the entire unimodal curve initially shifts upward and then gradually flattens. Note that the peak of the curve does not shift in position along the abscissa.

Returning to our original (and more general) set of predictions for unimodal prey-diversity responses (Figs. 3 and 4), we know of two relevant data sets:

Case 1. Subtidal reef flat in Hawaii. In a study off the island of Oahu, reef algae exhibited a unimodal diversity response to grazing by fishes (Hixon and Brostoff, 1983, 1985). Filamentous algae, which are generally preferred by all the herbivorous fishes, are abundant within the defended territories of the herbivorous damselfish *Stegastes fasciolatus*. Crustose coralline algae, which are subordinate competitors to filamentous algae but structurally defended against grazing (e.g., Paine, 1980; Lubchenco and Gaines, 1981; Steneck, 1982; Littler *et al.*, 1983), are abundant outside territories in areas exposed to intense grazing by numerous parrotfishes and surgeonfishes. Benthic algal diversity was quantified on 50 cm² coral-rock surfaces exposed to one of three grazing treatments. (1) protected within cages (low predation intensity); (2) exposed inside damselfish

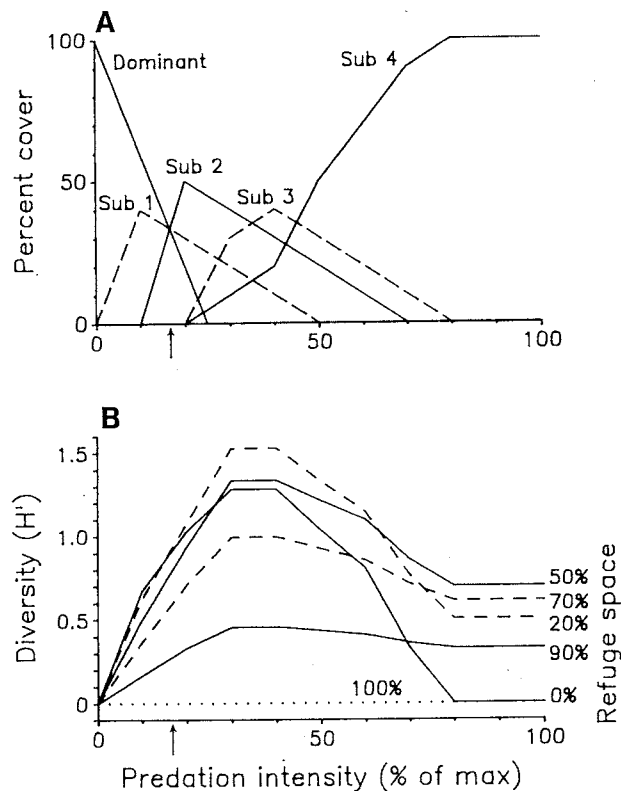


FIG. 5. (A) A five-prey system in the absence of prey refuges. The dominant is extirpated at a low predation intensity. (B) Predicted effect of increased prey-refuge space on prey diversity in this system (cf. Fig. 4). The arrows along the abscissas indicate the predation intensity at which the dominant maximally contributes to diversity in the absence of prey refuges.

territories (moderate intensity); and (3) exposed outside territories to abundant herbivorous fishes (high intensity). Relative predation intensity was estimated directly using the density of fish bite marks on the experimental surfaces (Hixon and Brostoff, 1983). Refuge space was varied within each grazing treatment by including pieces of coral rock of similar surface areas that were either flat (0% refuge space) or naturally irregular (about 10% refuge space, based on the distribution of fish bite marks). Thus, this factorial experiment included three predation intensities and two

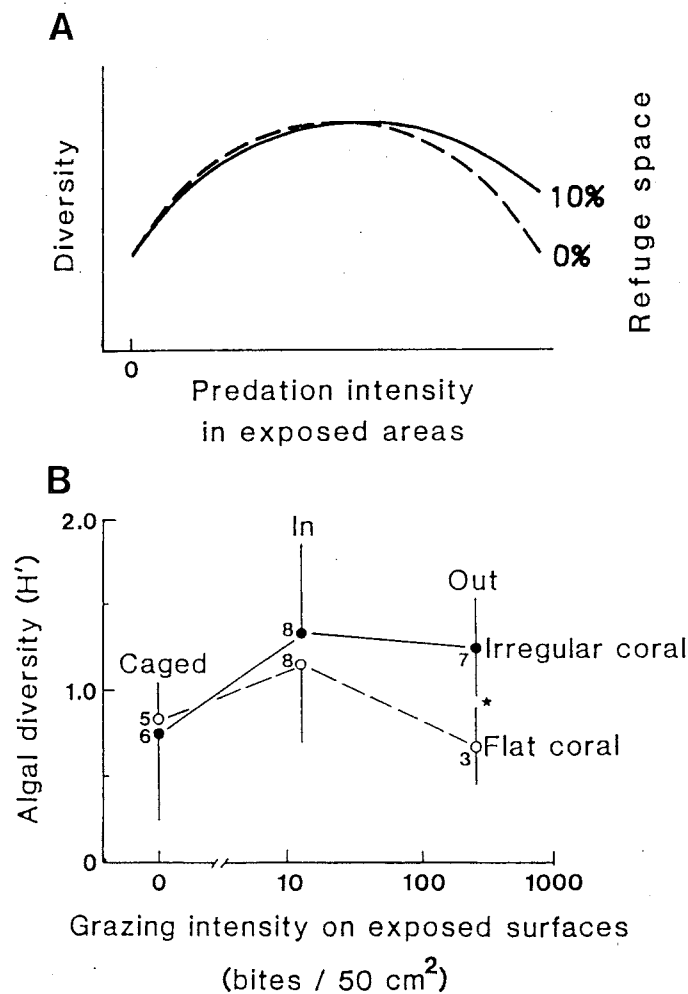


FIG. 6. (A) Predicted effect of increasing prey-refuge space from 0 to 10% (see Fig. 3). (B) Benthic algal diversity as a function of fish grazing intensity on irregular coral pieces (providing about 10% refuge space) and flatly cut coral plates (0% refuge space) after 1 year on a Hawaiian reef. The three treatments were caged, exposed inside damselfish territories ("In"), and exposed outside damselfish territories to parrotfishes and surgeonfishes ("Out"). Grazing intensity was measured as the "standing crop" of fish bite marks on the plates. Each symbol gives the mean Shannon-Weiner diversity index value and 95% confidence interval (Hutcherson, 1970) for seven settling surfaces. Samples separated by the asterisk are significantly different ($P < 0.05$, Wilcoxon signed-ranks test). The number by each symbol indicates the average species richness per plate. Data are from Hixon and Brostoff (1985).

levels of habitat complexity, with seven replicates of each treatment combination, for a total of 42 surfaces.

After 1 year, algal diversity was significantly greater on irregular surfaces than on flat surfaces at high but not moderate or low grazing intensities (Fig. 6B). Species composition and subhabitat use also different with substratum complexity at high but not moderate or low grazing. With high grazing on flat surfaces, crustose corallines dominated, while on irregular surfaces a mix of crustose corallines (on exposed areas) and filamentous algae (in crevices) occurred (Hixon and Brostoff, 1985). Because no new prey species were observed on the irregular surfaces, regardless of treatment, these results suggest that substratum complexity in this system introduced prey refuges, but not competitive refuges. Overall, the results of this experiment (Fig. 6B) are consistent with the predictions of the model (Fig. 6A).

Case 2. Rocky shores in Panama. In a study on the Pacific coast of Panama, intertidal benthos also exhibited a unimodal prey-diversity response (Menge *et al.*, 1985). Here, rocky surfaces are dominated by crustose algae, sessile invertebrates, and foliose algae (Menge and Lubchenco, 1981; Lubchenco *et al.*, 1984). To determine the response of prey diversity to predation, the composition and density of the consumer assemblage was experimentally varied (Menge *et al.*, 1985, 1986). Twelve treatments were established, producing a gradient of predation intensity from high (all consumers present, the normal condition) to none (all consumers absent). Two to four 0.25 m² plots of each treatment were monitored over 3 years. The abundances of sessile organisms were also estimated in 20 additional unmanipulated plots, all of which were exposed to normal levels of predation. Quantification of substratum complexity combined with estimates of the biomass of predators which could enter the holes and crevices suggested that prey-refuge space ranged from near 0 to about 60% in this set of 51 plots.

To compare the results of this experiment with the predictions of the model, we estimated prey diversity, predation intensity, and substratum complexity per plot. Diversity (H') and substrate heterogeneity (I_h) were quantified as detailed in Menge *et al.* (1985). Predation intensity was estimated indirectly as the average biomass of consumers per plot. Consumer biomass was calculated using size and density measurements converted to weights (see Menge, 1983, for methodological details). This analysis produced 51 prey-diversity values distributed over the consumer biomass (increasing predation intensity) vs substratum heterogeneity (increasing refuge space) plane, projected onto a three-dimensional surface by a computer graphics program (Fig. 7B). For comparative purposes, Fig. 7A is a projection of the predicted prey-refuge effect illustrated in

Fig. 3B, but truncated at 60% refuge space, the approximate maximum in this system (see above).

Two results of this analysis are consistent with the predictions of the model (Fig. 7). As the proportion of refuge space increased: (1) prey diversity increased and then decreased slightly in plots subjected to high predation intensities, and (2) the peak of the unimodal curve shifted to the right. However, at low predation intensities, diversity increased slightly with increasing substratum complexity (Fig. 7B). This pattern indicated that complexity also introduced new microhabitats for new species, corroborated by the fact that some species were found only in crevices regardless of predation levels.

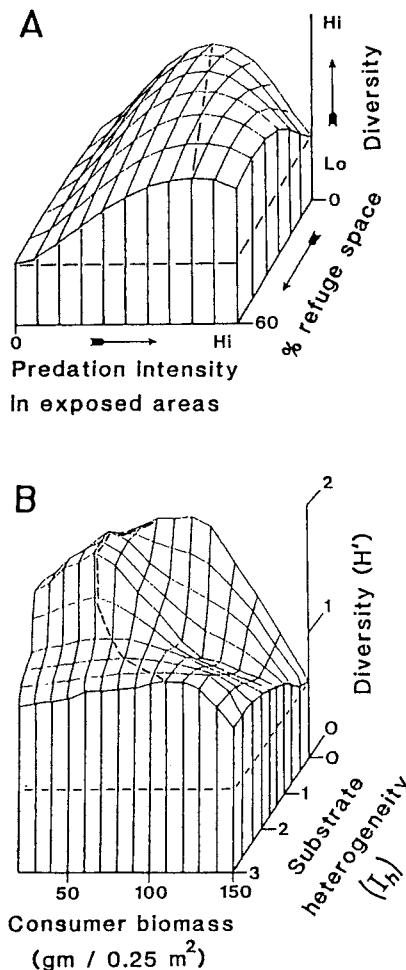


FIG. 7. (A) Predicted effect of increasing prey-refuge space from 0 to 60% (see Fig. 3). (B) The diversity of benthic species in a Panamanian rocky intertidal system along two gradients: consumer biomass (increasing predation intensity) and substratum heterogeneity (refuge space increasing from 0 to about 60%). On each surface, the dashed line follows the peaks of successive diversity-response curves.

3.3. Bimodal Prey-Diversity Response

Sebens (1987) modeled the effects of predation (or physical disturbance) on the diversity of the same kind of sessile prey examined in our models. In this case, however, competitive dominance among the prey was indeterminate, such that any species could outcompete any other with some

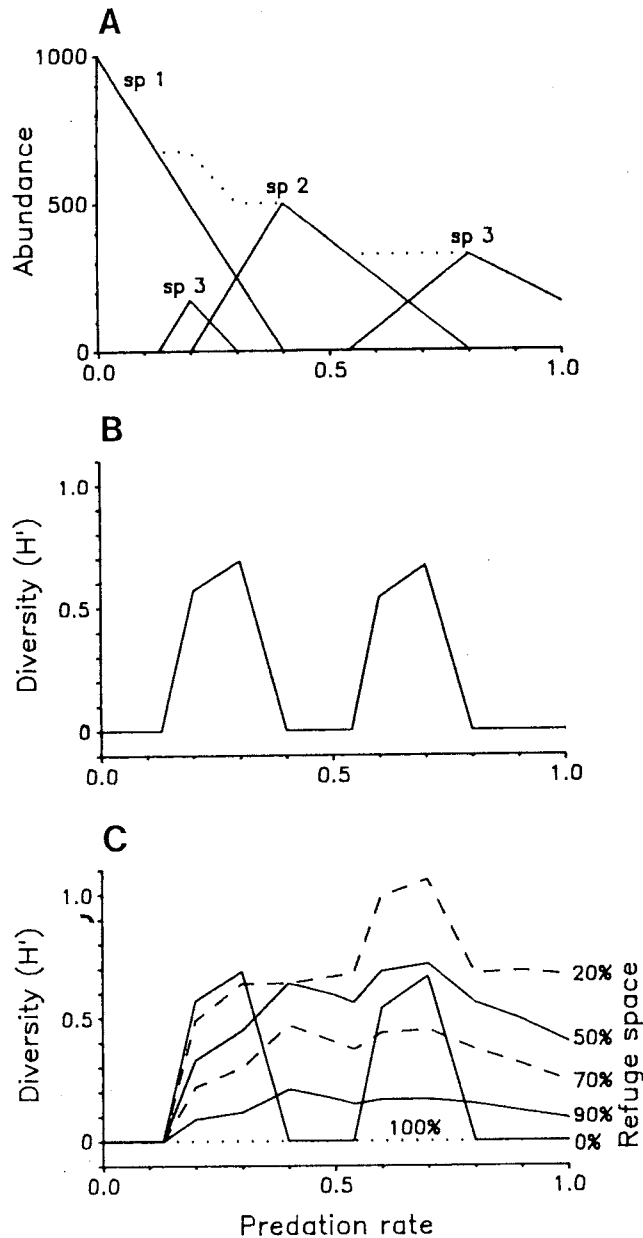


FIG. 8. (A) Outcome of Sebens' (1987) model of the effects of predation on three competing sessile prey. An "abundance" of 1000 equals 100% cover, so total cover (dotted line) decreases with increasing predation. "Predation rate" is a measure of density-independent mortality. (B) Sebens' result converted to species diversity. (C) Predicted effect of increased prey-refuge space on Sebens' result. The original bimodal prey-diversity response gradually shifts to a unimodal pattern, which subsequently flattens.

probability. Among other scenarios, Sebens examined a system of three prey species: a dominant competitor (species 1), a species with the most rapid recruitment rate (species 3), and a species of intermediate capabilities in competition and recruitment (species 2). As expected, species 1 excluded all others in the absence of predation, and species 2 monopolized space at high predation rates. However, for certain parameter values, species 2 could monopolize space at intermediate predation rates because it could recruit more rapidly than species 1 and still outcompete species 3 (Fig. 8A). Converting these results to prey diversity, we see a bimodal prey-diversity response (Fig. 8B).

Adding prey refuges to Sebens' result, which assumed an exposed and homogeneous substratum (i.e., 0% refuge space), illustrates the changes that can occur in a bimodal combination of the two kinds of unimodal responses discussed above: one where the competitive dominant is present in nonrefuge areas over most of the unimodal curve (e.g., Fig. 4), and the other where the competitive dominant is extirpated early on (e.g., Fig. 5). As illustrated in Fig. 8C, the results of progressively adding prey refuges differed predictably for the two diversity peaks, depending upon whether the competitive dominant was present in nonrefuge space (left peak) or absent (right peak; Figs. 8A and B). The change in the left peak (between predation rates of 0.1 and 0.4 in Fig. 8C) is qualitatively similar to that illustrated in Fig. 3 and 4 and results from the same mechanisms. The change in the right peak (between predation rates of 0.5 and 0.8) is similar to that illustrated in Fig. 5: the entire unimodal curve initially shifts upward and then gradually flattens (Fig. 8C).

Considering the overall prey-diversity response of Sebens' model over the entire range of predation rates, increasing the abundance of prey refuges gradually changes the response from a bimodal to a unimodal pattern, which eventually flattens (as it must) toward 100% refuge space (Fig. 8C). We know of no data set for testing this prediction.

Note that one of the differences between Sebens' bimodal system and our unimodal systems is his assumption that the total abundance (or percent cover) of prey decreases with increasing predation intensity. The fact that the left unimodal curve in his system responded similarly to those in our Figs. 3 and 4 and the right unimodal curve responded similarly to that in our Fig. 5 shows that our models are robust with respect to total percent cover. This is simply a result of diversity indices incorporating relative (rather than absolute) species abundances.

4. DISCUSSION

Our models explore how local prey diversity is affected by simultaneous variation in three factors: predation, interspecific competition, and prey-

refuge space. Although our approach is simple, some of the resulting predictions are not. For each type of prey-diversity response in a homogeneous habitat lacking refuges, progressively increasing prey-refuge space produces different patterns. First, a negative response simply flattens gradually (Fig. 1). Second, given a unimodal response in which the competitive dominant persists at the predation intensity where diversity peaks, rather dramatic changes occur. Increasing refuge space causes a monotonic decline in diversity under low predation and a unimodal response in diversity under high predation, such that initially the peak of the original curve shifts to the right, then the curve becomes monotonic and gradually flattens (Figs. 3 and 4). Third, given a unimodal response in which the competitive dominant is extirpated at low predation intensity, the curve simply shifts upward then flattens at most predation intensities, without a shift in the position of the peak along the abscissa (Fig. 5). Finally, prey refuges may transform bimodal responses into unimodal responses (Fig. 8).

The reality and importance of these multifactorial effects are indicated by the experiments summarized above. All three studies produced results which indicate that the responses of prey diversity to predation and competition depend on the proportion of refuge space in the habitat. Although none of these studies was designed to test our models, and more explicit tests are clearly needed, the data suggest that future tests will be productive. Of course, the detection and interpolation of such complex interactions in nature depends heavily on labor intensive, factorial experimental methods (review by Sih *et al.*, 1985).

Critical to understanding interactions between habitat complexity and predation is identifying the mechanistic nature of spatial prey refuges, which requires knowledge of the relative responses and capabilities of predators and their prey. The essential characteristics of an absolute spatial refuge are that, first, the feeding apparatus of the smallest predator is incapable of reaching the prey, and, second, the prey can continuously and safely occupy the refuge when predators are in the area. Partial spatial refuges pose another challenge (review by Woodin, 1978). Determining when a particular microhabitat is safe for which prey and from which predator requires considerable knowledge of the natural history of the organisms involved. For example, a partial refuge may provide a place to hide, but not intrinsically exclude predators (e.g., a herbivore hiding in vegetation from a carnivore). The ability of the predator to detect prey occupying such refuges will depend upon the predator's sensory capabilities and the extent to which the prey and refuge hinder those senses.

Another important goal is to predict the effects of competitive refuges as well as refuges from predators on prey-diversity responses. As described above and illustrated in our empirical examples, competitive refuges can be detected by examining the effects of adding refuges to systems where

predators have been removed or are naturally absent. For sessile marine organisms, such substratum complexity can allow normally subordinate species to outcompete dominants (e.g., Walters and Wethey, 1986). We suggest that a fertile area for future research will be theoretical and empirical studies of the effects of competitive refuges over broad ranges of predation intensity, especially as they interact with prey refuges.

In any case, given the individually documented importance of predation, competition, and habitat complexity in natural communities, it seems clear that studying the interactive effects of these factors on local species diversity is crucial to our understanding the mechanisms structuring ecological systems. We hope that the ideas developed here will stimulate more formal theoretical analyses of these phenomena, as well as additional multi-factorial field experiments.

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