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Species Diversity Gradients: Synthesis of the Roles of Predation, Competition, and Temporal Heterogeneity

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SPECIES DIVERSITY GRADIENTS:  
SYNTHESIS OF THE ROLES OF PREDATION,  
COMPETITION, AND TEMPORAL HETEROGENEITY

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A major goal of many ecologists working toward the development of a broad theory of community organization is to understand the causes of patterns of species diversity (Hutchinson 1959). Factors potentially affecting species diversity have been reviewed several times (e.g., Pianka 1966, 1967, 1974a; Ricklefs 1973) and include (1) time, (2) spatial heterogeneity, (3) competition, (4) predation, (5) climatic stability, and (6) productivity, plus several combinations of these (e.g., Pianka 1974a). Various attempts have been made to synthesize several of these hypotheses into a broad theory accounting for certain sets of observations or experiments. Among these are the predation hypothesis (Paine 1966, 1971), the stability-time hypothesis (Sanders 1968, 1969), and, most recently, a synthesis offered by MacArthur (1972). These syntheses focus mainly on theories (3)–(6) above but differ in their emphasis on the relative importance of each factor. This difference in emphasis revolves around the seemingly contradictory roles of competition and predation in the determination of community structure. Below we suggest that these roles are in fact complementary in their effects, the relative importance of each depending on the trophic level being considered and the overall trophic complexity in a community. We present data from the New England rocky intertidal zone supporting our contention and view this synthesis against patterns of environmental behavior and structural complexity. Our synthesis is not particularly new or novel. Hairston et al.'s classic paper (1960) makes essentially the same point, though it is concerned with regulation of populations and whole trophic levels and not species diversity. However, a realization of the fundamental lesson of their paper seems peculiarly absent from the controversy considered here.

Species diversity is here the number of species present in a community. Following MacArthur (1965), we distinguish between within-habitat comparisons (e.g., comparisons within rocky intertidal, grassland, or forest habitats) and between-habitat comparisons (e.g., comparisons between grasslands and forests, or rocky intertidal and kelp communities). In our view, terms such as lizard, bird, or plant "communities" are misleading and lead to confusion. We refer to such associations as "guilds," assemblages of species utilizing a specific type of resource (Root 1967). We reserve the term "community" for collections of interacting organisms of all trophic positions occurring in a given habitat.

We further define environmental "stability" as statistical variation in an environmental parameter (e.g., Margalef 1969; Holling 1973). Environmental "predictability" refers to the level of serial autocorrelation (Levins 1965; Lewontin 1969). Finally, environmental "stress" refers to the frequency that physical environmental conditions approach or exceed the physiological tolerance limits of an organism. These terms all have at least three temporal components: short term, or time scales of days or weeks; seasonal, or time scales ranging from months to 1 yr; and long term, or time scales greater than 1 yr. The former two scales generally correspond to ecological time (at least to macroscopic organisms), while the latter ranges from ecological to evolutionary time, depending on the organism. All of these factors may or may not be strongly correlated. That is, a predictable environment may be stable or unstable, a stable environment may be stressful or benign, etc. We combine these terms with levels and patterns of production and refer to them as "temporal heterogeneity" (e.g., Pianka 1974a).

#### THEORY

##### *Role of Predation and Competition*

The predation hypothesis (Paine 1966, 1971) suggests that selective predation on dominant competitors can maintain a relatively high local species diversity over ecological time by preventing the dominant competitors from monopolizing the major resource (food or space). By keeping species in lower trophic levels below their carrying capacities ( $K$ ), competition is alleviated and additional species can invade the system. Diversity may be further increased by a positive feedback mechanism whereby new invading predators can be supported by the new invading prey species (e.g., Dodson 1970). This process is presumably limited by the stability and level of primary production (Paine 1966). Severe predation, by creating genetically disconnected allopatric populations of a species, can presumably lead eventually to speciation, thus increasing diversity over evolutionary time (e.g., Stanley 1973). This theory is supported by several experimental studies (Paine 1966, 1971, 1974; Hall et al. 1970; Harper 1969) and a variety of comparative studies (Porter 1972a, 1974; Janzen 1970; Connell 1970b).

The competition hypothesis argues that highly diverse communities arise in environments which are stable over long periods of time as a result of competition-maintained niche diversification (Dobzhansky 1950; Pianka 1966, 1974a). Specifically, the argument maintains that interspecific competition is more intense in stable environments because such environments allow most species to reach carrying capacity. Theoretically, increased interspecific competition usually acts to reduce the array of habitats or patches used by a species (the "compression hypothesis" [MacArthur and Wilson 1967; MacArthur 1972; Schoener 1974b]). Interspecific competition thus selects for increased specialization, which serves to reduce competition intensity. Species diversity is then increased via successful invasion of additional species. The limit to this

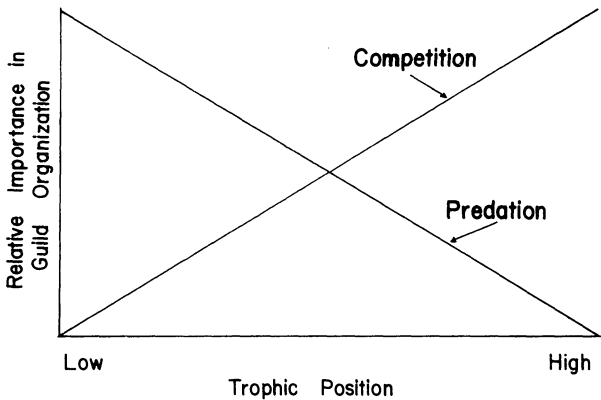
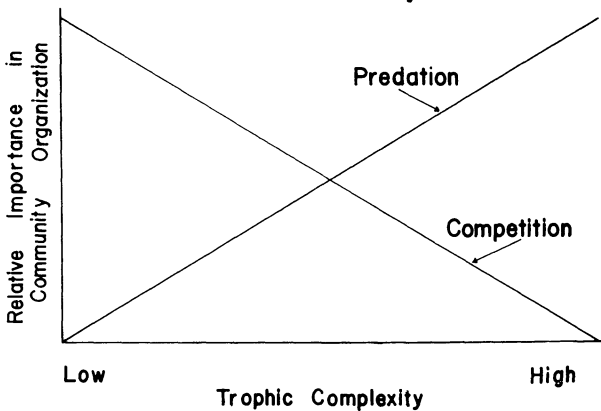
**A. Within Community****B. Between Community**

FIG. 1.—Qualitative models of the relative within-community (*A*) and between-community and habitat (*B*) importance of interspecific competition and predation in organizing and maintenance of diversity in communities. Trophic complexity is a function of several factors including at least the number of trophic levels, the number of species at each level, and the abundance and foraging strategy of each species. The relationships are linear for convenience; their precise shapes are not obvious and are unimportant for the purposes of this paper.

mechanism is theoretically a function of the number of discrete resources present (MacArthur 1965) or the maximum tolerable niche overlap on continuous resources (MacArthur and Levins 1967; MacArthur 1972), or both. Although maximum niche overlap is supposedly not directly sensitive to environmental variation (May and MacArthur 1972; Pianka 1974*b*), it should decrease as competition intensity increases (Pianka 1974*b*). Since increased competition intensity is theoretically a function of decreased environmental variation, maximum niche overlap is indirectly affected by environmental behavior. The ways in which the opposing effects of intra- and interspecific

competition interact to produce broad or narrow niches are currently a matter of debate (Van Valen 1965; Soulé and Stewart 1970; Roughgarden 1972). Indirect evidence that competition regulates diversity is available for birds (e.g., Orians and Horn 1969; Karr 1971), lizards (e.g., Schoener 1968; Pianka 1967, 1969, 1971), gastropods (e.g., Kohn 1967, 1968, 1971), fish (e.g., Zaret and Rand 1971), crustacea (e.g., Culver 1970; Vance 1972), and corals (e.g., Lang 1973; Connell 1973; Porter 1972*b*, 1974).

As indicated by Pianka (1966), these theories appear contradictory. Thus, in the predation hypothesis, predation is believed to allow high diversity by reducing competition intensity. In contrast, the competition hypothesis argues that diverse communities can only arise if differential specialization alleviates competition. This contradiction seems partly responsible for a recent exchange in the literature concerning the causes of diversity patterns in the deep sea (Sanders 1968, 1969; Slobodkin and Sanders 1969; Dayton and Hessler 1972; Grassle and Sanders 1973).

In fact, these theories are complementary rather than contradictory. The essential points of our hypothesis are (1) competition regulates the number of species in a guild only when the members of that guild actually compete, i.e., when they are at or near carrying capacity. This is usually true at relatively *higher* trophic levels because of the absence of other controlling factors, e.g., predation (fig. 1*A*). Conversely, (2) predation characteristically regulates the number of species present in guilds at relatively *lower* trophic levels (fig. 1*A*). Extending this hypothesis to between-community and between-habitat comparisons, we predict that in communities with few trophic levels competition will be relatively more important than predation as an overall organizing factor. As the number of trophic levels and the number of species per level increase, predation will become relatively more important as an organizing factor (fig. 1*B*).

#### ROCKY INTERTIDAL COMMUNITY ORGANIZATION

Species occupying the hard substrata of the rocky intertidal are either sessile (e.g., mussels, barnacles, algae) or slow moving (e.g., snails, starfish, limpets). The major limiting resource for sessile species is usually primary space on the rock substratum (e.g., Paine 1966, 1971, 1974; Connell 1961*a*, 1961*b*, 1970*a*; Dayton 1971) or, for algae, space in the light (Dayton 1975). Food, space, or both may limit more mobile species (Stimson 1970, 1973; Haven 1973; Menge 1972*b*; Sutherland 1970). However, because distribution and abundance patterns of sessile species are the dominant features of rocky intertidal community structure, we will focus below on patterns of utilization of primary space.

#### *New England*

The rocky mid-intertidal zone of New England harbors a very simple community, whose trophic organization is given in figure 2. Headlands exposed to the full force of storm-generated waves are usually typified by sharp zonation

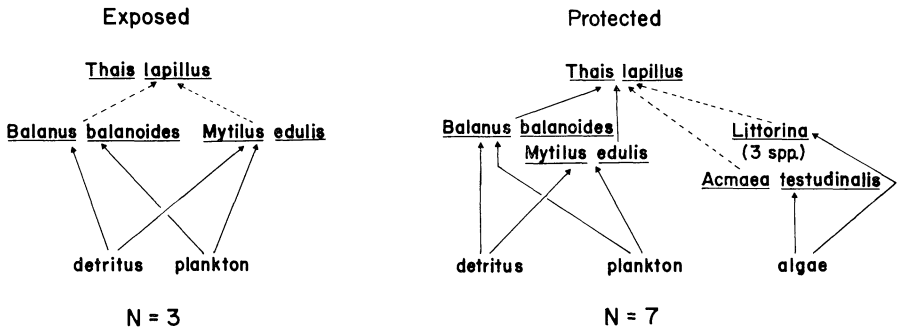


FIG. 2.—Generalized food webs at typical exposed and protected rocky intertidal communities in New England. The number of animal species occurring in each community is given below each web. The dashed lines indicate that *Thais* rarely preys upon the prey (protected) or has little effect (exposed).

and dense coverage of primary space by barnacles (*Balanus balanoides*, 69%–89%) in the high intertidal and mussels (*Mytilus edulis*, 64%–89%) in the mid intertidal (table 1). Moreover, exposed areas have relatively little free space (ranging from 2% to 25% in the mid intertidal [table 1]). At protected areas, the high intertidal also has a barnacle zone (table 1), but neither barnacles (0%–2% cover) nor mussels (25%–39% cover) occupy nearly as much space in the mid intertidal at protected areas as they do at exposed areas (table 1). Availability of free space at protected areas is generally high (e.g., 47%–72% at Grindstone Neck [table 1]).

The only mid-intertidal invertebrate predator in New England is the gastropod *Thais lapillus* (fig. 2). At all exposed areas, this species is relatively scarce (table 2) and seems confined to crevices (B. Menge, unpublished data). In contrast, mid-intertidal areas at more protected areas are characterized by higher predator densities (table 2), and from April to October these snails are dispersed widely throughout the mid intertidal. Other kinds of invertebrate predators observed in the mid intertidal on other coasts (e.g., starfish, crabs) are confined to the low (between +2.0 and –2.0 ft, or +0.61 and –0.61 m) intertidal and subtidal habitats in New England (B. Menge, unpublished data). Vertebrate predators (e.g., fish, gulls) evidently prey infrequently on the species in this food web (personal observations).

To determine the relative intensity of predation and competition in these communities, experiments similar in technique and design to those of Connell (1961a, 1961b, 1970a) and Dayton (1971) were performed at several areas in New England (B. A. Menge 1976). Briefly, each experiment, replicated four to eight times over 1–3 yr from 1972 to 1974, consisted of a stainless-steel mesh predator exclusion cage (10 × 10 × 3 cm), a mesh roof (10 × 10 cm), and a control (also 10 × 10 cm). The cage tests the effect of predation by excluding *Thais*, the roof tests the effect of shading by the mesh on survival of species settling under it, and the control provided the natural situation. These experiments were established on patches of substratum cleared of all sessile species in March of each year. In 1973 and 1974, a second cage from which

TABLE 1  
UTILIZATION OF PRIMARY SPACE AT AN EXPOSED AREA (PEMAQUID POINT) AND A RELATIVELY PROTECTED AREA (GRINDSTONE NECK)<sup>a</sup>

| INTERTIDAL<br>LEVEL AND DATE | % COVER<br><i>Balanus balanoides</i> |           |            |          | % COVER<br><i>Mytilus edulis</i> |           |            |          | % FREE SPACE <sup>b</sup> |         |            |          |
|------------------------------|--------------------------------------|-----------|------------|----------|----------------------------------|-----------|------------|----------|---------------------------|---------|------------|----------|
|                              | Pemaquid                             |           | Grindstone |          | Pemaquid                         |           | Grindstone |          | Pemaquid                  |         | Grindstone |          |
|                              | Point                                | Neck      | Neck       | <i>t</i> | Point                            | Neck      | Neck       | <i>t</i> | Point                     | Neck    | Neck       | <i>t</i> |
| High:                        |                                      |           |            |          |                                  |           |            |          |                           |         |            |          |
| August 1973.....             | 83 ± 6                               | 68 ± 15   | 2.04       |          | 15 ± 6                           | 0.1 ± 0.2 | 8.72**     |          | 1 ± 1                     | 32 ± 15 | 6.46**     |          |
| October 1973.....            | 88 ± 5                               | 67 ± 12   | 3.89**     |          | 10 ± 5                           | 12 ± 9    | 0.23       |          | 2 ± 2                     | 19 ± 12 | 4.81**     |          |
| December 1973.....           | 89 ± 5                               | 54 ± 15   | 5.31**     |          | 9 ± 5                            | 12 ± 15   | 0.51       |          | 2 ± 2                     | 34 ± 16 | 5.69**     |          |
| March 1974.....              | 69 ± 10                              | 48 ± 18   | 2.42*      |          | 10 ± 6                           | 9 ± 16    | 1.22       |          | 20 ± 6                    | 41 ± 19 | 1.99       |          |
| May 1974.....                | ... <sup>c</sup>                     | 62 ± 20   | ...        |          | ...                              | 3 ± 7     | ...        |          | ...                       | 28 ± 19 | ...        |          |
| July 1974.....               | 85 ± 7                               | 64 ± 17   | 2.51*      |          | 5 ± 3                            | 9 ± 12    | 0.14       |          | 10 ± 7                    | 28 ± 15 | 2.28*      |          |
| Mid:                         |                                      |           |            |          |                                  |           |            |          |                           |         |            |          |
| August 1973.....             | 11 ± 8                               | 2 ± 2     | 2.51*      |          | 81 ± 22                          | 42 ± 18   | 2.83*      |          | 8 ± 17                    | 47 ± 12 | 4.61**     |          |
| October 1973.....            | 7 ± 7                                | 0         | 2.72*      |          | 85 ± 21                          | 39 ± 27   | 3.37**     |          | 8 ± 14                    | 47 ± 24 | 4.06**     |          |
| December 1973.....           | 8 ± 7                                | 0         | 2.86*      |          | 89 ± 8                           | 37 ± 23   | 4.28**     |          | 2 ± 2                     | 51 ± 22 | 5.03**     |          |
| March 1974.....              | 5 ± 6                                | 0.1 ± 0.2 | 2.65*      |          | 79 ± 18                          | 25 ± 18   | 4.60**     |          | 16 ± 14                   | 72 ± 16 | 5.76**     |          |
| May 1974.....                | ...                                  | 0         | ...        |          | ...                              | 28 ± 22   | ...        |          | ...                       | 59 ± 24 | ...        |          |
| July 1974.....               | 8 ± 4                                | 2 ± 2     | 3.30**     |          | 64 ± 13                          | 26 ± 19   | 3.69**     |          | 25 ± 16                   | 53 ± 20 | 2.28*      |          |

<sup>a</sup> Mean percentage cover and 95% confidence limits of ¼-m<sup>2</sup> quadrats (*N* = 10) located randomly in the high and mid-intertidal zones of the study areas. Angular transformations (Sokal and Rohlf 1969) were performed on the data for *t* tests; degrees of freedom = 18 in all cases.  
<sup>b</sup> "Free" space is primary space on the rock which is either completely bare or covered with encrusting algae or lichens upon which mussels and barnacles will settle.  
<sup>c</sup> No data for May 1974 at Pemaquid Point.  
\* *P* < .05.  
\*\* *P* < .01.

TABLE 2

DENSITY\* OF *Thais lapillus* AT AN EXPOSED (PEMAQUID POINT) AND A PROTECTED (GRINDSTONE NECK) AREA

| AREA AND YEAR†   | INTERTIDAL ZONE   |                 |
|------------------|-------------------|-----------------|
|                  | High              | Mid             |
| Pemaquid Point:  |                   |                 |
| 1973 .....       | 0.1 ± 0.2<br>(10) | 4 ± 5<br>(10)   |
| 1974 .....       | 0<br>(10)         | 13 ± 8<br>(10)  |
| Grindstone Neck: |                   |                 |
| 1973 .....       | 130 ± 48<br>(15)  | 95 ± 21<br>(54) |
| 1974 .....       | 76 ± 41<br>(26)   | 60 ± 20<br>(40) |

\* Mean number/ $\frac{1}{4}$ -m<sup>2</sup> quadrat ( $\pm 95\%$  confidence limits). Number of quadrats in parentheses.

† Data are from June–August, since *Thais* are most active during the summer months.

*Thais* was excluded and mussels were removed was added to each experiment. This experiment tested the hypothesis that mussels would outcompete barnacles for space. The experiments were monitored every 2–4 wk. Abundance (percentage of primary substratum occupied) of mussels and barnacles in each treatment was estimated using the random-dot technique (e.g., Connell 1970a, Dayton 1971) either in the laboratory from photographs of the treatments or directly in the field.

Figures 3 and 4 show typical data from the mid intertidal at two exposed and two protected areas. At exposed areas such as Pemaquid Point and Little Brewster Point, barnacles settled in May, followed by mussels in July and August (fig. 3). Initially the barnacles rapidly occupied virtually all available space. However, mussels settled on and outcompeted the barnacles by late summer or early autumn. Since there was no important difference between predator exclusions and controls, predation seems to be an unimportant organizing agent at exposed areas. Here, competition for space between barnacles and mussels is apparently the dominant organizing biological interaction. Qualitative observations at seven other exposed headlands suggest these results are general for such shorelines.

At more protected areas, predation is more intense in the mid intertidal. Barnacles again settled before mussels, and in the exclusion cages *Balanus* were again overtaken and outcompeted by *Mytilus* by late summer to early autumn (fig. 4). Barnacles covered by mussels may survive for varying periods of time, but most are dead after 2 mo of complete coverage (B. Menge unpublished). In contrast, barnacles persist in the mussel removal cages, which supports the hypothesis that barnacles are outcompeted for space by mussels when predators are effectively absent (exposed areas) or excluded (protected areas). At protected areas, few barnacles or mussels survive through summer in the roof and



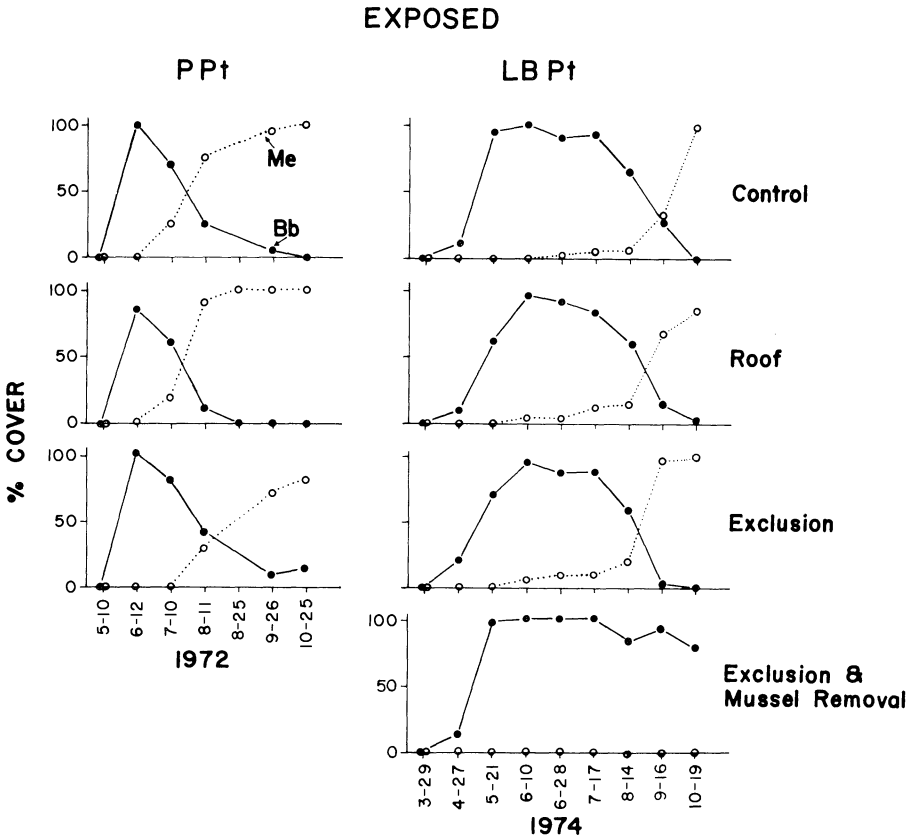


FIG. 3.—Results of exclusion experiments at two exposed areas in New England; PPt = Pemaquid Point, Maine; and LB Pt = Little Brewster Point, Outer Boston Harbor, Massachusetts; Bb = *Balanus balanoides*; Me = *Mytilus edulis*. See text for explanation of experimental design.

control. At these areas eventually all mussels and barnacles are eaten by *Thais*. Hence, space is rarely limiting and competition for space is relatively unimportant in structuring these areas (e.g., Grindstone Neck and Little Brewster Cove). Rather, predation seems largely responsible for the major observed patterns of community structure. However, observations and experiments at five areas for up to 3 yr indicate that even at protected areas, mussels occasionally escape predation and may occupy substantial amounts of space (e.g., 26%–42% cover at Grindstone Neck [table 1]). We conclude that in the trophically simple New England rocky intertidal, competition for space generally ranges from chronic (at exposed areas) to intermittent (at protected areas) and is a relatively important structuring agent. Further, the importance of competition in structuring New England communities evidently varies inversely with that of predation.

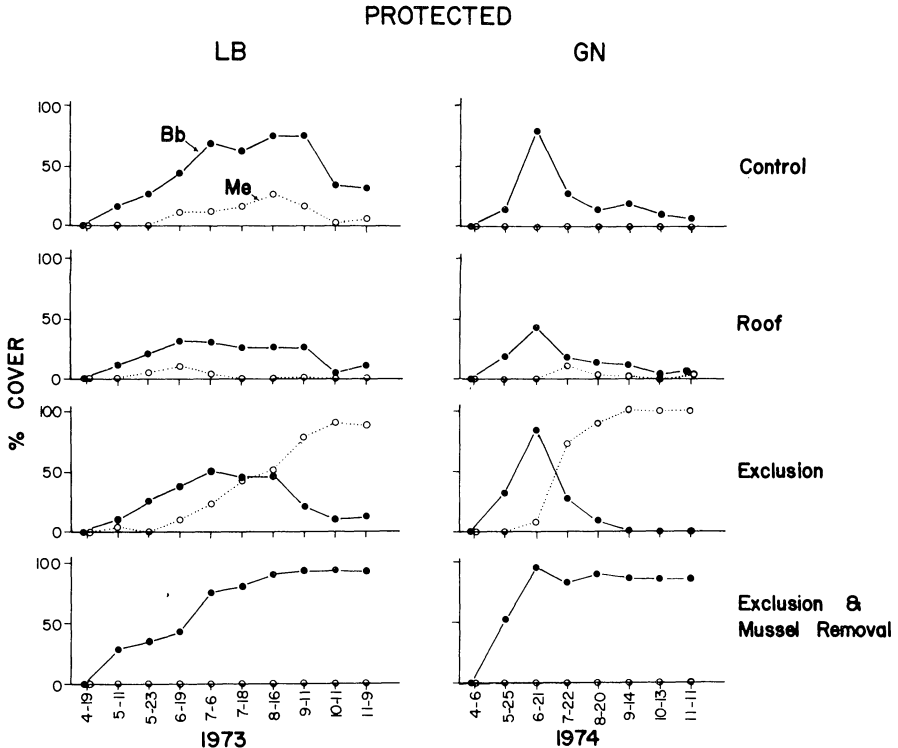


FIG. 4.—Results of exclusion experiments at two protected areas in New England; *LB* = Little Brewster Cove, Outer Boston Harbor, Massachusetts; *GN* = Grindstone Neck, Maine. See caption of fig. 3 for species code.

### *West Coast*

The mid intertidal of the northwest coast of North America is considerably more diverse than that of New England (fig. 5). The major functional differences between the West and East Coast communities are that the former has a secondary carnivore trophic level (starfish) and a much larger herbivore guild, including limpets, chitons, and gastropods. This community is structured largely by predation. Paine (1966, 1974) found that the top carnivore, *Pisaster ochraceus* (a starfish), increases the species richness in this community by preventing the mussel *Mytilus californianus* from monopolizing space in the mid and low intertidal. Dayton (1971) and Connell (1970a) have shown that this phenomenon is widespread on the West Coast and that primary carnivores (*Thais* spp.) also play an important, but subordinate, role in clearing space. Finally, Menge (1972b) has indicated that the small starfish *Leptasterias hexactis* may exert an important effect on intertidal community structure, especially when *Pisaster* is scarce. Hence, in the West Coast rocky intertidal, predation predominates in determining the distribution, abundance, and

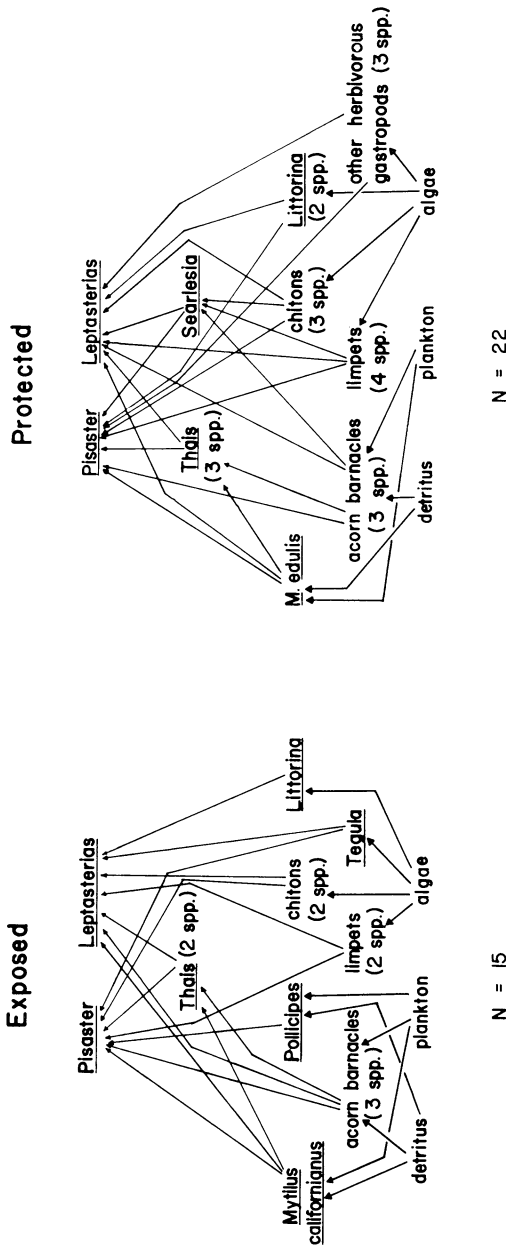


FIG. 5.—Generalized food webs at exposed and protected communities in Washington state. The left side represents open coast communities and is partly adapted from Paine (1966). The right side represents San Juan Island communities and is adapted from Menge (1972a, 1972b, unpublished data), Lounda (unpublished data), and Lloyd (1971). The number of animal species in each community is given below each web.

diversity of species occupying lower trophic levels (e.g., mussels, barnacles, limpets, herbivorous snails, etc.). Competition at lower trophic levels, at least among space users, appears to occur only sporadically.

At the top trophic level, Menge (1972*b*, 1974) and Menge and Menge (1974) have shown that *Pisaster* competes with *Leptasterias* and that, as a result, these cooccurring predators partition their food resources. Further, Connell (1970*a*) has suggested that three primary carnivores, *Thais* spp., also partition resources by habitat, presumably as a result of competition. We conclude that, on the West Coast, competition seems to be important only at high trophic levels and is generally unimportant overall in structuring the community in the mid-intertidal region.

#### *Within- and Between-Coast Comparisons*

The above evidence provides several insights concerning the relative intensity of competition and predation along gradients of temporal heterogeneity. If we compare local communities on the East Coast, the less stable (more variable over short-term and seasonal time scales), exposed headlands tend to have less dense predator populations (table 2) and hence functionally fewer trophic levels (fig. 2) than protected areas. As a result, competition for space between the suspension feeders (*Mytilus* and *Balanus*) occupying the "top" trophic level is largely responsible for the observed mid-intertidal community organization (fig. 3). At more protected areas, the predator *Thais* is more abundant and greatly reduces the occurrence of competition between barnacles and mussels (fig. 4). In other words, moving from exposed to more protected areas in New England effectively adds a trophic level (fig. 2) which results in a change from a competition-dominated to a predation-dominated community.

If we compare local communities along a comparable exposure gradient on the West Coast, predators (especially *Pisaster*) are almost always abundant enough to prevent competition for space in the mid intertidal regardless of local stability (fig. 5; see also Dayton 1971). Hence, predation is the predominant organizing factor along most of this intracoastal gradient.

If we contrast the two coasts, the East Coast rocky intertidal community appears to experience a more rigorous (less stable, more stressful, and, in some respects at least, less predictable) environment over at least short-term and seasonal time scales than does the West Coast rocky intertidal. Variability in wave shock, temperature, and precipitation is noticeably greater on the East Coast than on the West Coast (B. Menge, personal observations). Moreover, deaths of mid-intertidal organisms from freezing or overheating and desiccation seem to occur more frequently on the East Coast than on the West Coast (F. E. Smith, personal communication; B. Menge, personal observations). Finally, such events as severe storms and short-term weather variations appear less predictable on the East Coast than on the West. (These qualitative patterns will be considered more quantitatively in a future publication [B. Menge, in preparation].) Correlated with these patterns of environmental variation is a difference in the relative importance of predation and competition as structuring

agents in the rocky intertidal community. On the relatively more rigorous, trophically simpler East Coast, competition seems to be the dominant organizing factor for extensive segments of the shore (exposed areas), is responsible for the maintenance of the low diversity of these regions (via competitive exclusion), and hence may be at least partly responsible for the relatively low overall diversity in this community. On the relatively less rigorous, trophically complex West Coast, predation dominates community organization over most of the shore and seems mostly responsible for maintaining the relatively high diversity of this community.

#### DISCUSSION

An earlier synthesis, Sanders's "stability-time" hypothesis (1968; we use quotation marks to distinguish Sanders's terminology from ours), was specifically proposed to account for changes in diversity of marine soft-sediment infaunal communities arranged over gradients of decreasing environmental "stress" (shallow to deep sea). Sanders suggested that, where the environment is "severe" and "unpredictable," adaptations are primarily to the physical environment and communities are "physically controlled." Biological interactions between these eurytopic species are "unrefined," and their effects "are often drastic or catastrophic" (Sanders 1969). In "benign" and "predictable" environments, adaptations are primarily to other organisms and the community is "biologically accommodated." These adaptations are thought to ameliorate the intensity of biological interactions, e.g., by the production of narrow, nonoverlapping niches. He offers the hypothesis that "the resulting stable, complex, and buffered assemblages are always characterized by a large number of stenotopic species" (Sanders 1968).

In our view, the usefulness of this synthesis is impaired by the failure to recognize that (1) animals are usually physiologically adapted to their environment such that they are rarely stressed by it (e.g., Wolcott 1973) and (2) all communities have trophic organization, i.e., interactions occur between (predation) as well as within (competition) trophic levels.

First, those species which do not possess the appropriate physiological adaptations are probably simply absent from the habitat. However, there is no reason to believe that the biological interactions between the remaining species are any less "refined" or that their effects are any more "drastic or catastrophic" (Sanders 1969). Thus, there is considerable evidence for "biological accommodation" in the rocky intertidal (Connell 1961*a*, 1961*b*, 1970*a*, 1970*b*; Paine 1966, 1969, 1974; Dayton 1971, 1975; Menge 1972*b*, 1974; Menge and Menge 1974) and some for the muddy intertidal as well (Woodin 1974; Fenchel 1975*a*, 1975*b*), communities which are termed "physically controlled" by Sanders (1968) and Grassle and Sanders (1973).

It seems more appropriate to label a community "physically controlled" only if environmental catastrophes are a direct, and primary, cause of distribution and abundance patterns. In these habitats, biological interactions are likely to be of lower intensity or absent rather than "unrefined." Catastrophic mortality

is probably a typical result of physiological stress primarily in such areas as the upper intertidal zone, the upper reaches of estuaries, ice-scoured benthic habitats, mountaintops, etc. (see Paine 1974). For example, Sutherland (1970) demonstrated a reduced level of food competition and an increase in the effects of physical factors with increasing tidal height in the limpet, *Acmaea scabra*.

The second consideration affecting the value of Sanders's synthesis is the failure to recognize that all communities have trophic organization. In Sanders's view, the increase in infaunal diversity he observed (1968, 1969) in sampling increasingly deeper benthic habitats results from an increase in "biological accommodation" as environmental "stress" is reduced. Here "biological accommodation" evidently means tighter species packing and finer resource subdivision via competition. We reinterpret Sanders's data to be a reflection of (1) a probable increased number of predator species, total predator abundance, and perhaps trophic levels with decreasing temporal heterogeneity and, consequently, (2) fewer occurrences of competitive exclusion as a result of the increase in predation intensity (see also Dayton and Hessler 1972). In addition, there are probably an unknown number of species which disappear with increasing temporal heterogeneity (i.e., in shallow habitats) because they do not possess the physiological adaptations necessary to survive. Support for this interpretation comes from the work of Jackson (1972), who found an increased predator effect on bivalves with depth, and of M. Rex (in preparation), who has found that the fraction of gastropod species which are apparently predators in samples of deep-sea gastropods (i.e.,  $H'$  gastropod predators/ $H'$  total gastropod species) increases with depth, at least down to the abyssal plain. These patterns are consistent with the above reinterpretation of causes of variations in patterns of deep-sea diversity.

### *Role of Temporal Heterogeneity*

Temporal heterogeneity may affect community organization both directly and indirectly. Some direct effects have been suggested by other workers. For example, with trophically simple communities consisting of either primary producers (e.g., grasslands) or primary space occupiers (e.g., rocky intertidal), local physical disturbance (a local stress) creating patchiness may increase species richness (e.g., Loucks 1970; Taylor 1973; Levin and Paine 1974). In these examples, physical disturbances (fires, wave-borne logs) occur frequently enough so that competitively inferior opportunists are maintained in the system. Hence, physical disturbance may "switch" some systems from ones in which competitive exclusion would lead to reduced richness to ones where disturbance-mediated competitive coexistence occurs. However, if the disturbance is more frequent and widespread, diversity may be reduced (e.g., Dayton 1971) and, at the extreme, the community may be "physically controlled" or essentially nonexistent.

As trophic complexity increases, the ways in which temporal heterogeneity can affect community organization also increase. First, trophic complexity itself is undoubtedly a function of temporal heterogeneity. The precise number

of trophic levels in a community is probably dependent in part on the rate and predictability of primary and secondary production (Hutchinson 1959; Paine 1966; Connell 1970*b*), which in turn is probably influenced by environmental stability and predictability (Connell and Orias 1964). Several studies indicate there may be fewer trophic levels with increasing temporal heterogeneity (Pianka 1967; Jackson 1972; MacArthur 1972; Tinkle and Ballinger 1972). One effect of increased temporal heterogeneity is undoubtedly the elimination of more specialized consumers of high trophic status, since the array of resources becomes less predictably available (e.g., Menge 1972*a*). For example, Connell (1970*a*) suggested there are three species of *Thais* on the West Coast of North America and only one (*T. lapillus*) in England (and New England) because food resources are spatially and temporally more predictable on the West Coast. A second potentially important effect of temporal heterogeneity on trophically higher species is to make the environment unfavorable for certain periods of time (e.g., winter in temperate and boreal regions, gales, summer in deserts and certain other habitats). This would reduce the foraging period of consumers and might permit prey species to escape predation. For example, this effect seems partly responsible for the ineffectiveness of *Thais* at exposed areas in New England (table 2 and fig. 3 herein; and B. Menge, in preparation).

In general, then, we suggest that commonly observed reductions in within-habitat species richness along gradients of temporal heterogeneity (Sanders 1968; Johnson 1970; Jackson 1972) are due in large part to the increased incidence of competitive exclusion as trophic levels are lost or become ineffective. However, if highly localized physical disturbances or stresses occur with sufficient frequency, the diversity of such simple systems may be increased. Local physical disturbance apparently enhances the effects of predators in trophically complex systems (Dayton 1971).

### *Role of Spatial Heterogeneity*

The effect of competition or predation on diversity is strongly influenced by the structural complexity or spatial heterogeneity (number of habitats) of a given locality. Thus, in the absence of regular local disturbance in structurally simple environments (i.e., two-dimensional habitats like the rocky intertidal or grasslands), competition can reduce diversity through the process of competitive exclusion (e.g., fig. 4). On the other hand, predation evidently increases and then decreases diversity as it increases in intensity in structurally simple environments (e.g., Paine 1966, 1971, 1974; Paine and Vadas 1969; Emlen 1973; Harper 1969; J. Menge, in preparation). Thus, when predation intensity is low, competition will be intense and competitive exclusion will reduce species diversity (figs. 1*A* and 4). As predation intensity increases, diversity increases (fig. 1*B*) until a point is reached where predation becomes so intense it reduces diversity (e.g., Emlen 1973).

Structurally complex localities with many habitats may allow the co-existence of many more species through competition-induced habitat specialization or through moderation of predation. Both theory (the "niche compression

hypothesis'' [see MacArthur and Wilson 1967; Schoener 1974*b*]) and available evidence (e.g., MacArthur 1964; Schoener 1974*a*) implicate habitat segregation as the major means of coexistence between competing species. Hence, at high trophic levels, competition in structurally complex environments can maintain high diversity through the production of narrow, nonoverlapping niches. At lower trophic levels, structural complexity may moderate predation and increase diversity in two ways. First, such localities might provide many more refuges for prey species than might structurally simple localities. Both in theory (Rosenzweig and MacArthur 1963) and in nature (Paine 1969; Dayton et al. 1974; Connell 1972), refuges stabilize otherwise unstable predator-prey interactions. Hence, more refuges should result in a higher diversity of prey. Second, structurally complex environments might decrease the foraging efficiency of the predator, which is another stabilizing influence on predator-prey interactions (Rosenzweig and MacArthur 1963). For example, Ware (1972) demonstrated that trout forage less efficiently in more complex habitats. Thus, the overall effect of structural complexity should be to increase diversity at all trophic levels.

Finally, a refuge of potentially great significance is that of size. This may be an especially important refuge at the primary producer level. In the low intertidal on the West Coast, Dayton (1975) has shown that interspecific competition between kelp species is an important structuring agent in this habitat. Dayton suggests these algae essentially "escape" control by herbivores, i.e., many individuals survive and grow large because the herbivores are decimated by predators. Terrestrial forests may represent an analogous situation; adult trees surely must compete for light (e.g., Horn 1971), and few consumers are capable of eating whole trees. In other words, trees have evidently also escaped control from herbivores. However, (1) predation by higher trophic levels may be indirectly responsible for these kinds of escapes, and (2) herbivores may still regulate diversity of primary producers by preying selectively on juvenile stages of the plants (e.g., Janzen 1970; Connell 1970*b*). Hence, predation may have important direct and indirect effects on overall community structure. Obviously, a key refinement of our hypothesis will be the examination of the regulation of the structure of such primary-producer associations.

#### SUMMARY

We suggest that the "predation" and "competition" hypotheses of community organization and species diversity are complementary. Maintenance of high diversity by competition appears to be relatively more important at higher trophic levels, while maintenance of high diversity by predation seems relatively more important at lower trophic levels. Further, predation is probably the dominant organizing interaction in trophically complex communities, while competition is probably the dominant organizing interaction in trophically simple communities. These hypotheses are supported on a local scale by experimental studies in the rocky intertidal communities of New England and the West Coast. A probable consequence of its greater temporal heterogeneity (i.e.,



a less stable, less predictable, and more stressful environment) is that the East Coast is trophically more simple and has an increased incidence of competitive exclusion. As a result, diversity is lower on the East Coast compared with the West Coast. A similar interpretation is possible for differences in diversity along other gradients of temporal heterogeneity such as the shallow to deep-sea soft-sediment communities.

In structurally simple environments, competition reduces diversity through competitive exclusion. On the other hand, predation first increases and then decreases diversity in spatially simple environments, presumably because refuges are few and hence overexploitation of a resource is more probable. In structurally complex environments, competition may increase diversity through increased habitat specialization. Such environments undoubtedly have more refuges and reduce predator foraging efficiency, both of which may allow the coexistence of more species. Predator-mediated escapes by primary producers from herbivores may explain the apparent importance of interspecific competition in certain primary producer associations.

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