

ECOLOGICAL DETERMINISM IN THE COMPETITION FOR SPACE

The Robert H. MacArthur Award Lecture
Presented on 9 August 1983
Grand Forks, North Dakota

by

R. T. PAINE

Department of Zoology, University of Washington, Seattle, Washington 98195 USA



R. T. Paine
MacArthur Award Recipient

Ladies and gentlemen, fellow ecologists. It is appropriate that we recognize the role played by Robert MacArthur in the conceptual evolution of ecology, and I am truly moved by the opportunity to participate. It has not been an easy task to determine the tone and focus of my lecture. I am obviously not the person to evaluate MacArthur's many enduring contributions to an impressive variety of ecological subjects. That task is best left to historians of science and, in my opinion, the analysis should be made at some future date. Nor am I the one to enlighten you with novel mathematical treatments of important ecological processes—something Robert MacArthur excelled at. Rather, I plan to do the following. I will develop my own views on the importance of interspecific competition, a subject with which his name is inexorably linked. Although the topic has recently fallen on hard times (Simberloff 1982),

I will ask whether such a strong indictment is reasonable for certain marine systems. To some extent, I will be relying heavily on observation. MacArthur continually urged ecologists to draw their inspiration from naturally occurring patterns and to use their naturalist's intuition. I have followed this advice in pursuing my interests in the occurrence and relative importance of interspecific competition between organisms resident on marine rocky shores. I will deal specifically and solely with the sessile moiety, both plant and animal, and the outcomes of their contests for a required and limiting resource, space.

MARINE MONOCULTURES

In marine nearshore communities single species or aggregates of comparable life forms often occur as monocultures. Although there is a spatial and taxo-

onomic vagueness to this term which is unfortunately unavoidable, I have employed it in the following sense. Monocultures are defined to occur if, in the guild (Root 1967) or stratum being examined, some single species occupies at least 80% of the space. At places monocultures may be broken into smaller aggregations; the intervening gaps are usually important sources of community enrichment and may harbor monocultures of their own. The spatial extent of a monoculture is arbitrary: it may cover just a few square centimetres, as is the case for barnacles occupying a pebble or shell, or hundreds to thousands of square metres as in certain mussel or tunicate beds (Paine and Suchanek 1983). Monocultures often have a rich associated community, for instance mussel beds (Suchanek 1979) or kelp forests (North 1971), and their general presence has stimulated the naming of universal schemes of intertidal zonation (Stephenson and Stephenson 1972). Finally, the term is a descriptive one, is most usefully employed relative to events, potential or realized, within a guild or life-form grouping, and bears no implications about the nature of the ecological processes underlying the observed resource monopolization. Within the context, then, of exploring the causes of resource monopolies I will develop and examine three quite different scenarios from the exposed rocky shores of western North America, and pose three general questions.

1) Is the formation of a monoculture deterministic? That is, can we identify with absolute certainty some specified result? Or do alternate states (Sutherland 1974) lurk within the community nexus?

2) Are the monocultures, as observed naturally or generated experimentally, formed through the action of interspecific competition? Or, alternatively, do they simply represent aggregations of the most resistant local species, where resistance is to such factors as desiccation, wave action, or biological forces like predation?

3) Finally, how can the great species richness characteristic of many exposed rocky shores be explained? Obviously, numerous factors are involved (i.e., Pianka 1966), but in general, is the capacity of sessile, space-using species to coexist determined by properties intrinsic to their interacting populations, or must extrinsic agencies, for instance predation or disturbance, be invoked?

The three segments of research described below were performed on the exposed coast of Washington State ($\approx 48^\circ\text{N}$ latitude), at sites described in general detail by Dayton (1971) and Paine and Levin (1981). Seven factors, taken collectively, underlie the rich and ecologically persistent character of the biota. The Pacific ocean is an ancient one with a minimal age estimate of ≈ 300 million years, ample time for evolutionary processes of every imaginable sort to occur. The sites are characterized by continuous stretches of rocky as opposed to sandy shore, a feature known to be important in a biogeographical context. Thus solid substrata are a ma-

ajor physical component of the biotope rather than existing as minor elements or islands. Three attributes of the assemblage's overall environment render it relatively benign: surface water temperatures vary only between $\approx 6^\circ$ and 13°C (Roden and Groves 1959); floating ice never occurs, and thus ice scouring of intertidal surfaces is a nonfactor; in summer, coastal fogs are often coincident with the time of maximum low tides, which thus protects the organisms from extreme desiccation or heat effects. Two biological factors whose general importance remains unknown help complete the picture. The region is one of moderately high productivity (Thompson 1981), and grazing fish, known to be significant elements in reconstructions of more tropical regions, simply do not occur as a major trophic component. I believe these factors, operating in some complementary fashion, and in conjunction with generally heavy wave action, have been conducive to the local development of an extraordinarily rich community. With little effort, the "local" could be extended to include similar exposed sites from $\approx 29\text{--}58^\circ\text{N}$ latitude.

On many rocky shores there is little relationship between the tidal height at which organisms exist and the limits to water height given in tide tables (Lewis 1964). In other words, descriptions of organism level, standardized by tide table data and ignoring local factors which easily distort such inferences (for instance, wave surge which can extend organism distribution upwards, vs. insolation or winter freezes which tend to depress upper limits relative to exact tidal levels), can be very misleading. The assemblages I am discussing here, and have discussed previously (Paine 1966, 1971, 1974, 1980), are all mid- or low intertidal groupings despite their existence at tidal heights approaching the predicted limits of extreme high water. Many of the organisms are extremely long lived. To the casual observer the overall pattern seems constant from year to year, an opinion supported by measurement (Paine 1974). I stress these points to emphasize the differences between the above situation and that "mid-shore" assemblage ably studied by Underwood et al. (1983, and literature cited therein). That assemblage in southeastern Australia occupies a series of heterogeneous sites which seem mid- to upper intertidal on physiological grounds. Certainly, the major biological components (limpets, barnacles, littorine snails, and small carnivorous gastropods) are highly reminiscent of the fauna of other, earlier studies (Hatton 1938, Dayton 1971) in which pattern was not persistent and prediction difficult because of unsettled biological interactions and those many capricious events characteristic of relatively extreme environments. In any event, the ecological character of such sites is simply not comparable to those at more benign lower levels. Here, the dominant species are typically long lived and spatially persistent, and even an order-of-magnitude annual variation in recruitment intensity is averaged out by

TABLE 1. Completely deterministic recovery of mussel beds at Tatoosh Island, following both natural and experimental gap formation. From Paine and Levin (1981).

Patch type	No. patches	Number reverting to <i>Mytilus californianus</i>	Number reverting to any alternate terminal state
Experimental	152	152	0
Natural	360	360	0

the long-lived adults. I now describe three scenarios suggesting a regularity, potentially leading to the formation of monocultures, underlying community organization at physiologically mid- and low tide levels.

SCENARIO ONE: MONOCULTURES OF *MYTILUS CALIFORNIANUS*

Mussels, predominantly *Mytilus californianus*, are a conspicuous biological component of exposed rocky shores of western North America. At suitable sites the stands can be continuous; where the topography is broken, mussels usually occur most densely on the outer tips of promontories most exposed to wave action. The lower limit to these beds is set by starfish predation (see Paine 1966, 1974, and below). The beds harbor an extraordinarily rich associated community of no fewer than 300 species (Suchanek 1979) and are frequently disrupted into patches or gaps (Paine and Levin 1981). Their pattern of disturbance and recovery is monotonously regular; Simon Levin and I have followed the fate of both natural patches and those we have made (Table 1). Both types inevitably revert to a complete cover of mussels, and though the rate and

TABLE 2. Densities of *Hedophyllum sessile* and *Alaria nana* holdfasts within nine gaps in natural and experimental mussel beds, and in the surrounding mussels. Data are based on counts within 0.09-m² replicate samples at Tatoosh. As the gaps close and revert to mussels, these algae and many other species disappear.

Date	Site state	No. samples	Density (holdfasts/m ²)	
			<i>Hedophyllum</i>	<i>Alaria</i>
Jun 1970	Gap	10	89	22
Sep 1976	Gap	7		274
Sep 1976	Mussels	7		0
May 1978	Gap	10	6	
Jun 1978	Gap	17	4	30
Jun 1978	Mussels	8	0	0
May 1980	Gap	12	9	
Jul 1980	Gap	15	32	
May 1983	Gap	9	122	
Aug 1983	Gap	10		159
Aug 1983	Gap	20	16	
Aug 1983	Mussels	24	0.5	0

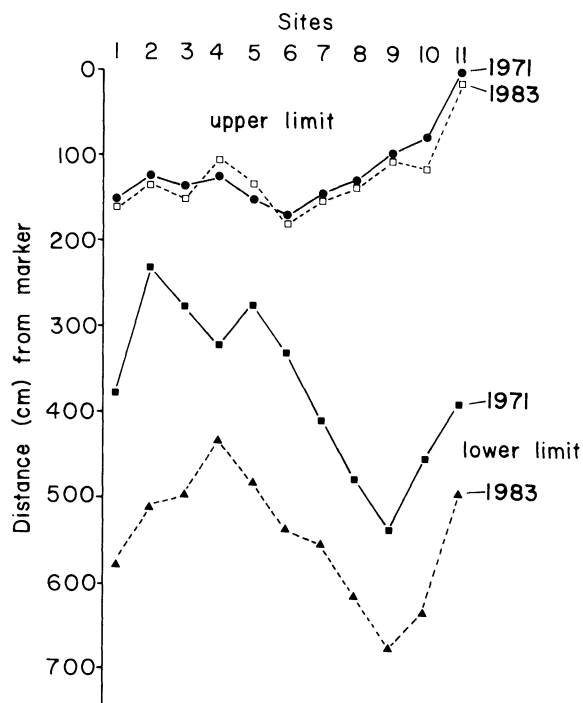


FIG. 1. Relative changes in the upper and lower limits of the mussel *Mytilus californianus* at Tatoosh Island in the maintained (since September 1970) absence of its major predator, as measured from 11 fixed reference points (sites). Sample dates are 4 September 1971 and 23 April 1983. Site 1 is at the south end of the channel.

within-patch events are highly variable, there is but a single end point. These constant results imply a highly deterministic process; by themselves they do not necessarily prove competitive superiority in that process. For that we require other sorts of data.

I have manually removed the starfish *Pisaster ochraceus* from short stretches of the Washington outer coast. The initial experiment, lasting 5 yr (1963–1968), demonstrated major increases in mussel distribution and percent cover, and associated disappearance of a number of co-occurring species (Paine 1966, 1974). The basic design has been extended to the offshore island Tatoosh, and the result repeated. Starfish removal began in September 1970 from a long surge channel on the southwest side of the island and has continued to date. Changes in mussel distribution have been quantified since September 1971 by measuring the distance of major bed features from 11 stainless steel screws set at 2–3 m intervals along the channel. Changes have been progressive (Fig. 1) at the bed's lower limit, as mussels gradually extend their domination lower into the intertidal. The upper distributional limit, and the lower limit at control sites with *Pisaster* (Paine 1974 and R. T. Paine, *personal observation*), have shown no such shifts.

These changes have resulted in major alterations in

TABLE 3. Results of experimental burns of 1–2 m² *Hedophyllum*-dominated areas at Waadah Island. Data are given as mean values, \pm one standard deviation. The first row provides data on individual burns initiated at variable dates throughout the indicated period. The remaining rows give data on simultaneous, replicated burns.

Date initiated	No. areas	% cover at recovery	Maximal observed % cover	Months to recovery
Apr 1970– May 1973	10	76 \pm 15	87 \pm 14	34 \pm 11
Aug 1975	6	77 \pm 12	93 \pm 8	39 \pm 6
May 1976	4	77 \pm 3	92 \pm 11	35 \pm 12
Oct 1976	3	69 \pm 3	96 \pm 4	17 \pm 3

the abundance patterns of, for instance, two species of large benthic algae. Occasional sampling of various gaps and the adjacent mussels indicate (Table 2) that *Hedophyllum sessile* and *Alaria nana* often are abundant in gaps within the mussel bed but are unable to persist once the encroaching mussels have made physical contact. The numbers of these macrophytes within gaps are highly variable due to variation in algal size structure, differences in sample tidal height, and perhaps also age, of the gap. For another species of large brown alga, *Postelsia palmaeformis*, I have demonstrated that local extinction is inevitable in the presence of mussels, but that persistence is the rule when the mussels are continually removed (Paine 1979 and R. T. Paine, *personal observation*). Finally, one can simply observe the brute force competitive capacities of *Mytilus* in action: small barnacles are smothered; larger species such as *Semibalanus cariosus* are overgrown and then abraded to death; the goose-necked barnacle *Pollicipes* is gradually crushed; and so on.

This encroachment by mussels into the lower intertidal, usually forbidden by *Pisaster*, has at places approached 3 m. The advance has occurred over a wide range of exposure and habitat types. Measures with a transit indicate an average vertical downward extension, to date, of 0.84 m at the 11 sites, or $\approx 27\%$ of the maximal tidal range at Tatoosh. Wave forces are judged to be severe at the south end and more moderate at the north, and the slope ranges from 0° to almost 60°. Since the basic Tatoosh substrate is a turbidite, a marine conglomerate, the advance has been over many different rock types. Furthermore, the advancing front of mussels has treated all rock irregularities or microsites equally. In sum, observations on *Mytilus californianus* yield no suggestions of this species being a habitat specialist. It recovers previously inhabited space, or invades, as the opportunity permits, new terrain of a wide variety of sorts, and it does so by being competitively superior. Both the recovery and invasion events appear totally deterministic: mussels thus form persistent monocultures in a broad range of habitats in the absence of predation or disturbance.

SCENARIO TWO: MONOSPECIFIC STANDS OF CANOPY ALGAE

Conspicuous stands of benthic algae are major features of the Washington State outer coast (Rigg and Miller 1949, Dayton 1975). Probably the most important intertidal species, judged by the criteria of canopy percent cover or simply mass per square metre, is *Hedophyllum*. A "meadow" of it exists on the exposed side to the north of the Waadah Island breakwater. At places this may be 30–50 m wide, and *Hedophyllum* can be found growing to the tops of 1–2 m high rock slabs as well as on the level surfaces. The species is a perennial, attaining ages of 4–5 yr. Dayton (1975) believed that it achieved its canopy dominance in spite of herbivores, and I concur. It is also easily removed, and Table 3 gives summary data on 23 sites on large boulders or rock walls which were first scraped and then burned. I believe the initial sterilization to have been effective; no attempt was made to control for herbivores, which rapidly recovered due to recruitment and adult immigration. Sea urchins, *Strongylocentrotus purpuratus*, the one species capable of excluding *Hedophyllum* (Paine and Vadas 1969, Dayton 1975), were absent from these high-angle surfaces, and the chiton *Katharina tunicata*, capable of influencing kelp abundance (Paine 1980), is not common.

The results are straightforward (Table 3). *Hedophyllum* was judged to have recovered once canopy cover, estimated from replicated samples using a plastic sheet with 39 randomly positioned dots, was equivalent to that of control, unburned sites. Observations on recovery of the canopy were continued at all sites: eventual recovery averaged in excess of 85% canopy cover for each series of burns, and at many individual sites the mid- or late summer canopy was composed entirely of *Hedophyllum*. Clearly, recovery is highly deterministic despite the fact that the rate varies seasonally (Table 3) and great variation characterizes the identity of the transition states (Paine 1977).

There are many indications that the recovery pattern is repeatable spatially as well as temporally. I found *Hedophyllum* that invaded urchin-removal plots to account for >50% of the algal mass after 2–3 yr at Mukkaw Bay (Paine and Vadas 1969). Dayton (1975) found a range of canopy cover values at removal sites: slower recovery values in the protected San Juan Islands of Washington State, intermediate values at Portage Head and Shi-Shi Beach, and values roughly comparable to mine at Waadah. The results at Tatoosh (Fig. 2) following careful scraping of large areas (5–15 m²), repeated through time for 3 yr and with a modification in a 4th yr, are essentially identical in outcome though not in recovery rate. *Hedophyllum* recovers within about a year; the control sites show the same trends of seasonal variation in canopy dominance as illustrated by Dayton (1975) at Waadah.

Collectively these manipulations, done as they were

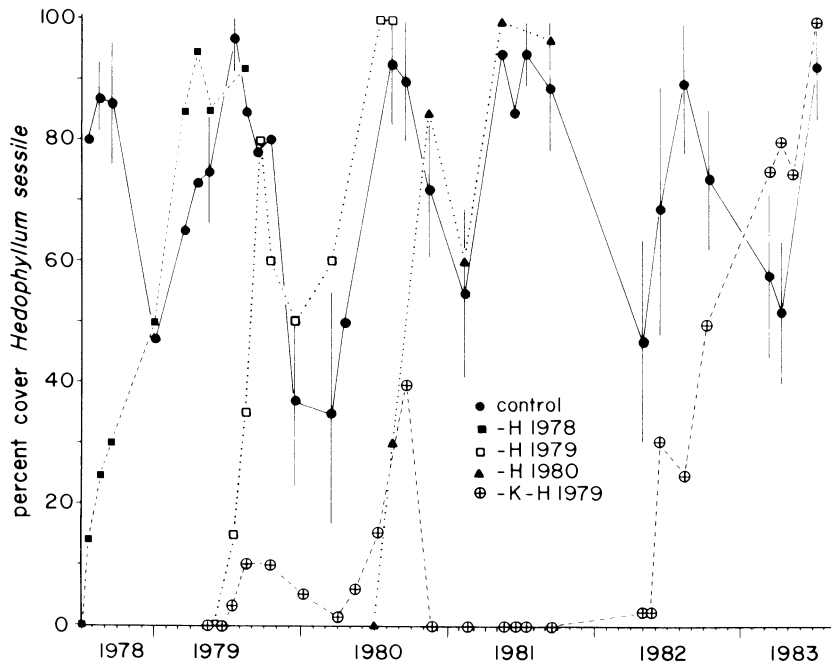


FIG. 2. Patterns in the percent canopy cover of the brown alga *Hedophyllum sessile* at Tatoosh Island. Controls are natural, unmanipulated population. Error bars are \pm one standard deviation based on 3–28 quadrat samples. The notation “-H” preceding the year indicates that all *Hedophyllum* were scraped from the surface once. The notation “-K-H” refers to the simultaneous removal of *Hedophyllum* and the chiton *Katharina*. This last treatment was maintained from 1979 to September 1981, at which point the site was allowed to revert to its natural state.

by different people at different places and times, suggest a very high level of process regularity: all transitional paths lead to a *Hedophyllum* canopy. But these examples, despite being highly deterministic, may have little or nothing to do with interspecific competition. If there is one truism that has developed from experimental studies on rocky shores it is that grazers have the capacity to control totally the species composition, distribution, and dynamics of the associated plant community (Lubchenco and Gaines 1981). None of the experimental removals of *Hedophyllum* mentioned above controlled for the presence and activities of grazers. Therefore, an equally acceptable alternative hypothesis about *Hedophyllum* is simply that canopy species are most resistant to invertebrate grazing, and that competitive abilities have little to do with its dominance.

A test of this possibility developed accidentally in the following way. Robert Steneck and I are investigating the ecology of crustose coralline algae (see below). These algae are experimentally tractable, so to examine the influence of specific grazers, the following manipulations were performed beginning in June 1981. Large ($\approx 3\text{-m}^2$) sites were established, and isolated by a 5–20 cm wide border of copper-based antifouling paint. Treatments consisted of one site without grazers, and three others in which near-normal densities of the chiton *Katharina*, or of one of two limpets, *Acmaea*

mitra and *Collisella pelta*, were maintained. An adjacent area was designated as the control and continues to be characterized by high grazer density: 20–40 *Katharina*/m²; 3–5 *A. mitra*/m²; 4–15 *C. pelta*/m²; and 10–18 other chitons/m². Later two other sites were added from which all grazers were manually removed, and all were sampled in late April 1983 for percent cover of the canopy algae. The results (Table 4) suggest a radical change in the identity of the canopy species depending on whether *Katharina* is present or not. Although this result seems clear, I have no understanding as yet of the underlying mechanisms, and the possibility exists that these are just short-term results. Thus *Hedophyllum* might be capable of dominating such sites, but with its eventual supremacy delayed because of an experimentally induced, persistent, transitional state. The data probably best serve to emphasize that near monospecific stands of canopy-forming algae can be produced in a variety of ways, some of which may have little to do with innate competitive abilities.

SCENARIO THREE: COMPETITIVE RELATIONSHIPS WITHIN A GUILD OF CORALLINE ALGAE

The research segment discussed next is being done at Tatoosh in collaboration with Robert Steneck. I present some of it here because the initial results, sup-

TABLE 4. The experimentally induced dominance of the alga *Alaria marginata* either in the enforced absence of all grazers ($N = 3$ sites) or in the general absence of all grazers except the limpets *Collisella pelta* or *Acmaea mitra* ($N = 2$ sites). At experimental sites with the chiton *Katharina tunicata* ($N = 1$), or controls with the normal complement of all grazers ($N = 1$), the brown alga *Hedophyllum* dominates (see Fig. 2). Estimates based on four 900-cm² quadrat samples within each treatment. Treatments with a common underline are statistically indistinguishable from each other; the two groups are significantly different, $P < .05$, Student-Newman-Keuls test.

<i>Katharina</i> present		<i>Katharina</i> absent				
Control (all grazers present)	Minus all grazers except <i>Katharina</i>	Minus all grazers	Minus all grazers except <i>Collisella pelta</i>	Minus all grazers except <i>Acmaea mitra</i>	Minus all grazers	Minus all grazers
Mean percent canopy cover by <i>Alaria marginata</i>						
2.8	2.3	48.8	51.3	70.0	71.3	71.3

ported by a variety of experiments, are particularly germane to discussions of determinism in ecology.

Crustose and erect coralline algae, red algae which are 80–85% CaCO₃ by mass, are ubiquitous in the oceans' photic zone wherever appropriate substrate exists (Adey 1970, Steneck and Adey 1976). They seem especially well developed at sites characterized by intense grazing pressure. Thus, at Tatoosh, if one pushes

aside the *Hedophyllum* canopy at the 0 m tidal level one finds a landscape dominated by coralline algae, with the genera *Pseudolithophyllum*, *Lithothamnium*, *Bossiella*, and *Corallina* being especially prominent. These and other similar plants belong to the same guild because of morphological similarity and use of a comparable resource (space) in roughly similar ways. The limits to guild membership are arbitrary; the guild could be expanded to include fleshy crustose algae and a variety of recumbent animal morphologies such as thin-bodied sponges, certain bryozoa, and hydrocorals. Large benthic algae and large-bodied animals such as the barnacle *Balanus nobilis* and mussels would be excluded. The larger algae, in particular, bear an enigmatic relationship to this guild; their holdfasts have the capacity to outcompete all the above groups for space, yet their presence is essential since most members of the understory plant community require shade (Paine 1980).

Competitive relationships are easily observed in coralline crusts, and the crusts themselves seem to provide exceptionally tractable experimental material (Steneck and Adey 1976, Paine 1980, Steneck 1982). In fact, marine ecologists have had little difficulty in identifying competition or overgrowth from a wide variety of taxa and environments: coral reefs (Lang 1973), fouling or piling communities (Sutherland 1974, Quinn 1982, Russ 1982), marine "caves" (Buss and Jackson 1979, Jackson and Buss 1975), and subtidal rock walls (Sebens 1982). There is little questioning of the fact of extensive interspecific competition for space, and most of the authors have concluded that the interacting sets of species show a roughly hierarchical (transitive) arrangement (Quinn 1982). However, there are hints of networks (intransitive loops), as in cryptic coral reef assemblages where growth is often directional (Buss and Jackson 1979), and almost all authors have found pairs or trios of species in which the overgrowth relationships are highly indeterminate. In other words, reversals of the direction of competition via overgrowth are commonplace, as are apparent stalemates or other ambiguities. Some of these are illustrated (Fig. 3) for coralline algae. They clearly add uncertainty to the system, and thus contribute to potential coexistence

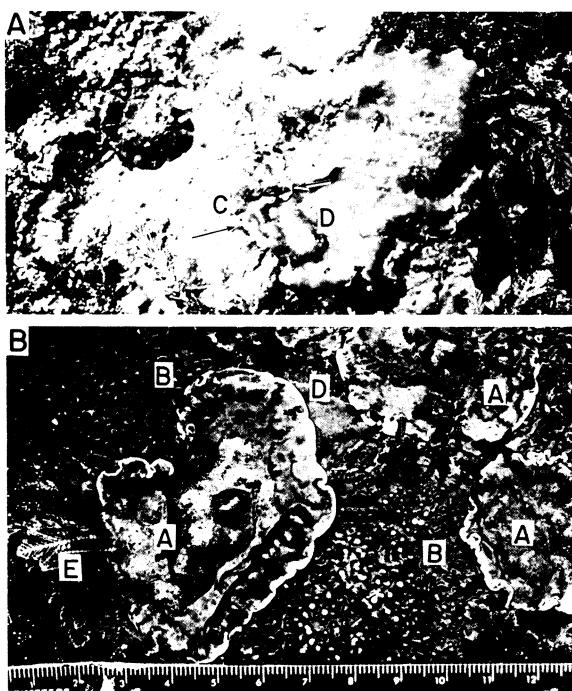


FIG. 3. (A) A competitive reversal (note arrows) on a natural rock surface along a common boundary between crust C (*Pseudolithophyllum whidbeyense*) and crust D (*Lithophyllum impressum*). The latter is also overgrowing some erect coralline algae. One grazer, the limpet *Collisella pelta*, is visible. (B) Competitive interactions on an artificial surface in the absence of grazers. Crust A (*Pseudolithophyllum lichenare*), the competitive dominant in this guild, is overgrowing crust B (*Lithothamnium phymatodeum*) and crust D. Other conspicuous overgrowths are: crust A over the erect coralline *Bossiella* sp. (guild member E); crust B over crust D; crust D over an erect species, probably *Corallina vancouveriensis*.

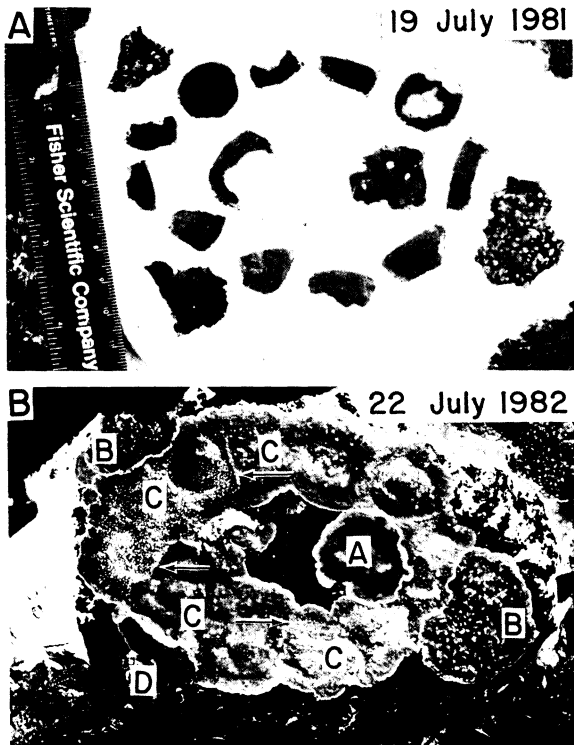


FIG. 4. (A) Putty island No. 36 on 19 July 1981 in a grazer-free area. (B) The same site on 22 July 1982. Letters indicate algal species as in Fig. 3. Boundaries (indicated by arrows) are visible between different clones of crust C, whereas fusion has occurred within clones. Visible overgrowths: crust C over crust D; crust B over crust C; crust A over crust C.

by retarding the rate of competitive exclusion. Furthermore, purely intransitive networks in which no competitive winner exists have been modelled (Gilpin 1975, May and Leonard 1975) and possibly observed in the field (Buss and Jackson 1979).

All the above assemblages are rife with competition for space, and yet they cannot be considered "competition communities" (an abstraction I consider highly unlikely) because few attempts have been made to identify the possible contribution of predation (or disturbance). However, it is possible to approach this ideal experimentally under natural conditions in the following way. I have been manually removing all herbivores for the last 2 yr from two large (1.9-, 4.3-m²) plots at about the 0-m tide level. Although the removals are not totally effective, I believe the herbivore load has been maintained at <10% of its original level. I have then staged competitive bouts between specific coralline crust species by transplanting algal chips onto Sea-Goin Poxty Putty (Paine 1980), a nontoxic aquarium cement. Crusts transplant easily, appear to flourish, and grow readily onto the putty in the near absence of grazers. The competitive interactions, both interspecific and intraspecific, are observed and recorded pho-

tographically as a time series. One such "island" of this easily replicated manipulation is illustrated in Fig. 4.

Three attributes of the experimental system seem especially valuable. The smooth putty surface at the time of transplantation effectively places all species on an initially equal footing and, in effect, controls for the possible influence of environmental heterogeneity on the outcome of competition. Once the crusts grow into physical contact and overgrowth interactions are initiated, the outcome is easily observed (see Fig. 3B). And last, some information can be gleaned on the intensity and outcome of intraspecific competition. Although I do not wish to develop this point further here, interclone (intraspecific) competition and overgrowth does not appear to be common, with stable boundaries being the rule if the pieces of an original thallus start their encounter as equals (Fig. 4). Further, using this

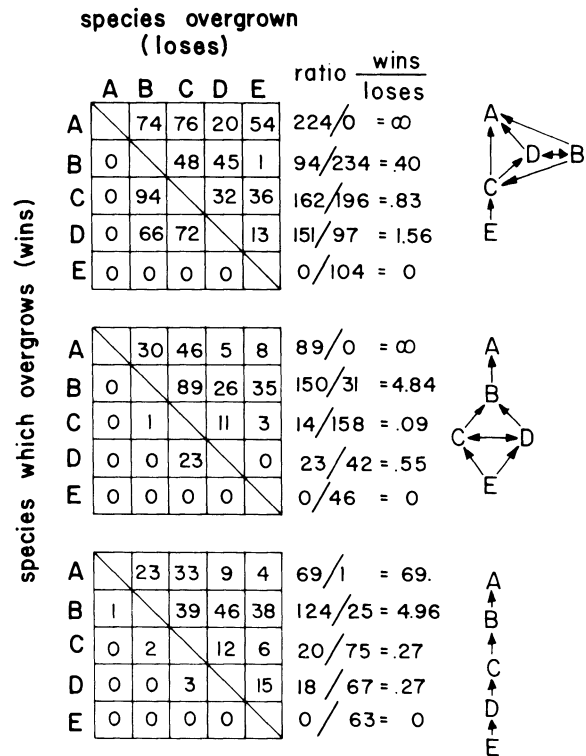


FIG. 5. Interspecific relationships within a guild of five coralline algal species under three different conditions. Top: with grazers, on natural surface; center: without grazers, on natural surface; bottom: without grazers, on smooth artificial surface. Letters refer to species as in Fig. 3: A, *Pseudolithophyllum lichenare*; B, *Lithothamnium phymatodeum*; C, *Pseudolithophyllum whidbeyense*; D, *Lithophyllum impressum*; E, *Bossiella* sp. Numbers in the array are observed overgrowths when two guild members come into contact. The column of wins to losses provides an index of each row species' relative competitive ability under the specified conditions. The diagrammed competitive interactions to the right of the ratios indicate the change of position induced under the various conditions. Arrows point from losers towards competitive winners. Two-headed arrows indicate that no significant bias exists in the interaction's direction.

TABLE 5. Results of the transplant to an herbivore-free arena of eight naturally occurring competitive interactions between *Lithothamnium* and *Pseudolithophyllum whidbeyense*. The "natural" column is based on the observations from unmanipulated rock surfaces reported in Fig. 5. The overgrowth pattern is reversed, and the uncertainty removed, by the elimination of grazers.

<i>Lithothamnium</i>	Natural	Experimental
Wins	48	8
Loses	94	0
Fisher exact probability test, $P = 2.7 \times 10^{-4}$.		

technique, Steneck and I have not been able to discover any competitively superior genotype within four species examined to date. The implications are that the potential contribution of both intra- and interspecific competition to coexistence, so basic to understanding the dynamics of competition (Gause 1934, MacArthur 1972), can be evaluated under field conditions.

A preliminary analysis of some of these transplant experiments is given in Fig. 5. I have chosen to restrict consideration to five typical guild members: *Pseudolithophyllum lichenare*, a superior competitor for space at these morphological scales; three competitively intermediate crust species, *Lithothamnium phymatodeum*, *Lithophyllum impressum*, and *Pseudolithophyllum whidbeyense*; and *Bossiella* sp., an erect coralline species whose basal system is crust-like in appearance. The numbers represent directly observed interactions in which a winner, as determined by visible overgrowth along much or all of the common interface, was apparent. Stalemates, or situations in which the issue was in doubt, have not been included. Three blocks of data are compared: interaction observed on adjacent sites with a normal herbivore complement, i.e., the real world; interactions on natural rock surfaces within the two sites from which herbivores were manually removed; and interactions on putty islands in these same herbivore-exclusion areas. I have also shown a schematic representation of the competitive relationships between these species to suggest the degree of transitivity.

At least three patterns are apparent. First, the proportion of observed reversals diminishes significantly in the absence of grazers, reflecting increased transitivity of the interactions. Thus, in the real world, 20% of all interactions (125/631) are reversals, with a loser observed overgrowing a winner. In the absence of grazers, the proportion is greatly reduced: 4% (12/288) on natural rock surfaces and 3% (6/231) on the putty. Although the latter two are statistically indistinguishable ($\chi^2 = 1.09$, $P > .30$), both are significantly different from the situation with normal herbivore densities ($\chi^2 = 39.1$, $P < .001$). If the analysis is confined to the three intermediate species, a similar pattern appears: species tending to win lose significantly more often ($\chi^2 = 37.8$, $P < .001$) than they would in the absence

of consumers. Second, all pairwise interactions become polarized in the absence of herbivores on the putty islands, whereas in the real world or on natural surfaces some competitive ambiguity remains. Thus in the real world the relationship between *Lithothamnium* and *Lithophyllum* suggests competitive equality ($P > .05$, two-tailed Binomial Test), and on a natural surface uncertainty persists at the boundaries between *Pseudolithophyllum whidbeyense* and *Lithophyllum*. This situation may be enhanced by the tendency for the latter species to occupy topographic highs, rendering its overgrowth more difficult. And last, in the absence of grazers, some species change ranks (i.e., *Lithothamnium*), a feature reflected in systematic changes in the ratio of wins to losses.

The implication of such comparisons is obvious. Grazers introduce competitive uncertainty into the natural system, and in the process generate the high level of reversals which can promote coexistence. In the absence of grazers, the system is hierarchical and cannot persist for long in this condition. Even given the stately growth rate of the winner, *Pseudolithophyllum lichenare*, this "competition community" should gradually become a monoculture as the losers are eliminated.

I have made a number of explicit experimental tests of these patterns in the following way. Just as small fragments of some single species of crust can be transplanted, so can the actual interspecific competitive bouts. These can be chosen where one species is overgrowing a second. With luck, sometimes a three-way interaction can be found. These are chipped from the rock and transplanted to the grazer-free areas. Preliminary analysis of eight transplants in which *Lithothamnium* and *Pseudolithophyllum whidbeyense* were originally competing for space in the presence of grazers gives evidence for the development of a polarized pattern when interspecific competition is encouraged in the grazer-free compound (Table 5). The implied determinism provides independent confirmation for the observed rank changes.

The competitive relationships are transitive within this guild of coralline algae. To me there seems solid evidence for a dominant species, which implies the formation of a spatial monopoly at a rate determined primarily by the growth capacities of the winner. That such domination does not occur naturally on a larger spatial scale, though it is readily observed in interspersed 10–1000 cm² patches, can be attributed to the combined influences of grazing and biologically mediated disturbance. Thinner calcareous crusts, which include the growing front of *Lithothamnium*, are highly susceptible to invertebrate grazing pressures. Thus the potential competitive advantage of high growth rate and excellent overgrowth capability is countered by consumers. Thicker crusts, especially those with raised growing edges like *Pseudolithophyllum lichenare*, tend to be competitively superior, even being able to "push

over" erect corallines like *Bossiella* or *Corallina* (Fig. 3B). They also are more resistant to grazers because of their thick thallus, a situation extensively documented by Steneck (1982) for western Atlantic species. However, no single species is apt to be a jack-of-all-trades (MacArthur 1961). Thick calcareous crusts are attacked by boring sponges and often are riddled with holes produced by other invertebrates, especially the worm *Dodecaceria fewkesi* or the clam *Hiatella arctica*. The resultant weakened structure renders them much more susceptible to mortality from wave action. In this sense, then, although at different phyletic and morphological scales, the organization of the crust guild is comparable to that headed by *Mytilus californianus* and even the sea grass *Phyllospadix* (Dethier 1984): the domination by a competitive winner, with its implied potential spatial monopolization, is thwarted by a variety of extrinsic influences, resulting in a complex mosaic of coexisting, yet locally competing, species.

CONCLUDING REMARKS

If I could catch the essence of these three examples it would be as follows.

1) Single sessile species on some marine rocky shores are capable of forming resource monopolies. Experimentation seems to be the best and perhaps the only way to determine whether competitive prowess or superior capacity to resist predation or other external pressures are responsible for their formation and maintenance. In the cases developed above, *Mytilus californianus* and *Pseudolithophyllum lichenare* can acquire and hold space competitively better than other members of their respective guilds. The outcome of these interspecific interactions seems deterministic, perhaps entirely so in the case of mussels. The coralline-algae guild is unlikely to be completely deterministic even under the most extreme experimental conditions (total herbivore exclusion, smooth artificial surface) because of artifacts introduced by the procedures. However, to date these artifacts, involving damage to the crust during transplanting, unknown initial differences in physiological or reproductive state, or minor variations in position or individual size, generally seem of little consequence to the overall directions of multispecies competition which develop in the absence of grazers. Thus a single-species monoculture should eventually appear regardless of the initial conditions. A comparable determinism characterizes the spatial domination by the brown algae *Hedophyllum* and *Alaria*, in which the expression is demonstrably influenced by grazers but where, unfortunately, the causal mechanisms also remain unknown.

2) The potential (or realized) formation of large-scale spatial monopolies only in the enforced absence of predation or disturbance suggests that "competition communities," assemblages or guilds, where the capacity to coexist is *intrinsic* to the group, do not exist when space is the resource in short supply, and the

species involved are primarily or entirely sessile. These results imply that such popular ecological terminology as niche diversification or resource partitioning, as due to competition, should not be generally applicable to sessile marine organisms. For mobile species exploiting discrete and ecologically discontinuous prey, the terminology probably retains its utility, although the relative importance of interspecific competition as the evolutionary cause often remains in doubt. When sessile species coexist, the result seems to be brought about by events *extrinsic* to the resource. As in the coralline algal guild discussed above, coexistence is characteristic of ecologically uncertain relationships. When the sources of environmental uncertainty are eliminated, the capacity for multispecies coexistence is significantly reduced.

3) Although some may perceive the above view as a heresy, I believe it offers many compensatory benefits to those attempting to understand how, or even whether, natural communities are organized. The outcome of interspecific competition under broadly homogeneous conditions is perceived as a single-species stand or resource monopoly. Though it may seldom be realized in nature, it is both theoretically and experimentally respectable, as the Lotka-Volterra equations predict and numerous bottle experiments show. Further, the monopoly provides an idealized null state or standard against which to measure departures in the real world. In the absence of such benchmarks it is difficult to evaluate the relative importance of the many individual processes which, collectively, generate community pattern.

4) Finally, observational and experimental studies such as the above, rather than diminishing the importance of interspecific competition, illustrate its central position in community ecology. I agree with the recent assessment of Schoener (1983): we as ecologists are in the early, not terminal, phases of our understanding of species coexistence and competition, the theoretical elaborations of which are primarily due to the many insights of Robert MacArthur.

ACKNOWLEDGMENTS

It has been a joy to recall during the preparation of this lecture the many pleasant associations formed during my 20 yr of research on the Washington State outer coast. J. P. Sutherland, P. K. Dayton, J. W. Drescher, R. L. Vadas, B. A. Menge, K. P. Sebens, T. H. Suchanek, J. F. Quinn, S. A. Levin, E. G. Leigh, and S. R. Palumbi have been especially stimulating. The continuing work on coralline algae would have been impossible without the collaboration of R. S. Steneck, and the manuscript has benefitted from his inspection and that of J. Lubchenco, B. Menge, K. Sebens, and S. Palumbi. Some of the photographs and all of the better ones were taken by A. Wertheim. Research on Tatoosh Island remains possible because of permission and a helping hand from the United States Coast Guard, and has been supported in its entirety by the National Science Foundation. To all the above, and many others, I remain deeply grateful.

LITERATURE CITED

- Adey, W. H. 1970. The crustose corallines of the north-western North Atlantic, including *Lithothamnium lemoineae* n. sp. *Journal of Phycology* **6**:225-229.
- Buss, L. W., and J. B. C. Jackson. 1979. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *American Naturalist* **113**:223-234.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**:351-389.
- . 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs* **45**:137-159.
- Dethier, M. N. 1984. Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. *Ecological Monographs* **54**:99-118.
- Gause, G. F. 1934, reprinted 1964. *The struggle for existence*. Hafner, New York, New York, USA.
- Gilpin, M. E. 1975. Limit cycles in competition communities. *American Naturalist* **109**:51-60.
- Hatton, H. 1938. Essais de économie explicative sur quelques especes intercotidales d'algues et d'animaux. *Annales de l'Institut Oceanographique de Monaco* **17**:241-348.
- Jackson, J. B. C., and L. W. Buss. 1975. Allelopathy and spatial competition among coral reef invertebrates. *Proceedings of the National Academy of Sciences (USA)* **72**:5160-5163.
- Lang, J. C. 1973. Interspecific aggression by scleractinian corals. II. Why the race is not only to the swift. *Bulletin of Marine Science* **23**:260-279.
- Lewis, J. R. 1964. *The ecology of rocky shores*. English Universities Press, London, England.
- Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics* **12**:405-437.
- MacArthur, R. H. 1961. Population effects of natural selection. *American Naturalist* **95**:195-199.
- . 1972. *Geographical ecology*. Harper and Row, New York, New York, USA.
- May, R. M., and W. J. Leonard. 1975. Nonlinear aspects of competition between three species. *Society of Industrial and Applied Mathematics (SIAM) Journal of Applied Mathematics* **29**:243-253.
- North, W. J. 1971. The biology of giant kelp beds (*Macrocystis*) in California. *Beihefte 2. Nova Hedwigia* **32**:1-600.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65-75.
- . 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology* **52**:1096-1106.
- . 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berlin)* **15**:93-120.
- . 1977. Controlled manipulations in the marine intertidal zone and their contributions to ecological theory. *Special Publication Academy of Natural Sciences Philadelphia* **12**:245-270.
- . 1979. Disaster, catastrophe and local persistence of the sea palm *Postelsia palmaeformis*. *Science* **205**:685-687.
- . 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**:667-685.
- Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs* **51**:145-178.
- Paine, R. T., and T. H. Suchanek. 1983. Convergence of ecological processes between independently evolved competitive dominants: a tunicate-mussel comparison. *Evolution* **37**:821-831.
- Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnology and Oceanography* **14**:710-719.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* **100**:33-46.
- Quinn, J. F. 1982. Competitive hierarchies in marine benthic communities. *Oecologia (Berlin)* **54**:129-135.
- Rigg, G. B., and R. C. Miller. 1949. Intertidal plant and animal zonation in the vicinity of Neah Bay, Washington. *Proceedings of the California Academy of Science* **26**:323-351.
- Roden, G. I., and G. W. Groves. 1959. Recent oceanographic investigations in the Gulf of California. *Journal of Marine Research* **18**:10-35.
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* **37**:317-350.
- Russ, G. R. 1982. Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. *Oecologia (Berlin)* **53**:12-19.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* **122**:240-285.
- Sebens, K. P. 1982. Competition for space: growth rate, reproduction and escape in size. *American Naturalist* **120**:189-197.
- Simberloff, D. 1982. The status of competition theory in ecology. *Annales Zoologici Fennici* **19**:241-253.
- Steneck, R. S. 1982. Adaptive trends in the ecology and evolution of crustose coralline algae (Rhodophyta, Corallinaceae). Dissertation. Johns Hopkins University, Baltimore, Maryland, USA.
- . 1982. A limpet-coralline alga association: adaptations and defenses between a selective herbivore and its prey. *Ecology* **63**:507-522.
- Steneck, R. S., and W. H. Adey. 1976. The role of environment in control of morphology in *Lithophyllum congestum*, a Caribbean algal ridge builder. *Botanica Marina* **19**:197-215.
- Stephenson, T. A., and A. Stephenson. 1972. *Life between tidemarks on rocky shores*. W. H. Freeman, San Francisco, California, USA.
- Suchanek, T. H. 1979. *The Mytilus californianus* community: studies on the composition, structure, organization, and dynamics of a mussel bed. Dissertation. University of Washington, Seattle, Washington, USA.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. *American Naturalist* **108**:859-873.
- Thomson, R. E. 1981. Oceanography of the British Columbia coast. *Canadian Special Publication of Fisheries and Aquatic Science* **56**:1-291.
- Underwood, A. J., E. J. Denley, and M. J. Moran. 1983. Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia (Berlin)* **56**:202-219.