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# Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality

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## Abstract

Evidence for the geographic generality of the causes of intertidal zonation and the indirect effects of a 'keystone' predator, the sea otter, on subtidal kelp assemblages was examined. Most research on intertidal algal assemblages has been done at a few protected sites where zonation is distinct. Surveys of wave-exposed intertidal sites in central and northern California show that assemblage structure is highly variable. This indicates that our present understanding of assemblage organization, including the effects of mussel-algal interactions, may not be widely applicable. Surveys of kelp forest habitat along the entire coast of California suggest that deforestation by sea urchins is uncommon in the absence of sea otters. These examples indicate that the generality of commonly accepted causes of algal assemblage structure in the Northeast Pacific may be an illusion based on assumptions of environmental homogeneity.

## Introduction

The Northeast Pacific coast covers the large geographic range from near the tip of Baja California, Mexico (23 deg. N, 110 deg. W) to the Aleutian Islands, U.S.A. (53 deg. N, 178 deg. E) and its intertidal and subtidal algal assemblages are among the most diverse and well publicized in the world. The coast has a long history of taxonomic work, natural history description and observation, and ecological experimentation. The composition and geographic distribution of the flora (e.g. Abbott & Hollenberg, 1976; Scagel *et al.*, 1986) have been described, and natural history and ecological information summarized and reviewed (Carefoot, 1977; Littler, 1980; Foster & Schiel, 1985; Ricketts *et al.*, 1985; Dayton, 1985; Harrold & Pearse, 1987; Foster *et al.*, 1988).

I define 'assemblage organization' to be the cause(s) of assemblage structure, and 'assemblage structure' to be the temporal and spatial distribution and abundance of co-occurring populations in an area. In this context, many studies in the Northeast Pacific have become 'classics' as a result of their influence on our ideas about how macroalgal assemblages are organized. The work of Doty (1946) on tide factors, Paine (1974) on sea star-mussel-algal interactions, Dayton (1975a, b) on exposure, grazing and interspecific competition, North & Pearse (1970) on sea urchin grazing, Estes and Palmisano (1974) on sea otter-sea urchin-algal interactions, and Sousa (1979a, b, 1980) on disturbance are a few examples. The results of many studies either directly or indirectly related to the organization of algal assemblages have been generalized to the entire region (Estes & Palmisano, 1974; Paine, 1974; Dayton, 1975b; Duggins, 1980; Leigh *et al.*, 1987).

This apparent wealth of knowledge suggests that we have a good understanding of algal assemblage organization in the Northeast Pacific, and that an overview would be appropriate here. Recent reviews of both assemblage structure in the region and its causes, however, are available (cited above). Rather than reviewing this information again, I will focus on the evidence for generality of the causes of two commonly observed patterns in algal assemblages in the region, intertidal zonation and variation in the abundance of subtidal kelp assemblages.

By generality, I mean over what proportion of the coast in some defined geographic region does a particular organization apply. Other criteria have been used to argue for the generality of causes. Dayton (1984) examined generality of organization in marine systems by using the literature to determine in how many different systems (rocky shores, soft bottoms, etc.) a particular organization had been demonstrated. Others have used the relative number of papers that have shown an organizational process to occur as an indication of its importance or generality (Connell, 1983; Schoener, 1983; Sih *et al.*, 1985). However, understanding patterns in nature, not the published literature, is the goal of ecology. The literature upon which such paper surveys are based may reflect the ecological bias of the original investigators (Underwood & Fairweather, 1986), and the results may not be typical of the systems or geographic areas in which the studies were done. A geographic criterion seems the most realistic way to evaluate how well we understand assemblage organization.

Hurlbert (1984), Underwood & Denley (1984), Underwood (1986a), and Underwood and Fairweather (1986) have suggested that difficulties in understanding assemblage organization arise, in part, because much of the evidence for many of the purported causes of structure in marine benthic assemblages is poor. Methods and experimental designs often fail to evaluate adequately alternative hypotheses for observed patterns. I conclude that even if causes have been unequivocaly identified, inadequate descriptive information and lack of replicated sites often make it impossible to know how generally the results of studies at one or a few sites apply to even a few kilometers of coastline, let alone the Northeast Pacific. As Underwood & Denley (1984) have pointed out, a greater appreciation of the information and approaches necessary to determine the importance and generality of assemblage organization will put our eventual understanding on a more solid scientific foundation.

## Intertidal zonation

### *Organization at sites with distinct zones*

The extant literature on the distribution of algae in the Northeast Pacific intertidal zone suggests that species occupy discrete vertical zones; Doty (1946) described six zones on shores in Oregon and California, and further examples can be found in Ricketts *et al.* (1985) and Foster *et al.* (1988). These patterns, summarized primarily from qualitative observations on shores protected or semi-protected from wave exposure, suggest that such non-overlapping distributions with high within-zone abundances of the characteristic species are the norm for the region. Shorelines with these attributes have been the focus of studies on the causes of zonal boundaries (Doty, 1946; Lebednik, 1973; Hruby, 1976; Hodgson, 1980; Foster, 1982a).

Doty (1946) suggested that zonal boundaries may be entirely set by differences in physiological tolerance along the intertidal exposure gradient. More recent studies (Hruby, 1976; Hodgson, 1980; Foster, 1982a) have generally concluded that lower limits are set by competition with plants below, and upper limits by physiological tolerance. Underwood (1980) has pointed out that many such experiments, especially on upper limits, have failed to consider alternative explanations such as lack of dispersal into higher areas on the shore.

We (Foster & Mair, unpublished) found that only a few isolated plants of *Iridaea flaccida* established a few cm above their normal range on rocks at Point Cabrillo, Monterey [see Foster

(1982) for site description] when limpet and littorine grazers were either removed by hand or excluded with fences. These plants were small relative to those below, and did not reproduce during two years of observation. There was no significant increase in *I. flaccida* in portions of the experimental areas seeded with suspensions of carpospores and tetraspores. Like the data for *Gastroclonium coulteri* at the same site (Hodgson, 1980), these results suggest that physiological stress, rather than settlement or post-settlement biological interactions, is the most important factor limiting the upward expansion of *I. flaccida* at this site. In contrast to Underwood's (1980) findings, grazing effects were relatively minor. Neither study at Point Cabrillo, however, evaluated the alternative of lack of natural spore settlement.

As found in many studies in the region (e.g. Cubit, 1984), a large increase in ephemeral algae, especially *Porphyra* spp., occurred at Point Cabrillo after grazers were removed. In the absence of grazers, the splash zone alga, *Prasiola meridionalis*, also colonized the rocks at Point Cabrillo even though these rocks were 2 m below this alga's natural lower limit. Anderson (1987) used grazer exclusion fences to show convincingly that the lower limit of *P. meridionalis* at this site was determined by grazers.

These examples from one protected site with very discrete zones illustrate the diversity of demonstrated and potential causes of zonal boundaries. The only generalization that emerges is that the species investigated are physiologically capable of growing below their natural lower limits. When other experimental studies from this huge geographic region are included (reviewed in Foster *et al.*, 1988), it is clear that only a few species have been investigated at only a few sites. Thus, even at sites where zonation is clear, it is not apparent which causes are most general.

Sites at more exposed locations can also have distinct zones. Most of our information on such shores comes from Tatoosh Island in Washington (Paine, 1974; Dayton, 1971, 1975a), where *Lessoniopsis littoralis* dominates the low intertidal zone, while mussels and *Postelsia palmaeformis* form a zone more than 2 m above this (Dayton, 1971). Observations and experiments at this and other nearby sites have indicated that the lower boundary is controlled by sea star predation, and that mussels competitively displace other sessile plants and animals within this zone (Paine, 1966; 1974). This organization, centered around the sea star acting as a 'keystone' species, has been suggested as a general phenomenon on the open coast of the Northeast Pacific (Paine, 1966), and has certainly achieved paradigm status in ecology.

### *Are sites with distinct zones and high cover general?*

Most studies of zonation on rocky shores in the Northeastern Pacific have been done near marine laboratories at sites with massive rock shores, relatively even surfaces, gentle slopes, and with sufficient area for experiments (Foster *et al.*, 1988). Similar experiments at sites with varying physical and biological features are rarely done. Instead, if generality is suggested, it is usually based on claims that the site used is typical of a larger area (assuming similar structure represents similar organization, which may not be correct; Dethier & Duggins, 1988). There are, however, no published, quantitative surveys over even localized sections of coasts from which one can determine how general the species composition and zonation patterns are.

In the absence of quantitative information, most rocky shore studies that generalize do so by suggesting their sites are 'typical' based on information in various geographic overviews, particularly editions of *Between Pacific Tides* (latest edition: Ricketts *et al.*, 1985). This is an excellent natural history book, but does not treat variability within major habitat divisions, and does not give any quantitative information on the relative proportions of different types of sites in the Northeast Pacific. Ricketts *et al.* (1985) divided the coast into protected and exposed, and then discussed in a qualitative overview the common animals and a few plants that occur in each. It would be quite remarkable to find a site that was not 'typical' of the Northeast Pacific as it is described in this book.

The second way of suggesting generality is to list other papers with similar conclusions, or which are suggested to provide evidence for assertions of geographic generality. While the former may help verify the assumption that similar structure is caused by similar organization, it says nothing about how typical the particular sites are. Citations for the latter may not cover the region claimed or, if they do, the data are often based on general natural history observations. For example, Leigh *et al.* (1987) state, 'In general, intertidal zones of the Northeastern Pacific are more completely covered by plants and animals the more exposed they are to wave action (Dayton, 1971: Table 1).' The sites in this table did include both protected and exposed, but all were in northern Washington, and covered a latitudinal range of 0 deg., 18 min., roughly 1% of the Northeast Pacific coast.

That our knowledge of the structure and organization of intertidal assemblages may not apply generally is suggested by descriptive surveys associated with an ongoing study of seasonal variation and succession on rocky intertidal benches along the open coast in central and northern California (Foster *et al.*, in progress). In this study, large intertidal benches distributed over the region were required to cover the necessary geographic range and to accommodate unmodified and cleared plots. Sites were selected by flying over the entire coast from Point Conception to the Oregon border (Fig. 1) when the tide was low, and noting all such benches. Twenty sites that spanned the region and were accessible by land were selected

*Table 1.* Mean Percent Cover of Characteristic Sessile Organisms and Bare and Overstoried Rock (see text for definitions) in Six Assemblages at 20 Sites in Central and Northern California. Site locations shown in Figure 1. Means are from 5 transects/site (4 at sites 6, 7, and 8). A 'plus' indicates that the assemblage was present at the site but not encountered on transects. When two taxa were dominant, their abundances were combined. C/B, *Chthamalus* spp./*Balanus glandula*; P/P, *Pelvetia fastigiata*/*Pelvetiopsis limitata*; E/M, *Endocladia muricata*/*Mastocarpus papillatus*; Myt, *Mytilus califorianus*; Iri, *Iridaea flaccida*; N/O, *Neorhodomela larix*/*Odonthalia floccosa*); BR, bare rock; OR, overstoried rock; *s*, standard deviation; *, *n* = 17.

| Site no. | Assemblage | | | | | | Rock | |
|---|---|---|---|---|---|---|---|---|
| | C/B | P/P | E/M | Myt | Iri | N/O | BR | OR |
| 1. | 7 | 0 | 26 | + | 10 | 15 | 6 | 22 |
| 2. | 9 | 2 | 9 | 44 | 1 | 1 | 39 | 5 |
| 3. | 9 | 2 | 12 | 20 | 1 | 4 | 32 | 20 |
| 4. | 9 | 0 | 20 | 0 | <1 | 1 | 72 | 9 |
| 5. | 8 | 5 | 31 | 1 | 3 | 3 | 55 | 10 |
| 6. | 5 | 1 | 19 | 9 | 2 | 15 | 16 | 12 |
| 7. | 10 | 0 | 4 | 7 | 2 | 5 | 40 | 14 |
| 8. | 6 | 3 | 13 | 1 | 2 | 6 | 38 | 22 |
| 9. | 3 | 2 | 11 | 8 | 6 | 0 | 16 | 7 |
| 10. | 2 | 17 | 16 | 1 | 9 | 3 | 43 | 14 |
| 11. | 2 | 1 | 26 | 1 | 15 | 9 | 31 | 5 |
| 12. | 0 | <1 | 30 | + | 17 | <1 | 8 | 13 |
| 13. | 3 | 3 | 32 | 5 | 11 | <1 | 35 | 5 |
| 14. | 1 | 7 | 37 | 0 | 3 | 0 | 38 | 11 |
| 15. | <1 | 2 | 27 | 0 | 19 | <1 | 32 | 9 |
| 16. | 0 | 0 | 19 | + | 6 | 1 | 18 | 13 |
| 17. | 6 | 4 | 22 | 9 | <1 | 5 | 32 | 7 |
| 18. | 1 | 14 | 7 | 2 | 4 | 4 | 18 | 9 |
| 19. | 2 | 3 | 2 | 11 | 0 | 0 | 32 | 14 |
| 20. | 1 | 1 | <1 | 0 | 0 | 4 | 46 | 16 |
| Mean = | 4 | 3 | 18 | *7 | 6 | 4 | 32 | 12 |
| *s* = | 3.4 | 4.5 | 10.6 | 11.0 | 5.9 | 4.5 | 15.9 | 5.2 |

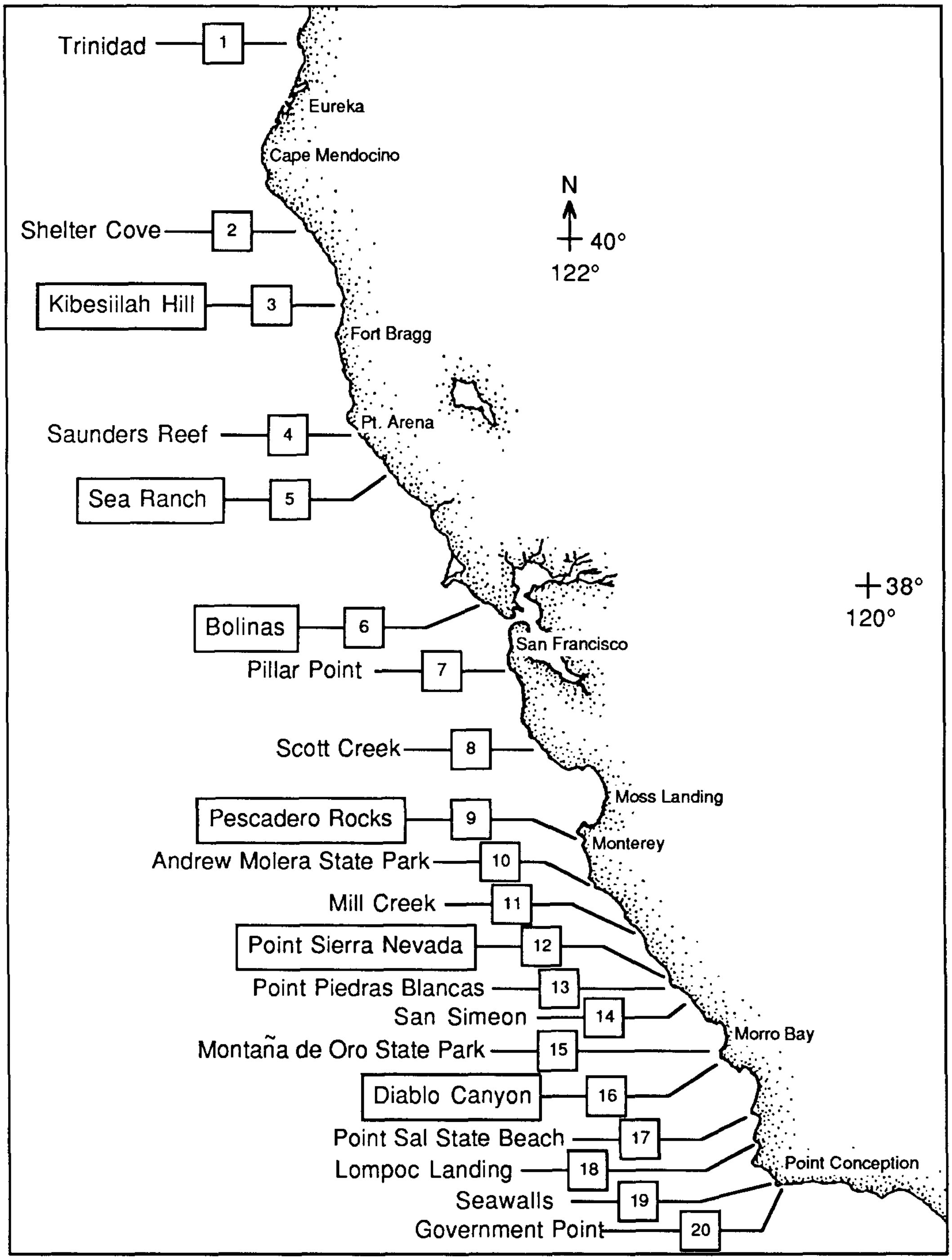

*Fig. 1.* Locations, Names and Site Numbers of Intertidal Sites Surveyed in Northern (Oregon/California Border to San Francisco) and Central (San Francisco to Point Conception) California. Boxes indicate sites where the *Endocladia muricata*/*Mastocarpus papillatus* and *Mytilus californianus* assemblages were sampled with quadrats. Oregon/California border is 100 km north of Trinidad.

for sampling (the larger number in the south reflects both greater accessibility and more benches; Fig. 1).

The abundance and distribution of sessile plants and animals were surveyed at the sites during low tides in March, April, and May, 1984. If the site was very large, we picked a 50-100 m wide (parallel to shore) area that contained the most visually obvious assemblages. Otherwise, the shore baseline equaled the width of the upper part of the bench (generally 20-50 m wide). Five transect lines, running from the upper limit of sessile organisms to the water's edge, were then randomly positioned along the baseline at each site. Species and unoccupied substrata were noted under 100 evenly spaced points (3 mm dia. metal rods) along each line. The spacing between points varied with substratum slope and tidal height at the time of sampling. All species and unoccupied substrata (layering) were recorded under each point. The tidal heights along each transect were determined with a transit and stadia rod, and assuming sea level at the time of sampling was as predicted by tide tables.

Our first objective was to determine the abundance and distribution of the most common assemblages of both plants and sessile animals in the region. Six assemblages were chosen based on a qualitative assessment of species or species pairs [assemblages based on most characteristic (abundant) species] which, after all surveys were done, appeared to be most abundant at most sites. The abundance of these characteristic species was then determined for each site (Table 1). Assemblages below Mean Lower Low Water (e.g. *Phyllospadix* spp.) were not examined because they were infrequently accessible.

These data show that even given our bias in picking the most common assemblages, consistent abundance patterns were not apparent. There was considerable variation in assemblage abundance among sites, including the barnacle (*Chthamalus/Balanus*, 0-10%; Table 1) and mussel (*Mytilus*, 0-44%; Table 1) assemblages commonly suggested as characteristic of the open coast (reviewed in Foster *et al.*, 1988). The standard deviation was similar to or exceeded the mean for all but the *Endocladia/Mastocarpus* assemblage (Table 1). Some assemblages were not detected by the method used at some sites (e.g. *Pelvetia/Pelvetiopsis* at sites 1, 4, 7, and 16; Table 1). Point Conception is the only well established area of biogeographic change in the region (Foster *et al.*, 1988) and, with the exception of the absence of the *Iridaea flaccida* assemblage and the reduction in cover of the *Endocladia/Mastocarpus*

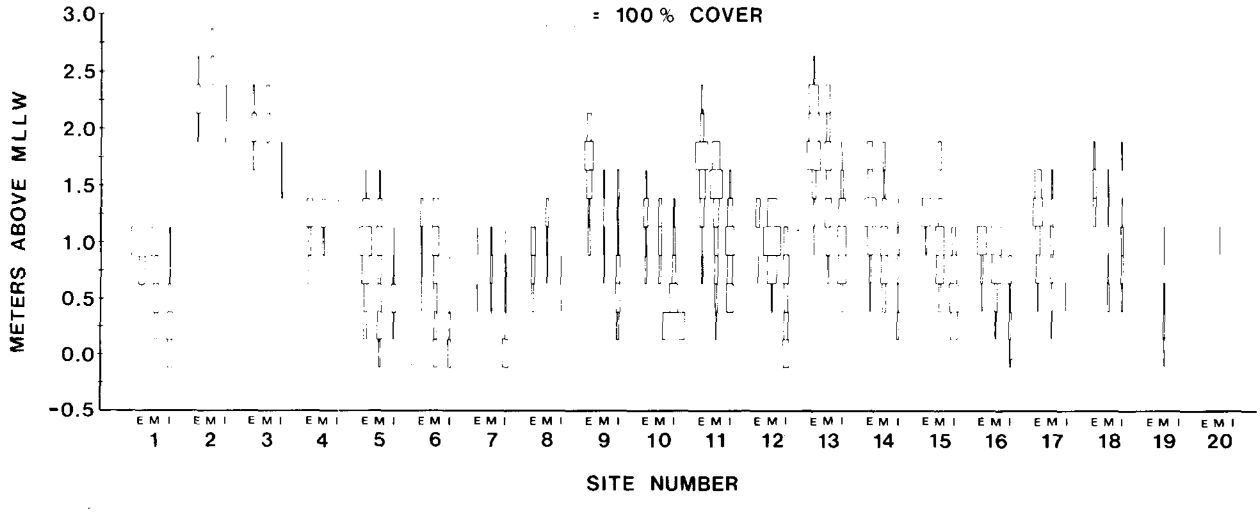

*Fig. 2.* Vertical Distribution and Mean Abundance (% cover) of *Endocladia muricata* (E), *Mastocarpus papillatus* (M), and *Iridaea flaccida* (I) at the 20 Sites in Fig. 1. Abundances are in 0.25 m vertical increments. Data are means of four transects at sites 6,7, and 8, and five transects at the rest of the sites. MLLW, Mean Lower Low Water.

assemblage at Point Conception (sites 19 and 20; Fig. 1, Table 1), there were no clear trends in abundance with latitude.

Space is commonly suggested to be limiting in the intertidal zone because the zone is limited in extent and appears to be dominated by diverse and abundant sessile organisms (Connell, 1972; Paine, 1966, 1974; Carefoot, 1977; Dayton, 1984; Ricketts *et al.*, 1985; Nybakken, 1988; but see Dayton, 1971: Table 1). Thus, the total amount of rock unoccupied by attached organisms was unexpectedly large (mean = 44%) and variable among sites (Table 1). Bare rock (no attached organisms and no overstory) had a mean cover of 32% and overstoried rock (no attached organisms but with an overstory canopy above) a mean of 12%. Unoccupied space did, however, tend to decline with decreasing tidal height, especially in the mussel assemblage (discussed below).

### *Are boundaries and abundance of assemblages constant?*

The distribution and abundance data for *Endocladia muricata*, *Mastocarpus* ( = Gigartina) *papillatus*, and *Iridaea flaccida*, the three most common mid to high intertidal species, also show that there was considerable site to site variation in absolute vertical position, relative vertical position, and abundance (Fig. 2). Variation in absolute vertical position and range was probably related to differences in wave exposure and slope, but these factors have not yet been evaluated.

Prior studies have indicated that *E. muricata* and *M. papillatus* occur in the same high intertidal zone (Doty, 1946; Abbott & Hollenberg, 1976; Ricketts *et al.*, 1985) and Doty (1946) suggested that *M. papillatus* has a slightly broader vertical range than *E. muricata*. These species did have overlapping distributions at all 18 sites where both occurred (Fig. 2), but their relative vertical limits varied from site to site. *E. muricata* occurred higher than *M. papillatus* at five sites, while the reverse occurred at three sites. Their upper limits were identical (within 0.25 m) at ten sites.

Lower limits were less variable, with *Mastocarpus papillatus* usually extending lower than *Endocladia muricata* (12/18 sites). The reverse occurred at 3/18 sites, and the lower limits of these two algae were the same at three sites (Fig. 2).

More surprising was the distribution of *Iridaea flaccida*. Prior studies have indicated that this alga is typical of the mid intertidal region, occurring below *Endocladia muricata* and *Mastocarpus papillatus* (Doty, 1946; Abbott & Hollenberg, 1976; Foster, 1982a). Its center of distribution was below these species at 15 of the sites where all three were found. However, rather than forming a distinct band with an upper limit below that of the algae in the higher zone, the range of *I. flaccida* overlapped those of *E. muricata* and *M. papillatus* at all sites where the species co-occurred. In addition, the cover of *I. flaccida* was often relatively large within the range of these other species (eg. sites 5, 11, 12, 13; Fig. 2). These distributions suggest that, contrary to the results of Hodgson (1980) and Foster (1982a) for *Gastroclonium coulteri* and *I. flaccida* at a protected site, it is unlikely that the lower limits of *E. muricata* and *M. papillatus* are generally set as a result of competition with *I. flaccida*.

### *Are large densities common? Do they imply competitive exclusion?*

Additional sampling at some of these sites raises further questions about generality. Contractual and logistical constraints dictated that only two assemblages, *Endocladia muricata*/*Mastocarpus papillatus* and *Mytilus califorianus* at six of the 20 sites be selected for further study, and that these six be distributed fairly evenly over the region (Fig. 1). Our primary question concerned differences in succession with latitude (only undisturbed plots are discussed below) and resources were not available to examine this question over a range of assemblage densities at the same site. Therefore, we picked two subsites at each site, one with the greatest abundance of the *Endocladia*/*Mastocarpus* assemblage and one with the greatest abundance of the mussel assemblage. Three (1 x 2 m) plots were selected randomly within each subsite, and these have been surveyed twice per year since Spring, 1985. Plots are surveyed by randomly choosing three point quadrats (25 x 25 cm) within each plot, and then surveying 20 random points (as discussed above for transects) within each quadrat. For the analyses below on the data from Spring, 1985, all points (60) in a plot were combined so each sample ($n$) was a single plot and $n = 3$ per site.

Although areas with the greatest cover were selected for sampling, the average cover of *Endocladia muricata* per site ranged from 4-73%, and *Mastocarpus papillatus* from 2-36% (Table 2). It might be expected that these two co-occurring species compete for space, resulting in an inverse relationship in abundance. This may occur at high densities (e.g. sites 1 and 12; Fig. 2), but there was no overall inverse correlation between the abundances of the two species at the 20 sites ($r = 0.08$; $p = 0.75$) or in the plots at the six sites ($r = 0.006$, $p = 0.99$). Total unoccupied substratum (bare plus overstoried rock) was again unexpectedly abundant, ranging from 15% at site 9 to 57% at site 12 (Table 2).

In contrast to the dense and extensive mussel assemblages studied by Paine (1974) at sites at Tatoosh Island (60-90% cover from +2 ft to > +10 ft above MLLW; Dayton, 1971), the percent cover of mussels at our sites on open coast rocky shores was smaller and highly variable, ranging from 0 to 44% (Table 1). Mussel cover in the plots was larger because these were chosen in subsites of large density (Table 2). Even using this criterion, however, very large densities could only be found in patches at three sites (3,5,6; Table 2). As a result of both high mussel and high algal cover, the abundances of bare and overstoried rock in these plots were clearly lower (< 10%) and less variable (with the exception of site 16; Table 2) than in the *Endocladia muricata/Mastocarpus papillatus* assemblage.

Paine (1974) also found that mussels displace other animals and algae, resulting in a reduction in the cover of the displaced species and the overall richness of attached species. In our data from the plots (Table 2), there was no significant correlation between the cover of mussels and either the number of algal species ($r = -0.5$, $p = 0.33$) or the cover of algae ($r = -0.4$, $p = 0.45$). This resulted in part because extensive algal stands

*Table 2.* Percent Cover of Characteristic Species, Bare Rock, and Overstoried Rock (see text for definitions) in the *Endocladia muricata/Mastocarpus papillatus* and *Mytilus californianus* Assemblages at Six Sites. See Figure 1 for site locations; data are mean (standard deviation); $n = 3$.

| | *Endocladia/Mastocarpus* Assemblage Site | | | | | |
|---|---|---|---|---|---|---|
| | 3 | 5 | 6 | 9 | 12 | 16 |
| *E. muricata* | 49(12) | 50(22) | 4(6) | 73(9) | 23(17) | 48(7) |
| *M. papillatus* | 4(3) | 13(7) | 36(14) | 34(15) | 2(2) | 23(3) |
| Bare Rock | 11(5) | 6(3) | 12(6) | 2(3) | 13(4) | 17(11) |
| Overstoried Rock | 39(10) | 25(7) | 18(9) | 13(7) | 44(11) | 16(7) |
| | *Mytilus* Assemblage | | | | | |
| | 3 | 5 | 6 | 9 | 12 | 16 |
| *M. californianus* | 93(5) | 86(3) | 90(7) | 27(7) | 66(7) | 42(13) |
| Bare Rock | 3(3) | 6(5) | 4(5) | 8(7) | 1(1) | 38(9) |
| Overstoried Rock | 0 | 2(3) | 2(3) | 6(3) | 4(4) | 4(3) |
| Total Algal Cover (1) | 8(5) | 19(5) | 40(11) | 49(17) | 52(36) | 18(13) |
| No. Algal Species (2) | 2.0<br>(1.1) | 3.3<br>(1.2) | 3.2<br>(0.8) | 5.7<br>(1.4) | 6.5<br>(3.1) | 2.8<br>(1.3) |

1. Total cover of algae in plots; 2. Number of algal species, not cover.

occurred attached to mussel shells at some sites (especially 6 and 12; Table 2; see also Dayton, 1975; Suchanek, 1979; Sousa, 1984). An analogous association can occur between the alga, *Iridaea flaccida*, and the barnacle, *Tetraclita rubescens* (Foster, 1982a). When such layering occurs, it may be that the total species richness of sessile species is increased rather than decreased as at Paine's (1974) site. In any case, these data indicate that both mussel abundance and the competitive effects of mussels on algae vary among sites along the open coast, and that the suggested 'cardinal interaction' structuring this assemblage at selected locations in Washington (Paine, 1974) may not be generally cardinal.

The variable nature of exposed rocky shores in central and northern California was recognized by Doty (1946). He mentioned that rough shores and boulder fields can have 'anomalous intermixtures' of species, and zones that vary in presence/absence, relative abundance, and relative position. He also noted that up to ten distinct zones can be found under other conditions, and that gaps between zones at some locations suggest a lack of competition. Zonation research, however, has focused on shores with distinct patterns. The surveys reported here indicate that such patterns may not be common.

Are these benches typical of rocky shores in central and northern California? Qualitative observations from the aerial surveys indicate that the most common types of open coast rocky shores are irregular rocky outcrops and boulder fields (Hardin *et al.*, in prep.), habitats that are rarely studied (e.g. Seapy & Littler, 1978; Sousa, 1979a, b; 1980). Thus, generalities concerning the structure and organization of algal assemblages on the benches may not be general for rocky shores in the region.

### *Algal abundance in subtidal kelp assemblages*

The nearshore subtidal zone in the Northeast Pacific is noted for its diversity of kelps, and especially for its extensive subtidal stands of those kelps that form surface canopies. Various species of the latter occupy particular portions of this large geographic range (Druehl, 1970), and the associated understory can be rich and abundant (reviewed in Foster & Schiel, 1985). However, there are very few studies that have quantitatively assessed the abundance of kelps and associated species along the complete depth gradient over which they can occur. Furthermore, I am aware of only one published account of variation over this gradient with time (Neushul, 1967), and none over even a small geographic range (Schiel & Foster, 1986). Numerous qualitative observations have been made, especially in California, and these are summarized in Foster & Schiel (1985). I know of only two field experiments that have examined the causes of subtidal zonation in the region: Pearse & Hines (1979) on the effects of sea urchin grazing at one site, and Kastendiek (1982) on competitive interactions at another.

Research in these forests has concentrated on the causes of within assemblage structure. For a variety of reasons discussed by Foster & Schiel (1988) for the Northeast Pacific and Harrold & Pearse (1987) worldwide, much of this research has focused on the effects of the hierarchical interaction between predators on sea urchins, sea urchins, and the abundance of kelp assemblages. In the Northeast Pacific, the emphasis has been on a particular predator, the sea otter. This interaction has been generalized as 'extremely' or 'most' important in organizing kelp assemblages in this region (Estes & Palmisano, 1974; Dayton, 1975b; Duggins, 1980), and appears to have achieved the status of a paradigm (Estes & Harrold, 1988; Levin, 1988). As such, it has been incorporated into the popular literature, ecology texts, ecological reviews (e.g. Kitching, 1986), and management decisions (reviewed in Foster & Schiel, 1988).

Is this interaction as general as suggested in the literature cited above? We (Foster & Schiel, 1988) recently tabulated all known subtidal surveys of the abundances of sea urchins and benthic macroalgae at sites in California outside the present range of the sea otter. This analysis revealed that, contrary to the predictions of the paradigm, less than 10% (19/224 sites) contained large abundances of sea urchins and were deforested over large areas ('urchin-dominated barrens'). Less than 20% were either entirely deforested or composed of large (20-50 m dia.) deforested patches among similar sized patches of kelp and associated algal species. These data strongly suggest this hierarchical interaction is not 'most' important in California and, as shown by Laur *et al.* (1988), the effects of the interaction likely vary with the physical characteristics of particular sites. The effects also probably vary with other site characteristics such as sea urchin recruitment (Ebert & Russell, 1988), kelp recruitment (Harrold & Reed, 1985), and disease (Pearse & Hines, 1979). While numerous factors have been identified, the multi-factor, multi-site studies necessary to determine their relative contributions to kelp forest dynamics have not been done. Our data also suggest that until unbiased site descriptions and appropriate experiments are available for the rest of the Northeast Pacific, the question of generality for areas outside of California remains unanswered.

It has been suggested that other predators may have functionally replaced sea otters in southern California (Dayton, 1984), thus preserving the keystone paradigm but changing the predator(s). As this suggestion was based on correlative evidence from three sites within one kelp forest (Tegner & Dayton, 1981), one hopes that it will remain a suggestion until better evidence is available.

### *From heterogeneity to generality*

The difficulties with rigorously answering questions about the organization of algal populations, assemblages, or communities in a system that exhibits considerable small scale variation seem to be of two types. The first is that of structuring the research so it adequately tests hypotheses about the causes of distribution and abundance at the location(s) where the research is done. This type of difficulty has been discussed by Dayton & Oliver (1980), Underwood & Denley (1984), and Underwood (1986a, b). Underwood (1981), Hurlbert (1984), and Welden & Slauson (1986) provide information on appropriate experimental designs and analyses of results. The latter also discuss the distinction between intensity and importance, possible statistical techniques for determining importance, and the effects this lack of distinction has had on current debates about the importance of competition (see also Schiel, this vol.).

The second difficulty is determining how generally the results of a study apply geographically. The results and review above indicate that multi-site surveys can reveal considerable heterogeneity in the structure of assemblages. This suggests that some current and widely acknowledged claims of generality for assemblage organization based on studies at one or a few sites are unfounded. Field ecologists in particular are often caught in the dilemma of wanting to determine the generality of particular processes but not having the financial and logistical resources to do so in a rigorous manner. Field experiments at a particular site are not a way out of this dilemma; while they can provide better tests of hypotheses than descriptive-correlative studies or 'natural' experiments (Connell, 1974), their results are not necessarily more broadly applicable.

A more rigorous way out is to be able to compare the structure of research sites (samples) with that of unbiased estimates of the general structure of sites in the region of interest (population). This is certainly not a new idea; Choat & Schiel (1982) discussed this approach and their study is an excellent example of its utility in examining the generality and range of organization in subtidal kelp assemblages. Andrew & Mapstone (1987) and Underwood and Kennelly (this vol.) also pointed out the importance of adequate sampling to the interpretation of experimental results, and the former reviewed sampling in marine ecology. Ultimately, the most complete generalities will be obtained when experimental sites span the range of site variability identified in the region of interest. The results of such efforts should give an indication of the conditions (e.g. exposure, irradiance, recruitment) under which particular processes (e.g. wave disturbance, grazing) have the greatest effects.

In the absence of such information, the current level of understanding could enhanced with better physical and biological descriptions of research sites. This would improve our ability to compare sites and, as suggested by Underwood (1986b), our understanding of the causes of possible differences in organization. Foster & Schiel (1988) point out that differences in the composition and dynamics of algal assemblages in *Macrocystis pyrifera* forests at different sites are correlated with differences in the physical characteristics of the sites. They suggest that this physical continuum might be stratified into a finite number of site 'types' to facilitate the identification, comparison, and understanding of differences in organization. Work in the Monterey Bay region indicates that there are a few such types generally present, and that each has a similar assemblage structure (Foster, 1982b; VanBlaricom & Foster, in prep.).

Continuing to create illusions of generality based on assumptions of homogeneity will perpetuate many of the problems that presently plague ecology. McIntosh (1987) argued that disagreements over approaches and philosophies have made community ecology appear to lack predictive ability and other characteristics of the 'hard' sciences. However, the lack of rigor concerning standards of evidence in hypothesis testing and generalization seems an even more important contributor to these problems. In the absence of good evidence for them, statements about spatial scales over which some organization applies lend misleading significance to results, especially to those unfamiliar with the area. The consequence is often controversy when information from additional sites is found to differ. 'Important' processes or factors may then become 'unimportant', waiting to be 'rediscovered' with the next experiment at the next site. The progress of the science is muddled, and other processes are depreciated. The cycle spreads to other fields such as paleontology (see discussion in Järvinen, 1986) and especially evolution, where adaptive 'strategies', morphologies, and chemistries rise and fall with the tide of ecological generalities [e.g. Estes & Steinberg (1988) on sea otters, sea urchins, and the evolution of kelp; Steneck (1983) on herbivory and the evolution of nongeniculate corallines].

We should cease making claims for generality in the introductions and discussions of papers without adequate data to support them. Such claims add apparent credibility to our results and, as noted in the case of sea otters above, can have significant theoretical and applied ramifications. Generality should be removed from the realm of allowed speculation and, like other results, be evaluated with higher standards of evidence.

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