



International Association for Ecology

Experimental Studies of Herbivory and Algal Competition in a Low Intertidal Habitat

Author(s): David O. Duggins and Megan N. Dethier

Source: *Oecologia*, Vol. 67, No. 2 (1985), pp. 183-191

Published by: Springer in cooperation with International Association for Ecology

Stable URL: <http://www.jstor.org/stable/4217711>

Accessed: 24/01/2010 18:23

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=springer>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Springer and International Association for Ecology are collaborating with JSTOR to digitize, preserve and extend access to *Oecologia*.

<http://www.jstor.org>

Experimental studies of herbivory and algal competition in a low intertidal habitat

David O. Duggins and Megan N. Dethier

Friday Harbor Labs, University of Washington, Friday Harbor, WA 98250, USA

Summary. Ecological factors regulating the species composition and abundance of the plant assemblage in the low intertidal zone were studied in the semiprotected San Juan Islands in Washington state. In particular, the roles of an abundant herbivore (the chiton *Katharina tunicata*) and competition among plants were evaluated experimentally. Densities of *Katharina* were manipulated in large areas to establish 3 treatments: *Katharina* removals ($N=2$), controls ($N=2$), and *Katharina* addition ($N=1$). These sites were monitored for 4 years. Over this time, algal abundance and diversity increased in the *Katharina*-removal areas; algae in most functional groups proliferated, and a multi-storied intertidal kelp bed eventually developed. In the *Katharina*-addition, the abundance of all plants except crusts, diatoms, and surfgrass decreased, and overall diversity declined. Control sites underwent year-to-year fluctuation in the abundance of the most conspicuous alga, *Hedophyllum sessile*, but remained otherwise unchanged.

At the end of the third year, the dominant space occupiers (the large brown algae) were removed from half of each of the *Katharina* removal and control areas. These kelps positively affect abundances of *Katharina* but are negatively correlated with limpet numbers. In the absence of competition from the kelps, the abundance and diversity of most other algal groups increased. This change was especially dramatic in the areas lacking both chitons and kelps, indicating that herbivory and competition have negative, additive effects on smaller algae. However, even in the absence of *Katharina*, abiotic disturbance (desiccation and storms) apparently mediates the competitive dominance of the kelps.

Plant assemblages in marine intertidal systems are controlled by grazing, physical disturbance, competition, physiological stress, and unpredictable recruitment events (e.g., Paine and Vadas 1969, Dayton 1975, Sousa 1979, Lubchenco 1980, Underwood and Jernakoff 1981, Jara and Moreno 1984, Dethier 1984). This study examines the roles of such ecological factors in the low intertidal zone of the northeastern Pacific. While these shorelines are among the most thoroughly studied ecological communities, their lowest levels have received little attention (due in large part to the logistic difficulties of working in an area so rarely emersed). The low zone is characterized by high algal diver-

sity and productivity and contains organisms found in association from northern California to the northern Gulf of Alaska. One of the most conspicuous elements in the assemblage is the chiton *Katharina tunicata*. While the role of temperate latitude intertidal grazers is well studied (reviewed by Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983), most research has concerned limpets and littorinid snails – very little is known about the ecological role of chitons. This paper presents the results of a set of nested experiments designed to examine 1) the interplay between *Katharina* and other members of the community (plants and other herbivores), and 2) the nature of competition within the benthic algal assemblage. We also discuss the mitigating effects of physical factors on the above biological interactions.

The study site and organisms

This study was conducted at Pile Point, on the wave-exposed side of San Juan Island (48° 29' N, 123° 05' W), in the northwest corner of Washington state. The habitat occupied by the chiton *Katharina tunicata* ranges from about 0.5 m above to 1.0 m below mean lower low water (MLLW). This zone is exposed only on the lowest tides, but because of the timing of low tides in the San Juans, it experiences considerable seasonal heating and freezing extremes.

The most prominent alga in the study site is a perennial intertidal kelp (O. Laminariales), *Hedophyllum sessile*. This alga has numerous stipeless, leathery blades up to 30 cm long, and is most abundant in lower areas (Table 1). *Hedophyllum* undergoes seasonal and year-to-year variation in abundance (see Results, and Dayton 1975, Paine 1980, 1984). Other macroalgae in this zone include articulated and encrusting coralline algae, a variety of filamentous and foliose red and green algae, and several species of fleshy crusts (Table 1). None of these algae is very abundant, with the exception of the crusts, which occupy much of the substratum. All are patchy in distribution (note the high variances in Table 1). The surfgrass *Phyllospadix scouleri* is found at the lower edge of this zone and in tidepools.

Sessile animals are rare at this site, except for the colonial polychaete *Dodecaceria fewkesi* (Table 1), which is most abundant in damp areas. Encrusting bryozoans, sponges, hydroids, ascidians, and spirorbid worms are found in low areas, but never exceed 5% cover. Barnacles (primarily *Semibalanus cariosus*) are found seasonally in the upper part of the study zone, but are generally consumed

Table 1. Abundances of the most conspicuous organisms in the study area, 20 upper (0 to +0.5 m above MLLW) quadrats and 22 lower (0 to -0.5 m) quadrats were censused at the beginning of the experiment, on May 12, 1979. Mean percent cover for bare space and for organisms found in >2% mean abundance (canopy for erect algae, cover on the rock for encrusting organisms), or number per 0.1 m² are given, with one s.d. *Hedophyllum* cover was unusually low in this year; in other years, canopy cover ranged up to a mean of 62% in the upper quadrats and 84% in the lower ones (see Fig. 2). "Other erect algae" consist primarily of *Callithamnion pikeanum*, *Gigartina* spp., *Spongomorpha* spp., and *Ulva* spp. Encrusting corallines are largely *Pseudolithophyllum whidbeyensi* and *Lithophyllum impressum*. Non-coralline crusts are primarily "Petrocelis middendorffii", *Ralfsia pacifica*, and *Hildenbrandia* spp. See text for other specific names

	Upper	Lower
<i>Hedophyllum</i> (canopy)	11.6 (18.3)	21.4 (17.6)
<i>Corallina vancouveriensis</i> (canopy)	5.1 (5.4)	5.0 (3.7)
<i>Bossiella plumosa</i> (canopy)	2.4 (2.7)	4.5 (3.8)
<i>Polysiphonia</i> spp. (canopy)	7.2 (13.9)	0.7 (1.4)
<i>Microcladia borealis</i> (canopy)	2.4 (5.4)	0.2 (0.6)
Other erect algae (canopy)	2.9 (4.0)	3.0 (7.6)
Encrusting corallines	10.2 (9.7)	20.2 (18.0)
Non-coralline crusts	34.9 (25.7)	26.0 (23.0)
Bare (or with thin diatoms)	38.2 (21.9)	37.2 (21.2)
<i>Dodecaceria fewkesi</i>	2.6 (5.9)	5.2 (6.4)
<i>Katharina tunicata</i>	4.4 (3.8)	8.4 (8.2)
Limpets (see text)	27.8 (23.6)	8.5 (7.8)
<i>Tonicella lineata</i>	0.9 (1.7)	3.3 (2.1)
<i>Acmaea mitra</i>	0.8 (1.4)	1.2 (1.2)

while small by *Nucella* (= *Thais*) spp. The other predator commonly encountered in this zone is *Leptasterias hexactis*. *Pisaster ochraceus* were rare in the study areas.

Herbivorous molluscs are the most conspicuous animals in the low intertidal zone. Most numerous are 3 species of acmaeid limpets: *Notacmea scutum*, *Collisella pelta*, and *C. strigatella*. These 3 species are hereafter referred to simply as "limpets". Their diets in this area are very similar, consisting primarily of microalgae (diatoms, bluegreens, and sporelings: Nicotri 1974, 1977). The encrusting coralline specialists (see Steneck and Watling 1982) *Acmaea mitra* (limpet) and *Tonicella lineata* (chiton) are present irregularly and in low numbers (Table 1). Other herbivores (*Cryptochiton stelleri*, *Mopalia* spp., *Cyanoplax dentiens*, and *Diodora aspera*) are rare and transient. The urchin *Strongylocentrotus droebachiensis* was seen occasionally at the lower edge of the zone.

Katharina tunicata is the most prominent herbivore, ranging up to 100/m² and reaching 12 cm in length. Populations show a marked size segregation with tidal height: mean chiton length in the upper half of its range = 4.8 ± 1.7 cm ($N=130$), in the lower half = 5.8 ± 1.3 cm ($N=120$) (t -test, $p < 0.001$). Juveniles less than 2 cm long are rarely found below MLLW, perhaps because predators (especially starfish) are more abundant in lower zones; on several occasions we have found *Leptasterias hexactis* eating small *Katharina* (see also Menge 1972).

Katharina in this region are generalist feeders, consuming benthic diatoms, articulated corallines, other macroalgae, and even small sessile animals (Dethier and Duggins, 1984). In their rather non-specific rasping of the substratum

they undoubtedly also eat spores and sporelings of macroalgae. We rarely have found *Katharina* eating full-size *Hedophyllum* blades; their main effect on algal population dynamics seems likely to be through the consumption of juvenile forms.

Observations of unmanipulated low-intertidal areas suggested to us that microhabitat use varied somewhat between *Katharina* and limpets: *Katharina* appeared to congregate (at low tide) under *Hedophyllum*, while limpets (excluding *Acmaea mitra*) were found in the barer areas between these patchy plants. Counts made in June 1981 in 10 haphazard quadrats (0.1 m²) containing *Hedophyllum* and 10 more at the same height lacking *Hedophyllum* corroborated these observations: *Katharina* were much more abundant in the quadrats with *Hedophyllum* than without it (7.2 vs. 2.0 chitons, U test, $P < 0.001$), and limpets showed the opposite pattern (0.5 vs. 14.3 limpets, $P < 0.001$). Two other herbivores were found more abundantly with *Hedophyllum*; *Tonicella* (2.0 vs. 0.5, $P < 0.01$) and *Acmaea mitra* (1.2 vs. 0.0, $P < 0.01$).

Methods

To determine the community role that *Katharina* plays in this region, we manipulated population densities of the chiton in intertidal areas, then monitored changes in the algal and herbivore assemblages over the next 4 years. All *Katharina* were removed from 2 promontories, each about 25 m² in area, and were added to a third site. At the start of the experiment (May 12–13, 1979), approximately 1000 *Katharina* were removed from one site and 1900 from the other (actual densities were not significantly different). After this, any immigrant or newly-settled chitons were removed every 4–5 months and added to the addition area. Since *Katharina* move slowly, these manipulations remained effective without the use of cages. In this way, densities remained at about 8% of original in the removals and 160–200% in the addition. Permanent quadrats were established near the center of the removal areas so that immigrants from the sides would have the least effect.

Algal and herbivore abundances were monitored in 8–10 permanent 0.1 m² quadrats in each of the 3 manipulations and in 2 nearby control areas. At each site there were 4 upper quadrats (0 to +0.5 m) and 4 lower (0 to -0.5 m), except in the larger removal area, where there were 6 lower quadrats. Since the assemblages in the upper and lower areas tended to differ (Table 1), most analyses were performed by comparing organisms in the 8 upper control quadrats with the 8 upper removals or the 4 upper additions, and likewise with the lower quadrats. By analyzing the data in such a manner, we are technically committing "pseudoreplication" (Hurlbert 1984). Pooling quadrats from the different sites and treating them as replicates requires that they be independent of each other; the statistical validity of this is questionable, and thus our tests using such data are interpreted with caution. However, our knowledge of this system suggests that the sites chosen were similar, and that chance events (nondemonic intrusions: Hurlbert 1984) are likely to impinge on quadrats independently rather than on a site-to-site basis; thus we do not feel that such pooling is unwarranted. Ideally, at least 3 sites should have been used for each treatment, but severe logistical constraints of working in this zone prevented this.

Algal abundance was quantified in two ways: as the

percent of the substratum occupied by crusts, diatoms, and the basal portion of erect species (primary space cover), and as the percent of the quadrat covered at low tide by the undisturbed canopy of erect forms (canopy cover). A quadrat covered with several layers of different algal species could thus have >100% canopy cover. All percent covers were visually estimated (see Dethier 1984), and these data were arcsine transformed for calculations of standard deviations. Since all sampling was non-destructive, algae often could be identified only to genus. Crusts were identified only as fleshy or coralline. Herbivores were counted in each quadrat and, when time allowed, were measured to the closest cm. Algal assemblages in the removals and controls were not significantly different at the beginning of the experiment (Table 2).

Experiments were begun on May 26, 1982 to examine the effects of the large, canopy-forming brown algae on the other plants and animals in this zone. All large browns (including kelps and *Desmarestia* spp.) were removed from half of each of the *Katharina* removal and control areas, leaving other algae as undisturbed as possible. Movements of herbivores into and out of these areas were closely monitored over the next 3 months in the permanent quadrats plus in additional, haphazardly located ones. Kelps were removed again in 8/82, 12/82, and 1/83.

The removal of large brown algae during the above experiment allowed us to compare kelp biomasses between *Katharina* removals and controls. On 5/26/82, all the brown algae in eight 0.25 m² areas (4 upper and 4 lower) were cut just above their holdfasts in each of the removal and control sites. The algae were brought to the laboratory, sorted by species, blotted, and weighed.

Algal diversity was analyzed in two ways: 1) Algal Richness – the number of species (or taxa, for the groups where species could not be identified in the field); 2) Diversity of all species with erect thalli – those for which we gathered percent cover (“canopy”) data. We used percent cover data in the absence of data on number of individuals, a figure that is meaningless for many of these plants. For each quadrat, we calculated a Shannon-Wiener index using the proportions of the total erect algal cover present on one date that were contributed by each erect species (or taxon). We thus could not include taxa such as diatoms and crustose algae, but did include both under- and over-story erect macroalgae.

Results

Katharina removals

The removal of *Katharina* had rapid and dramatic effects on the algal assemblages. Following an initial diatom bloom, there appeared a wide variety of macroalgae that had been absent or rare at the beginning of the experiment. The abundances of these algae are graphed in Figs. 1 and 2, where they are grouped by general growth form. We used algal functional groups similar to those described by Littler and Littler (1980) and Steneck and Watling (1982). These groups provide a useful way to look at ecological patterns in algae; species within groups show similarities in productivity, susceptibility to herbivores, successional status, and longevity. We have divided the common macroalgae seen in this zone into 4 groups, based on overall form, size, and apparent toughness; genera included in each

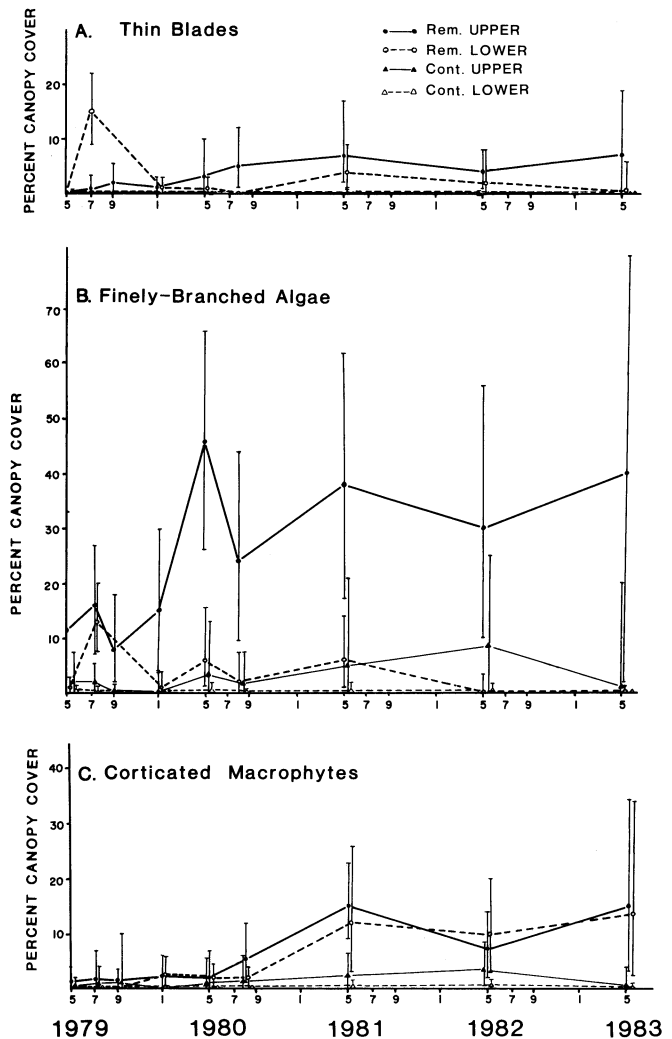


Fig. 1A–C. Canopy cover of three algal functional groups in the *Katharina*-removal areas and controls. Mean and 95% confidence limits are given ($N=8$ upper and 10 lower quadrats in the removals, 8 upper and 8 lower in the controls). Percent cover data were arcsine-transformed for calculation of confidence limits, then back-transformed for illustration. **A** “Thin blades” include ulvoids, *Porphyra* spp., *Petalonia fasciata*, and *Scytosiphon lomentaria*; **B** “Finely branched algae” includes *Polysiphonia* spp., *Callithamnion pikeanum*, *Spongomorpha* spp., and *Microcladia borealis*. **C** “Corticated macrophytes” include *Gigartina* spp., *Fucus* spp., *Rhodomela larix*, *Odonthalia* spp., *Botryoglossum* sp., *Plocamium* sp., *Iridaea* spp., and a variety of unidentified red blades

group are listed in the figure captions. Significant differences for each algal group between the removal and control areas are listed in Table 2.

“Thin blades”, including such forms as *Ulva* and *Porphyra*, appeared in many of the *Katharina*-removal quadrats within a month; they grew rapidly, especially in the lower quadrats (Fig. 1A), reaching a maximum of 40% canopy cover in one quadrat in July. After this they declined in importance, and remained abundant only in patches for the next 4 years. No more than 5% cover of this group was ever seen in any control quadrat (Fig. 1A and Table 2).

“Finely-branched algae” include simple filaments and a few more complex forms (e.g. *Microcladia*) that are small in cross-section and generally delicate. This group was present, especially in upper quadrats, at the start of the experi-

Table 2. Summary of changes in algal assemblages following the removal of *Katharina*. Significant differences are given for each date (May of each year) in percent cover (for algal groups), algal richness (number of taxa), and erect algal diversity (H') between the 8–10 removal quadrats and 8 control quadrats. — = no difference, * = $P < 0.05$, ** = $P < 0.01$, Mann-Whitney U tests. “Large brown algae” do not include *Hedophyllum*

	Differences between removals and controls				
	1979	1980	1981	1982	1983
<i>Upper quadrats</i>					
Thin blades	—	**	**	**	*
Finely-branched algae	—	**	**	($P = 0.052$)	*
Corticated macrophytes	—	—	**	—	*
<i>Hedophyllum</i>	—	—	—	—	—
Large brown algae	—	*	*	—	—
Algal richness	—	**	**	**	*
Erect algal diversity	—	**	*	*	*
<i>Lower quadrats</i>					
Thin blades	—	—	**	—	—
Finely-branched algae	—	*	*	—	—
Corticated macrophytes	—	**	**	**	**
<i>Hedophyllum</i>	—	*	*	—	—
Large brown algae	—	*	**	**	—
Algal richness	—	*	**	**	*
Erect algal diversity	—	*	**	**	—

ment (Fig. 1B), but became much more abundant in the second year in the removal areas and remained prominent (although patchy) thereafter. Lower quadrats contained much less of this growth form, especially in the *Katharina*-controls (Fig. 1B, Table 2).

“Corticated macrophytes” are larger, tougher, structurally more complex algae such as *Gigartina* and *Iridaea*. These appeared relatively late in the experimental areas, growing slowly and becoming abundant only 2 years post-removal (Fig. 1C, Table 2). Both upper and lower removal quadrats then retained moderate cover of these forms. As with the other algal groups, abundance remained low in the control quadrats.

The most dramatic change following the removal of *Katharina* was the increase of large brown algae (Table 2, Fig. 2). In the upper zone, chiton removals had no effect on *Hedophyllum* (Table 2). However, other large browns (primarily *Alaria* sp. and other kelps, but also *Desmarestia* spp.) became significantly more abundant in the upper removal areas than in the upper controls in 2 of the 4 years that the experiment ran.

In the lower zone, *Hedophyllum* increased in the first year in both the removal and control areas (Fig. 2A, 2B). 1979, the beginning of the experiment, was apparently a very bad year for *Hedophyllum* (Fig. 2A). However, the increase was much greater in the chiton removal areas, so that abundances were significantly higher there than in the controls in 1980 and 1981. Other large browns, in addition to *Hedophyllum*, colonized the chiton removal areas in 1981 (Fig. 2C), turning the low intertidal assemblages into flourishing kelp beds. The abundances of all large brown species pooled were significantly greater in the chiton removals than in the controls in 1980, 1981, and 1982 (U tests, P 's < 0.001).

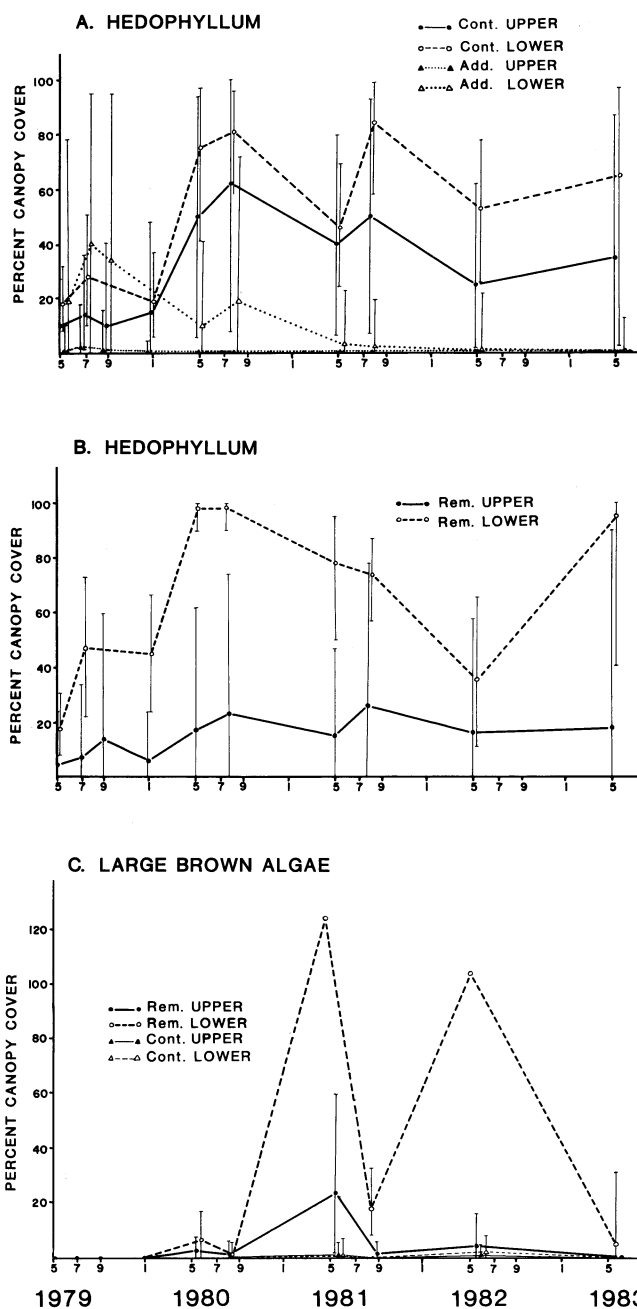


Fig. 2A–C. Canopy cover of large brown algae in the *Katharina* treatments. Data analyzed as in Fig. 1. **A** *Hedophyllum sessile* abundance in the *Katharina* controls and addition area; **B** *Hedophyllum sessile* in *Katharina* removal quadrats; **C** Canopy cover of other large brown algae; this group includes *Alaria marginata*, *Laminaria groenlandica*, *Nereocystis luetkeana*, *Costaria costata*, *Cymathere triplicata*, and *Desmarestia ligulata* and *D. viridis*. Layered canopies created 100% cover on 5/81 and 5/82; these data are thus untransformed (s.d. for 5/81 = 63%, for 5/82 = 29%)

Temporal variation in the abundances of large brown algae occurred both seasonally and from year to year, independently of herbivore abundance. Figure 2C shows that while the removal of one herbivore species allowed the upward extension of some subtidal kelps, these were generally unable to survive summertime physical stresses in this zone. When noontime low tides coincided with hot, calm days in May and June, the kelps and *Desmarestia* were seen

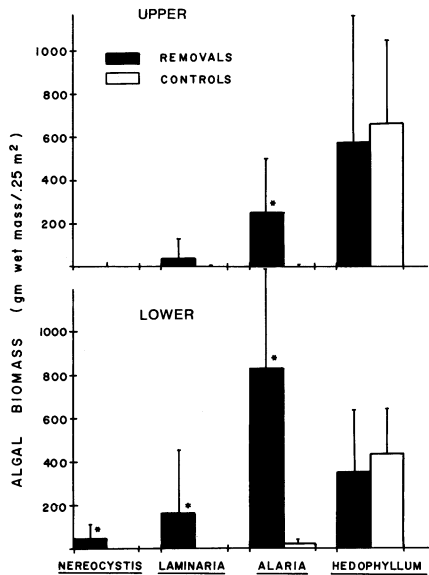


Fig. 3. Biomasses (blotted wet mass) of kelps from *Katharina* removals and controls, collected 5/26/82. Each bar represents mean (gm per 0.25 m²) of 8 samples, and one s.d. is shown. Small quantities of *Cymathere* and *Desmarestia* spp. were also found in the low Removal samples, but are not shown. * = significantly greater biomass in the Removals than in the Controls, Mann-Whitney *U* test, *P*'s < 0.01

bleaching and dying. By August, few of these plants were left. *Hedophyllum* occasionally had bleached or desiccated edges, but generally increased in cover during this warm, light period.

Figure 2A illustrates the seasonal nature of *Hedophyllum* abundance; plants grow rapidly in the spring and reach peak cover in late summer, then decline sharply over the winter, presumably due to storm damage. Each winter, the blades in our chiton removal and control areas were reduced to tattered straps only 10–20 cm long, and some adult plants disappeared. Thus the canopy cover of *Hedophyllum* dropped abruptly, exposing substantial amounts of bare space. While quantitative winter sampling was done only in Jan. 1980 (Fig. 2A), qualitative observations during the next 3 winters revealed similar, battered plants, and the reduced percent cover each spring reflected these losses.

Year to year variation in brown algal abundance is evident in the data in Figure 2. As mentioned, *Hedophyllum* was sparse in 1979 relative to other years. 1983 was a very poor year for the other large browns (Fig. 2C) which in previous years had flourished in the *Katharina* removal areas. A likely explanation for this absence is the unusually warm El Niño conditions of spring 1983. Raised air and water temperatures would be expected to affect the more-subtidal kelps to a greater degree than the *Hedophyllum*.

Large differences in brown algal biomass (on 5/26/82) resulted from the removal of *Katharina* (Fig. 3). *Alaria*, *Laminaria* and *Nereocystis* had greater biomasses in the removals than in the controls, especially in low quadrats. *Hedophyllum* biomass and percent cover, however, were not significantly greater in either the upper or lower quadrats on this date, probably due to suppression of growth by the other, abundant kelps. Total wet weight of all browns was significantly greater in the lower removals than the lower controls (*U* test, *P* < 0.001), but the upper treatments did not differ. Biomasses of other algal groups were not

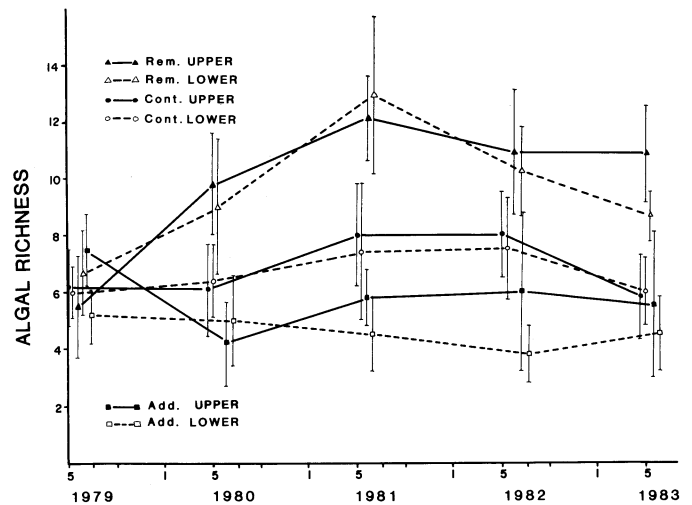


Fig. 4. Algal richness (mean number of taxa and 1 s.d.) in each of the *Katharina* treatments. Encrusting corallines and fleshy algal crusts were each counted as one taxon. Diatoms were excluded. The surfgrass *Phyllospadix* (although not an alga) was included

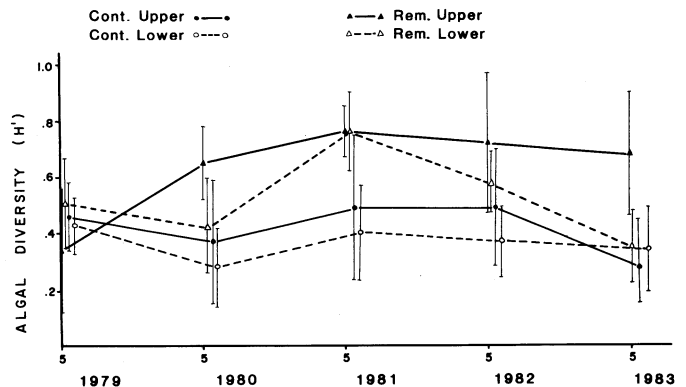


Fig. 5. Erect algal diversity in the *Katharina* removals and controls. For *Katharina* addition area, see Table 3. Calculation of diversity index is described in Methods

measured, but judging from differences in percent cover (Figs. 1 and 2), it is clear that the entire algal assemblage had a much higher biomass in the *Katharina*-removal areas than in the controls.

Encrusting coralline algae showed no discernable changes through time; their abundances fell and rose as the holdfasts of other algae covered them and disappeared. Articulated corallines also showed no clear differences among treatments. Fleshy algal crusts could not be sampled reliably without removing the microalgae and other transient organisms that covered them.

The diversity of the algal assemblage in the low intertidal zone was strongly affected by manipulations of *Katharina* (Figs. 4 and 5). At the beginning of the experiment, there were no significant differences in algal richness between any of the sites (*U* tests, *P*'s > 0.05). At every subsequent sampling period, however, richness was greater in the *Katharina*-removal quadrats than in the control quadrats at the same level (Table 2). A similar pattern is seen in the diversity of erect algae; diversity rose following the removal of chitons and remained high for 3 years (Table 2) (see below for a discussion of 1983 data).

Changes in the abundance of mobile and sessile animals

Table 3. Changes in algal assemblages in the *Katharina* addition area. For percent cover data, means and 1 s.d. were calculated on transformed data, then back-transformed to tabulate. No *Phyllospadix* was present in the upper quadrats. * = $P < 0.05$, ** = $P < 0.01$, U-tests comparing addition quadrats ($N = 4$) with controls ($N = 8$)

	5/79	5/80	5/81	5/82	5/83
<i>Upper quadrats</i>					
Thin blades	0.4 (0.5)	0.7 (1.1)	0.4 (0.5)	1.0 (1.4)	0.1 (0.3)
Finely-branched	6.5 (3.6)	0.1 (0.5)	0.8 (3.4)	3.1 (4.9)	8.6 (14.9)
Corticated macrophytes	0.6 (0.8)	0	0.1 (0.3)	1.0 (1.4)	0.1 (0.3)
<i>Hedophyllum</i>	0.6 (2.6)	0*	0*	0*	0*
Algal richness	7.5 (1.3)	4.2 (1.5)	5.8 (1.0)*	6.0 (2.8)	5.5 (2.6)
Diversity	0.57 (0.12)	0.14 (0.21)	0.35 (0.17)	0.41 (0.30)	0.22 (0.27)
<i>Lower quadrats</i>					
Thin blades	0.1 (0.3)	0.1 (0.3)	0.1 (0.3)	0	0
Finely-branched	0.1 (0.3)	0	0	0	0
Corticated macrophytes	0	0	0.1 (0.3)	0	0
<i>Hedophyllum</i>	18.8 (15.1)	10.2 (5.8)**	2.7 (4.3)**	1.3 (5.3)**	0.8 (3.1)**
<i>Phyllospadix</i>	1.3 (3.0)	4.4 (7.8)*	4.8 (11.5)	5.5 (11.9)	8.7 (13.0)
Algal richness	5.2 (1.0)	5.0 (1.6)	4.5 (1.3)**	3.8 (1.0)**	4.5 (1.3)
Diversity	0.27 (0.12)*	0.24 (0.19)	0.19 (0.14)*	0.08 (0.13)*	0.20 (0.20)

following the removal of *Katharina* followed no clear patterns, with the exception of the disappearance of limpets (Dethier and Duggins, 1984). Trends for other herbivores and for sessile animals were obscured by their low densities and high patchiness (Table 1). Much of the substratum in the *Katharina*-removals became covered by macroalgal holdfasts or decumbant branches of genera such as *Polysiphonia*; these may have inhibited the settlement or growth of sessile animals, but such interactions were not examined in detail.

Katharina addition

Changes in the algal assemblage in the *Katharina*-addition area generally were in the opposite direction from those in the removal areas, as expected. Densities of *Katharina* remained significantly higher than normal throughout the experiment, with means (May data) ranging from 6.2–9.8/0.1 m² versus 3.4–5.2 in the controls. Thin blades, finely-branched algae, and corticated macrophytes remained rare and patchy (Table 3), as in the control areas, and were found primarily in the highest quadrats (at the upper edge of *Katharina*'s range). *Hedophyllum* abundance dropped significantly relative to the controls (Table 3). Most quadrats contained no *Hedophyllum* at all after the first year, and no other large browns appeared.

Only two plant taxa thrived under the intense grazing pressure exerted by the chitons. The surfgrass *Phyllospadix*, an angiosperm, increased in the two low quadrats where it was present (from 3 to 15% and 15 to 50% cover); it may be unpalatable or indigestible for *Katharina*. Benthic diatoms were also abundant. Though eaten by the chitons, their productivity and turnover rates are so high that they survived, and seemed to even benefit from the absence of shading and sweeping by macroalgae (Dethier and Duggins 1984).

Algal richness dropped in the addition area, especially in the lower quadrats where grazing is most intense (Table 3 and Fig. 4). Erect algal diversity in the upper quadrats was similar to that in the controls, but the lower quadrats were significantly less diverse (Table 3). These differences disappeared in 1983, when diversity and richness in the control

areas were low (Figs. 4 and 5). Thus algal richness was generally highest in the chiton removal areas and lowest in the chiton addition, with the control areas at intermediate levels.

Kelp removals

Effects on algae. As with most other intertidal manipulations, the first result of removing the large brown algae was an influx of diatoms. Over the next year, there were substantial increases in other macroalgae (Table 4), suggesting that all had been negatively affected by shading or whip-lash from these larger forms. Similar responses to kelp removals have been seen by Dayton (1975), Hawkins (1979), Duggins (1980), and others. The responses of all three functional groups considered were greatest in the areas also lacking *Katharina*; the halves of the areas where we removed the kelp became covered by dense canopies of other algae that were sparse and patchy in unmanipulated areas (Table 4). Thus the abundance of these smaller algae rose substantially in the areas lacking both *Katharina* and kelp, attained intermediate levels with either chitons or kelp removed, and remained virtually absent in areas influenced by both factors (Table 4).

Algal richness and erect algal diversity showed significant increases following the removal of all large brown algae (Table 4). In the treatments with both chitons and kelp (the "normal" condition), both the grazers and the competitors suppressed the development of most algae. Removal of either the chitons or the kelps led to increases in diversity and richness over control levels (Table 4). In the sites where both herbivores and superior algal competitors were removed, diversity and richness were highest, at least over the short term (one year). Additive effects, observable on release from grazers and competitors, have also been demonstrated by Sousa et al. (1981) and Lubchenco (1982).

Effects on herbivores. The responses of herbivores to kelp removal were measured in June and August 1982 (2 and 11 weeks post-removal) and in May 1983 (1 year post-removal). Within 2 weeks of kelp removal, *Katharina* emigrated from or died in the kelp removals; densities became

Table 4. Algal canopy cover and algal richness and diversity in kelp-removal experiments in May 1983, one year after kelp removal. Percent covers and one s.d. (untransformed data) are given for each algal group. Differences between the 4 treatments are analyzed using Kruskal-Wallis multiple comparisons. A line drawn under 2 or more treatments indicates no significant difference ($P > 0.05$); otherwise all differences are below the $P = 0.025$ level. Kath/kelp represents areas in *Katharina* controls where kelps were undisturbed, Kath/no kelp where kelp was removed, etc. For the algal groups, $N = 8$ quadrats for each mean (upper and lower pooled). For the diversity and richness data, an additional 12 quadrats were haphazardly thrown in each treatment (thus $N = 20$)

	Kath/kelp	Kath/no kelp	No Kath/kelp	No Kath/No kelp
Thin blades	0.1 (0.2)	1.0 (1.4)	5.0 (5.4)	15.6 (10.7)
Finely-branched algae	2.2 (6.4)	4.1 (3.6)	21.2 (29.3)	37.5 (27.4)
Corticated macrophytes	0.5 (1.4)	6.2 (17.3)	15.4 (11.5)	31.9 (18.3)
Diversity	0.30 (0.12)	0.48 (0.13)	0.51 (0.24)	0.72 (0.19)
Richness	3.4 (0.8)	4.0 (1.4)	7.0 (2.6)	8.2 (1.9)

Table 5. Herbivore densities in the kelp-removal experiment (*Katharina* control areas), at the beginning and at three time periods following kelp removal (5/26/82). Densities (mean number (1 s.d.) per 0.1 m²) are compared between the kelp removals and adjacent controls using t tests ($N = 20$ quadrats, 5/23/82 and 6/10/82; $N = 40$, 8/17/82, $N = 20$, 5/83). * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Limpets were not sampled in 6/82

	5/23/82 (before)	6/10/82		8/17/82		5/31/83	
		with kelp	without kelp	with kelp	without kelp	with kelp	without kelp
<i>Katharina</i>	3.5 (1.9)	6.4 (3.2)***	1.9 (1.6)	4.9 (3.4)**	3.1 (2.3)	5.0 (3.5)**	2.2 (2.4)
Limpets (all)	18.1 (13.0)	—	—	21.4 (18.2)***	8.8 (4.4)	22.4 (17.7)**	43.8 (30.6)
< 1 cm	15.1 (12.6)	—	—	14.4 (14.0)***	4.6 (3.6)	16.6 (16.9)*	33.2 (27.7)
1–2 cm	1.9 (1.7)	—	—	5.3 (4.7)***	2.9 (1.9)	4.1 (3.3)**	8.4 (5.7)
> 2 cm	1.1 (1.6)	—	—	1.7 (1.8)	1.4 (1.3)	1.8 (1.9)	2.3 (1.8)

significantly lower than those in adjacent areas with kelp (Table 5). This effect persisted through August (Table 5). Dayton (1975) also found that *Katharina* numbers drop when kelp is removed. Limpets were not sampled in June but in August they, too, were less dense in the areas without kelps; both small and medium-sized limpets (Table 5) were affected. Several series of hot, dry, low tides occurred between May and August of 1982; the decline in herbivores may have been due to migrations into less stressful areas (e.g., under *Hedophyllum* elsewhere) or mortality from physical extremes or visual predators in the unprotected sites.

One year later, *Katharina* were still significantly more abundant in the presence than in the absence of kelps (Table 5). The limpets, however, showed the opposite pattern from the chitons and from their own distribution in 8/82; they were significantly more abundant in the areas without kelp (Table 5). Examination of the densities of different size classes shows that there was a large influx of small (< 1 cm) limpets. Observations made in the previous January indicated that hundreds of 1–3 mm long limpets had recruited into the areas without kelp. It is unknown whether these patterns were caused by preferential settlement into the diatom-rich kelp removals, or high mortality of recruits in the areas with kelp. Lewis and Bowman (1975) found that limpets have difficulty recruiting under an algal canopy. By May of 1983, a variety of macroalgae had colonized the kelp-removals. Limpet densities were low in areas with substantial macroalgal cover; there was a significant negative correlation between the density of limpets in a quadrat and the total canopy cover there ($N = 40$, $r = 0.38$, $P < 0.01$). Thus while the chitons are associated with macroalgae, the limpets avoid these areas – either because of the low diatom availability there, and/or because there is simply less space

where they can forage. Limpets in a *Laminaria*-removal experiment in Britain were similarly displaced by invading macroalgae (Hawkins and Hartnoll 1983).

Densities of two other herbivores, *Tonicella* and *Acmaea mitra*, remained too low in both kelp treatments to distinguish a response to kelp removals.

Discussion

In this paper we have described a community where one species of herbivore has wide-ranging effects. The herbivore exerts a strong influence over: 1) abundance; 2) species richness and diversity; 3) zonation; and 4) intensity of competition among plants. In a separate paper (Dethier and Duggins 1984), we also show that it affects the remainder of the herbivore guild, in that the chitons' removal caused the limpets to vanish. This herbivore plays a pivotal role even though other grazers are normally present in the system. Its importance, however, depends on the interactions of itself and of its prey species with the physical environment.

Katharina's important role in the low intertidal zone appears to stem from its size, density, and ability to eat a wide range of foods. The three species of limpets present are much more numerous but considerably smaller than the chitons, and their diets in this region consist primarily of microalgae (Nicotri 1977). In addition, limpet densities are suppressed by predators (Nicotri 1977), further reducing their ability to affect algal assemblages. The importance of crustacean herbivores such as amphipods and isopods is unknown, but is probably limited by their very low biomass. *Katharina*, however, are large and abundant and have radulae that enable them to eat a broad range of prey (Sten-

eck and Watling 1982). Thus their effect on algae is not restricted to the consumption of microscopic forms, as it largely is for the limpets. Similar large, generalist herbivores can control community development in the subtidal zone, as has been shown for urchins in temperate areas (e.g., Himmelman et al. 1983) and urchins and fishes in tropical areas (e.g., Hay 1984).

A number of algae do manage to coexist with the grazer assemblage in the low intertidal. These plants exhibit 3 different strategies: 1) attainment of an escape in size from their consumers. *Hedophyllum*, although susceptible when small, is seldom grazed at its full size (Dayton 1975, Paine 1980, Gaines 1985). 2) Tolerance of intensive herbivory gained through either a crustose growth form (Dethier 1981, Steneck 1982, Lubchenco et al. 1984, Paine 1984), calcification of erect portions (Padilla 1984), or other structural or chemical attributes (e.g., as seems to exist in the surfgrass). 3) Attainment of temporary escapes in space – the “fugitive” strategy – as seen in the fast-growing and short-lived diatoms, thin blades, and finely-branched algae. This strategy is successful because *Katharina* are slow-moving and patchy in distribution (cf. Lubchenco et al. 1984). Under normal grazer densities (e.g., Table 1), the low intertidal assemblage is a mosaic of algae using these 3 strategies. Such algal groups are characteristic of environments with high biotic disturbance (sensu Grime 1977; e.g., Littler and Littler 1984).

However, seldom can one plant's strategy be effective against all the environmental conditions it will encounter. *Hedophyllum*'s large size did not protect it from physical disturbances; every winter, much plant tissue was lost during storms, opening up space in the low zone and preventing this species from forming a monopoly. The loss of *Hedophyllum* from the chiton addition area probably resulted from such winter attrition of adults combined with lack of replacement due to grazing on sporelings. Thus this potential dominant is kept down by biotic disturbance (consumption) upon sporelings and abiotic disturbance upon adults.

The other large brown algae (primarily *Alaria*) that invaded the *Katharina* removal areas probably also can reach a size escape from the chitons. On the exposed coast, these browns appear to be better competitors than *Hedophyllum* (Dayton 1975, Paine 1984). However, the stressful summertime conditions in the San Juan Islands kill these kelps (Fig. 2), leaving *Hedophyllum* as the “dominant” alga. Thus, as noted by Paine (1984) and Dethier (1984), the canopy species in an area may simply be those most resistant to local disturbance, not necessarily the best competitors.

Assessment of the degree of competition among algae is confounded by behavioral aspects of the interaction between *Katharina* and the large brown algae. Kelp removals in the absence of chitons clearly showed that the browns suppressed the growth of smaller algal forms (Table 4). Under normal chiton densities, however, do the large browns have a similar effect? Kelp removals in areas with *Katharina* caused many of the chitons to emigrate; thus we cannot be certain whether the increase in algal abundance and diversity in these treatments resulted from decreased competition or decreased grazing pressure, or both (see also Dayton 1975). The interaction between the chiton and *Hedophyllum* is an interesting one, in that the chiton eats the young plants but relies on old plants (which have



Fig. 6. A One of the *Katharina* removal areas in May 1979, at the beginning of the experiment. Note the patchy *Hedophyllum* and the preponderance of bare space. B The same area in May 1980. The abundant algae this year were *Hedophyllum* and the finely-branched *Polysiphonia* spp

escaped consumption) for refuges from predation or physical stress.

The abundance of *Hedophyllum* varied substantially among the years of the study (Fig. 2A). In years when it was sparse (e.g. 1979), bare space was abundant (Table 1), and competition is unlikely to have been important in determining algal distributions and abundance. There was no evidence that *Katharina* dropped in abundance in response to sparse *Hedophyllum* populations. Observations suggest that they simply distribute themselves under available cover, except in drastic circumstances like our kelp removal, when many emigrated. In years when *Hedophyllum* is abundant, however, competition among algae for space and/or light may well occur. Our data are not detailed enough to document the relative importance of competition in different years due to the complex interaction between *Hedophyllum* and *Katharina*.

In other intertidal habitats, competition among algae is most likely to be important in low zones, where the physical environment is relatively benign and potential productivity high. The herbivores present are frequently unable to control algal growth, especially where they themselves are predator-limited (reviews in Branch 1981; Hawkins and Hartnoll 1983; for an exception see Lubchenco et al. 1984). This does not appear to be the case in the San Juans, although we do not know what limits *Katharina* populations (see Dethier and Duggins 1984). Higher in the intertidal zone, where physical stresses are greater but biomasses of herbivores are still often high, competition among algae would be predicted to be less important.

In summary, we have shown that the removal of *Katharina*, even in the presence of limpets and a variety of other grazers, released a wide variety of algae from grazing pressure and initiated the development of a new assemblage (Fig. 6). Morphologically simple, highly productive algal groups responded quickly (Fig. 1A–C), while more complex forms, including kelps usually found subtidally, appeared later. Removals of the kelps showed that they were suppressing the growth of smaller forms beneath them. A similar succession and onset of algal competition following urchin removal is discussed by Himmelman et al. (1983). But our grazer-removal experiments also disclosed the role of abiotic disturbance in this community; even in the absence of grazing, the plant assemblage is kept patchy and in an apparent non-equilibrium state by physical disturbances that remove the competitive forms.

Acknowledgments. We would like to thank the small army of friends who helped us pick chitons, especially Bob and Antonia Creese. The manuscript benefited greatly from comments by D Harvell, S Palumbi, RR Strathmann, RT Paine, and J Watanabe. Funding was provided in part by a National Science Foundation Graduate Fellowship (to MND), NSF grants to RT Paine and to Steneck and Dethier (OCE 80-25578), and a Friday Harbor Labs Postdoctoral Fellowship (to MND). Access to the field site was generously provided by Mr Lee Harvey. We gratefully acknowledge the space, facilities, and positive atmosphere at the Friday Harbor Laboratories provided by Dr. AOD Willows, Director.

References

- Branch GM (1981) The biology of limpets: physical factors, energy flow, and ecological interactions. *Oceanogr Mar Biol Ann Rev* 19:235–380
- Dayton PK (1975) Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol Monogr* 45:137–159
- Dethier MN (1981) Heteromorphic algal life histories: the seasonal pattern and response to herbivory of the brown crust, *Ralfsia californica*. *Oecologia* (Berlin) 49:333–339
- Dethier MN (1984) Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. *Ecol Monogr* 54:99–118
- Dethier MN, Duggins DO (1984) An “indirect commensalism” between marine herbivores and the importance of competitive hierarchies. *Amer Natur* 124:205–219
- Duggins DO (1980) Kelp beds and sea otters: an experimental approach. *Ecology* 61:447–453
- Gaines SD (1985) Herbivory and between-habitat diversity: the differential effectiveness of defenses in a marine plant. *Ecology* 66:473–485
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Amer Natur* 111:1169–1194
- Hawkins SJ (1979) Field studies on Manx rocky shore communities. PhD Thesis, University of Liverpool
- Hawkins SJ, Hartnoll RG (1983) Grazing of intertidal benthic algae by marine invertebrates. *Oceanogr Mar Biol Ann Rev* 21:195–282
- Hay ME (1984) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* 65:446–454
- Himmelman JH, Cardinal A, Bourget E (1983) Community development following removal of urchins, *Strongylocentrotus droebachiensis*, from the rocky subtidal zone of the St. Lawrence Estuary, Eastern Canada. *Oecologia* (Berlin) 59:27–39
- Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54:187–211
- Jara HF, Moreno CA (1984) Herbivory and structure in a midlittoral rocky community: a case in southern Chile. *Ecology* 65:28–38
- Lewis JR, Bowman RS (1975) Local habitat-induced variations in the population dynamics of *Patella vulgata* L. *J Exp Mar Biol Ecol* 17:165–203
- Littler MM, Littler DS (1980) The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Amer Natur* 116:25–44
- Lubchenco J (1980) Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology* 61:333–344
- Lubchenco J (1982) Effects of grazers and algal competitors on fucoid colonization in tide pools. *J Phycol* 18:544–550
- Lubchenco J, Gaines SD (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Ann Rev Ecol Syst* 12:405–437
- Lubchenco J, Menge BA, Garrity SD, Lubchenco PJ, Ashkenas LR, Gaines SD, Emlet R, Lucas J, Strauss S (1984) Structure, persistence, and role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). *J Exp Mar Biol Ecol* 78:23–73
- Menge BA (1972) Competition for food between two intertidal starfish and its effect on body size and feeding. *Ecology* 53:635–644
- Nicotri ME (1974) Resource partitioning, grazing activities, and influence on the microflora by intertidal limpets. PhD Thesis, University of Washington
- Nicotri ME (1977) Grazing effects of four marine intertidal herbivores on the microflora. *Ecology* 58:1020–1032
- Padilla DK (1984) The importance of form: differences in competitive ability, resistance to consumers, and environmental stress in an assemblage of coralline algae. *J Exp Mar Biol Ecol* 79:105–128
- Paine RT (1980) The third Tansley lecture. Food webs: linkage, interaction strength and community infrastructure. *J Anim Ecol* 49:667–685
- Paine RT (1984) Ecological determinism in the competition for space. The first MacArthur lecture. *Ecology* 65:1339–1348
- Paine RT, Vadas RL (1969) The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnol Oceanogr* 14:710–719
- Sousa WP (1979) Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol Monogr* 49:227–254
- Sousa WP, Schroeter SC, Gaines SD (1981) Latitudinal variation in intertidal community structure: the influence of grazing and vegetative propagation. *Oecologia* (Berlin) 48:297–307
- Steneck RS (1982) A limpet-coralline alga association: adaptations and defenses between a selective herbivore and its prey. *Ecology* 63:507–522
- Steneck RS, Watling L (1982) Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Mar Biol* 68:299–319
- Underwood AJ, Jernakoff P (1981) Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal community. *Oecologia* (Berlin) 48:221–233

Received October 29, 1984