

A functional group approach to the structure of algal-dominated communities

Robert S. Steneck and Megan N. Dethier

Steneck, R. S. and Dethier, M. N. 1994. A functional group approach to the structure of algal-dominated communities. – *Oikos* 69: 476–498.

We suggest that relatively few species attributes are of overriding importance to the structure of benthic marine algal communities and that these are often shared among taxonomically distant species. Data from the western North Atlantic, eastern North Pacific and Caribbean suggest that patterns in algal biomass, diversity and dominance are strikingly convergent when examined at a functional group level relative to the productivity and herbivore-induced disturbance potentials of the environment. We present a simple graphical model that provides a way to predict algal community composition based on these two environmental axes. This predictability stems from algal functional groups having characteristic rates of mass-specific productivity, thallus longevity and canopy height that cause them to “behave” in similar ways. Further, herbivore-induced disturbances have functionally similar impacts on most morphologically and anatomically similar algae regardless of their taxonomic or geographic affinities. Strategies identified for marine algae parallel those of a terrestrial scheme with the addition of disturbance-tolerant plants that characteristically coexist with and even thrive under high levels of disturbance. Algal-dominated communities, when examined at the functional group level, appear to be much more temporally stable and predictable than when examined at the species level.

R. S. Steneck, *Dept of Oceanography and Center for Marine Studies, Darling Marine Center, Univ. of Maine, Walpole, ME 04573, USA.* – M. N. Dethier, *Inst. for Environmental Studies and Friday Harbor Laboratories, Univ. of Washington, Friday Harbor, WA 98250, USA.*

Natural communities should be described in terms simple enough to be understood and detailed enough to convey useful information about their structure and functional components. There exists a broad spectrum of ways to describe patterns. At one end of this spectrum, species are the fundamental unit of measure. Because many factors contribute to the distribution and abundance of a given species, it is often impossible to predict its behavior consistently. At the other end of the spectrum are functional groups which categorize species according to features such as body plan, behavior or life history strategy. In this paper, we argue that analyzing community patterns for marine algae via groupings based on functional aspects of their morphology and anatomy provides sub-

stantial insight into community structure. A functional group analysis can be applied more broadly in space for making biogeographical comparisons, and in time for reconstructing paleocommunities, than is possible at the level of species or among related higher taxa.

Over the past three decades most community ecologists, following the lead of Hutchinson and MacArthur, stressed the *uniqueness* of species. That no two species can occupy the same ecological niche has been a driving axiom stimulating interest in a variety of topics including competition, niche compression, character displacement, resource partitioning and species diversification. However, many of these concepts have been questioned and recently criticized (e.g., see Sale 1977, Peters 1991, Bond

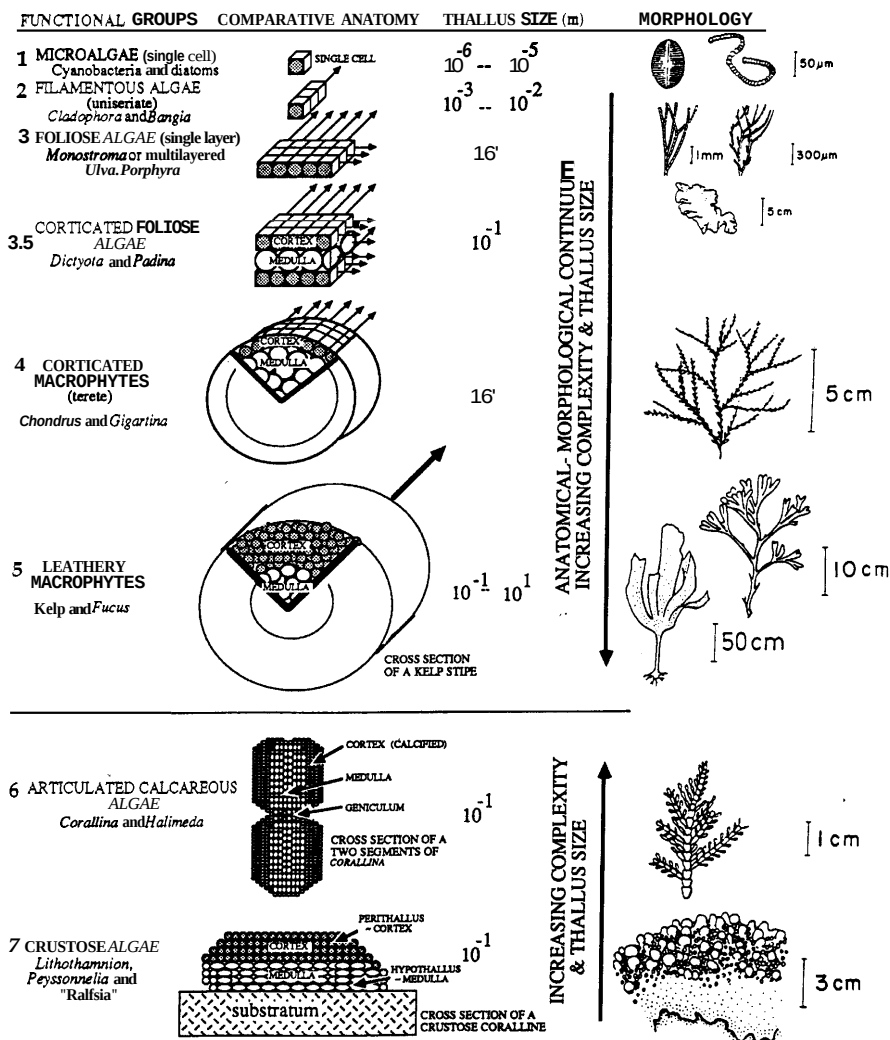
Accepted 17 September 1993

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ISSN 0030-1299

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Fig. 1. Diagrammatic representation of algal functional groups. Anatomical components are not drawn to scale, but illustrate tissue differentiation such as between the cortex and medullary regions of the thallus of a macroalga. The specific form of each functional group illustrated is indicated in parentheses. A few representative genera are given as examples for each group. Numbers at left, algal group ("AG") numbers, are for quick reference (rankings are described in Results). Note that groups of a given morphology with increased anatomical complexity (e.g., they are corticated) are designated by higher AG numbers. Thus, thinly corticated or polysiphonous filaments become AG 2.5 and similarly corticated foliose forms become AG 3.5.



et al. 1992). A functional group approach, in contrast, stresses similarities among unrelated species that share critical organismal features. We discuss the overriding importance of a small number of species attributes to the structure of benthic marine algal communities, and note that these attributes may be shared polyphyletically.

The functional group approach, although having received little attention among community ecologists, may have been foreseen by MacArthur (1972) when he predicted that "the future principles of the ecology of coexistence will... be of the form 'for **organisms of type A** in environment of structure B, such and such relationship will hold'" (boldface ours). We will consider the types of marine algae that live under specific marine environments (defined below). We offer data and examples in support of this approach as an alternative to other means of studying communities, rather than as a strict test of our hypothesis. Our objective is to examine patterns of algal functional group abundance, diversity and dominance

relative to extrinsic characteristics of their environment. To demonstrate the broad applicability of the functional group approach, we examined three biogeographically distinct regions: the western North Atlantic, the eastern North Pacific, and the Caribbean as exemplified by sites in Maine, Washington and St. Croix (U.S. Virgin Islands), respectively.

Definition of terms and rationale

We explore the hypothesis that observed patterns in the distribution and abundance of life forms of algae (functional groups) result largely from two environmental parameters: 1) productivity potential (factors that contribute to the maximum possible rate of biomass production) and 2) disturbance potential (factors responsible for the maximum possible rate of biomass lost). It is important to note

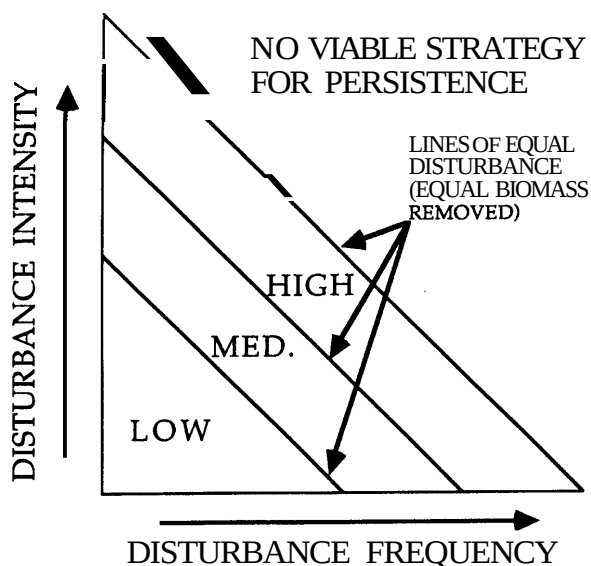


Fig. 2. The relationship between disturbance intensity and frequency. LOW, MED. and HIGH refer to disturbance levels.

that the productivity and disturbance potentials of the environment are theoretically independent of resident plant assemblages and thus may not directly reflect the observed level of productivity or disturbance in the system. Independence of structuring environmental components from organisms comprising the community is essential (e.g., Van der Steen and Scholten 1985, Southwood 1988) and thus we will carefully detail the intrinsic and extrinsic components of the community and their environment below. At this point we will develop this idea exclusively for herbivore-induced disturbances, although most aspects apply equally well to abiotic disturbances.

Functional groupings of algae are based on anatomical and morphological characteristics (Steneck and Watling 1982, Steneck 1988, Fig. 1) that often correspond to ecological characteristics (identified below). Thus they differ from guilds (sensu Root 1973), which are based strictly on similarities in resource utilization. We consider an algal-dominated community as an assemblage of functional groups, with the abundance of each group measured by its somatic biomass. Biomass is maintained by a dynamic balance between the rates of constructive forces of recruitment and net primary or biomass production and the destructive force of disturbance. The measurable result of these processes depends on both intrinsic properties of the organisms and extrinsic properties of the environment. This relationship can be expressed in biomass units for any given area as:

$$B_i = R_i + P_n - D_i, \text{ where}$$

B_i = Biomass of an algal species or functional group (i) that accumulates over some period of time. i = the

specific algal functional group(s) concerned i.e., 1–7 (see Fig. 1). The numeric designation in Fig. 1 is based on the ranking of mass-specific productivity (see Results).

R_i = Rate of recruitment, which is a function of

- 1) Intrinsic properties of the algal species or functional group (i) such as the number and viability of propagules.
- 2) Extrinsic properties of the environment or the recruitment potential of the environment (such as availability of free space for germination).

P_n = Rate of net primary productivity, which is a function of

- 1) Intrinsic properties of the algal species or functional group (i) or the “Mass-specific rate of production”.
- 2) Extrinsic properties of the environment or the “Productivity potential of the environment”.

D_i = Rate of herbivore-induced disturbance, which, assuming no refuge, is a function of:

- 1) Intrinsic properties of the algal species or functional group (i), which involves:
Resistance to disturbance (e.g., due to mechanical properties such as toughness and morphology), and deterrence of disturbance (e.g., chemistry of prey species affecting herbivore choice).
- 2) Extrinsic properties of the environment which we refer to as the: “Disturbance potential of the environment”. This can be measured as:
Rate of disturbance (e.g., from herbivores), involving:
Disturbance intensity (amount of biomass lost per event).
Disturbance frequency (events per unit time).

We define the “productivity potential of an environment” as being determined by the extrinsic factors that set an upper limit to the net primary productivity possible in that environment. A reduction in productivity potential of the environment by this definition equals an increase in stress (sensu Grime 1981). In the marine realm, factors influencing the productivity potential include light, nutrients, desiccation, freezing, and water motion (which controls both nutrient and gas exchange; e.g., Blinks 1955, Leigh et al. 1987). Thus the productivity potential on hard substrata decreases in a logarithmic fashion from maximum levels in the lower intertidal and shallow subtidal zone toward minimal levels in the upper reaches of the intertidal zone and the lower limits of the photic zone. Evidence for these gradients have been published from a variety of locations (Nicotri 1977, Raffaelli 1979, Round 1981, Keser and Larson 1984, Underwood 1984a, b, Hardwick-Witman 1985, Bosman et al. 1986, illustrated in Hawkins and Hartnoll 1983, Steneck et al. 1991).

Grime (1981: 39) defines disturbance to be “the mechanisms which limit plant biomass by causing its partial or total destruction”. Disturbance has two components: frequency and intensity (Reichle et al. 1975, Steneck 1988, Steneck et al. 1991). High levels of disturbance result

from conditions ranging from high frequency, low intensity disturbances to low frequency, high intensity disturbances (Fig. 2). If disturbance frequency and intensity are both high, organisms are unlikely to persist. Our concept of disturbance elaborates on Grime's (1981) by recognizing that there are agents of disturbance such as sea urchins or severe storms with the potential to destroy plant biomass, but which certain plants such as structurally robust, tough or highly elastic ones, can resist (discussed below). Thus, we speak of the "disturbance potential of an environment" as extrinsic to and independent of the resident algae, and note that the actual amount of biomass removed (i.e., the "disturbance") is in part a function of intrinsic properties of the plants.

We focus on herbivory as a source of disturbance because in many marine systems it is the most important cause for the loss of biomass (e.g., Lubchenco and Gaines 1981). This includes consumption and consequent losses due to dislodgement (e.g., Padilla 1987). Herbivory is by no means the only form of disturbance, but it is sufficiently ubiquitous and important to be the focal point of our research. We suggest that physical disturbances (or senescence) having a frequency and intensity similar to those caused by herbivores will have the same impact on the structure of algal communities (e.g., see Kendrick 1991).

Study sites and general methods

Study sites

We studied three biogeographically distinct locations, each of which had preselected target habitats which were located at different sites. Each habitat or zone was quantitatively sampled along transect lines where we quantified algal productivity and the biomass of herbivore and algal species.

Maine

Subarctic coastal research in the western North Atlantic was conducted on an exposed rock-ledge habitat near Pemaquid Point, Maine (44°30' N, 69°32' W) (see Steneck 1982 for detailed site description) and a protected intertidal habitat near the Darling Marine Center in Walpole (43°57'N, 69°35'W). Sampling transects were established along a depth gradient at seven discrete zones (i.e., high intertidal, +1.6 m; low intertidal -0.2 m; and subtidal depths of 1, 3, 10, 20 and 30 m). Multiple lateral transects were established at each depth zone. Offshore deep water research was conducted at Ammen Rock Pinnacle (42°52'N, 68°58'W) which is located 112 km southwest of Boothbay Harbor, Maine (see Vadas and Steneck 1988 for detailed site description). Sampling at this site used small manned submersibles. Scuba diving for biomass and productivity sampling at the 30 m depth station used mixed-gas NITROX techniques.

Washington

Boreal intertidal research in the eastern North Pacific was conducted at relatively protected sites on San Juan Island (48°30'N, 123°10'W) and at exposed sites on Tatoosh Island (48°25'N, 124°35'W) in Washington state. On San Juan Island transects were established at four zones around the island, sampling at very high, high, mid, low, and very low intertidal zones (ca >2, 1.3, 0.6, 0, and -0.6 m, respectively). Detailed descriptions of the San Juan Island sites appear in Dayton (1971). Tatoosh Island transects were established at very high, high, mid and low intertidal zones (ca >3, 2, 1, and 0 m respectively; see Leigh et al. 1987 for site details).

Caribbean

Tropical subtidal research was conducted on the Caribbean islands of St. Croix (Teague Bay reef; 17°46'N, 64°37'W and Salt River Canyon 17°48'N, 64°45'W) and Jamaica (18°28'N, 77°17'W). Productivity, herbivory and algal community structure were measured at three sites and nine depth zones distributed along the north shore of St. Croix (0-40 m depths, site details in Steneck 1983a). Seasonal comparisons in the structure of algal communities were made at a site on the south shore of St. Croix (site details in Adey and Steneck 1985). Long-term research transects in Jamaica were established on the western reef of Discovery Bay (site details in Woodley et al. 1981). Replicated transects were surveyed in 1978, 1982 and 1987 at target sites situated in the backreef (1 m); and shallow (3 m) and deep (10 m) forereef zones.

General methods

Patterns of distribution and abundance

At each target habitat along subtidal sampling transects, haphazardly tossed quadrats (25 cm x 25 cm) were sampled for algal percent cover, canopy height and biomass. Intertidal sampling used 10 x 10 cm quadrats which were also haphazardly tossed. Herbivores in each quadrat were identified, counted, and measured (length or test diameter). Algal biomass was estimated using a relatively non-destructive technique developed at our study sites in Maine. The heights of the algal canopies in quadrats were measured by repeatedly inserting a ruler or calibrated floating line to the substratum and measuring the longest fronds. Algal percent cover was visually determined. All algae were collected within randomly chosen quadrats for total biomass and canopy height determinations. The regression of algal biomass and algal canopy height is significant (F ratio = 59.1, $p < 0.001$) for quadrats having a 100% algal cover: $y = 134.8 + 7.76x$, $R^2 = 0.53$, $n = 53$, where y = dry mass of algae (g) per meter square and x = canopy height (mm). This relationship applies across species so that only the canopy height of algal mass and percent cover data were recorded for the majority of the intertidal zone biomass estimates at the Maine and Washington sites.

Biomass was measured directly for all sites in St. Croix

and Jamaica by harvesting all macroalgae within quadrats. Algae were then fixed, dried and weighed. Where only diminutive algae were found, substratum samples approximately 25 cm x 10 cm in size were taken to the laboratory, scraped, fixed, and decalcified for both algal community structure and biomass sampling (see Adey and Steneck 1985 for sampling details). The decalcified biomass samples were filtered onto preweighed millipore filters, dried and weighed. Ten control filters were handled identically except without algal samples to assess handling effects. Algal community composition was determined using the subsampling and point count technique of Adey et al. (1981).

Quantifying productivity potential of the environment

To assay the productivity potential at each target habitat, we measured the rate of dry mass production on hard substrata growing under herbivore free conditions. When possible, we recorded light levels and examined the correspondence between the two. Commensurability problems among different biogeographic regions were minimized by ranking target habitats from lowest to highest productivity potential within each region.

Maine

Dry mass production was determined from monthly algal biomass accumulation rates on epoxy putty substrata set in herbivore-free conditions for over a year. For this, rocks embedded in epoxy putty were surrounded by 1 cm long, 3 mm diameter pegs protruding every 1–2 cm² to exclude urchin grazing. The subtidal epoxy islands were placed on copper sheets to exclude limpets. Monthly inspection of the substrata for urchin and limpet bite marks indicated that the experiments remained herbivore free for the duration of the experiment. After monthly biomass estimates for percent cover and canopy heights, the epoxy putty substrata were scrubbed to a negligible level of remaining biomass from which would sprout next month's biomass. Subtidal light levels for target habitats were measured using a Licor underwater photometer (model Li 188b, integrating quantum meter) with a spherical sensor (Li 905B) during July at mid-day under clear calm conditions (from Vadas and Steneck 1988) to determine relative light availability.

Washington

Dry mass production was measured on San Juan Island, based on algal biomass accumulation over two weeks in August on epoxy putty under herbivore-free conditions in August. Herbivores were excluded by clearing a strip around each epoxy putty island and painting it with copper based antifouling paint (see Paine 1984). Biomass was estimated from canopy heights and percent covers (see above). The outer-coast site (Tatoosh Island) was assumed to have higher productivity potential per zone

because of the stronger wave action (Leigh et al. 1987) and the decreased desiccation stress there (due to fog, spray, and the timing of low tides; Dayton 1971).

St. Croix

Dry mass production was based on the rate of change in algal biomass growing on coral plates under herbivore free conditions (Steneck 1983a). For this, six scraped and six unscraped plates were suspended at each target depth in the water column away from the reef; after six days, new algal biomass was rescraped and taken as an indication of dry mass production. A *Thalassia* bioassay (Hay 1981a) and visual 5-min watches revealed no signs of grazing (Steneck 1983a). Productivity rates were also determined in situ using a portable respirometer for periods of 24 h at each site. Each 24-h run simultaneously recorded changes in oxygen concentration among three replicate unscraped coral plate samples. The chamber tops were composed of optically pure quartz glass. While recording oxygen concentrations, light intensity measurements were taken with a Licor light meter and every two hours the respirometer was flushed (see Porter 1980).

Quantifying disturbance potential of the environment

The disturbance potential of the environment involves both the intensity and frequency of disturbance. Herbivore-induced disturbance frequency was estimated differently for invertebrates than for fishes. Average invertebrate herbivore biomass per unit area for each target habitat was estimated from quadrat data by applying individual body size to biomass regressions (Menge 1972) and relating that to population density data. Disturbance frequency for herbivorous fishes was determined cinematically by recording bite rates (Steneck 1983a). Grazing intensity was estimated by categorizing herbivores by feeding ability from published studies based on impact per bite (i.e., excavating potentials) of gastropods, molluscs, urchins and grazing fish groups (methods of Steneck 1982, 1983a, b, 1988, 1990, Steneck et al. 1991). Grazing intensities by invertebrate groups are comparable among biogeographic zones (Steneck 1983b, 1990). Most estimates of frequency (i.e., herbivore biomass) and intensity (feeding capability) are correlated among zones for each region, facilitating the ranking of disturbance potentials of target habitats (see Results).

At Maine and Washington, three levels of invertebrate herbivore-induced disturbance intensity were identified based on impact per bite. They were 1) shallow-grazing molluscs such as littorinids, creating the lowest-intensity disturbances, 2) deep-grazing molluscs such as limpets, and 3) the intense-grazing urchins. Based on body size and population density, invertebrate herbivore biomasses < 10 g (dry)/m², 10 to 100 g (dry)/m² and > 100 g (dry)/m² were ranked as low, mid, and high disturbance potential

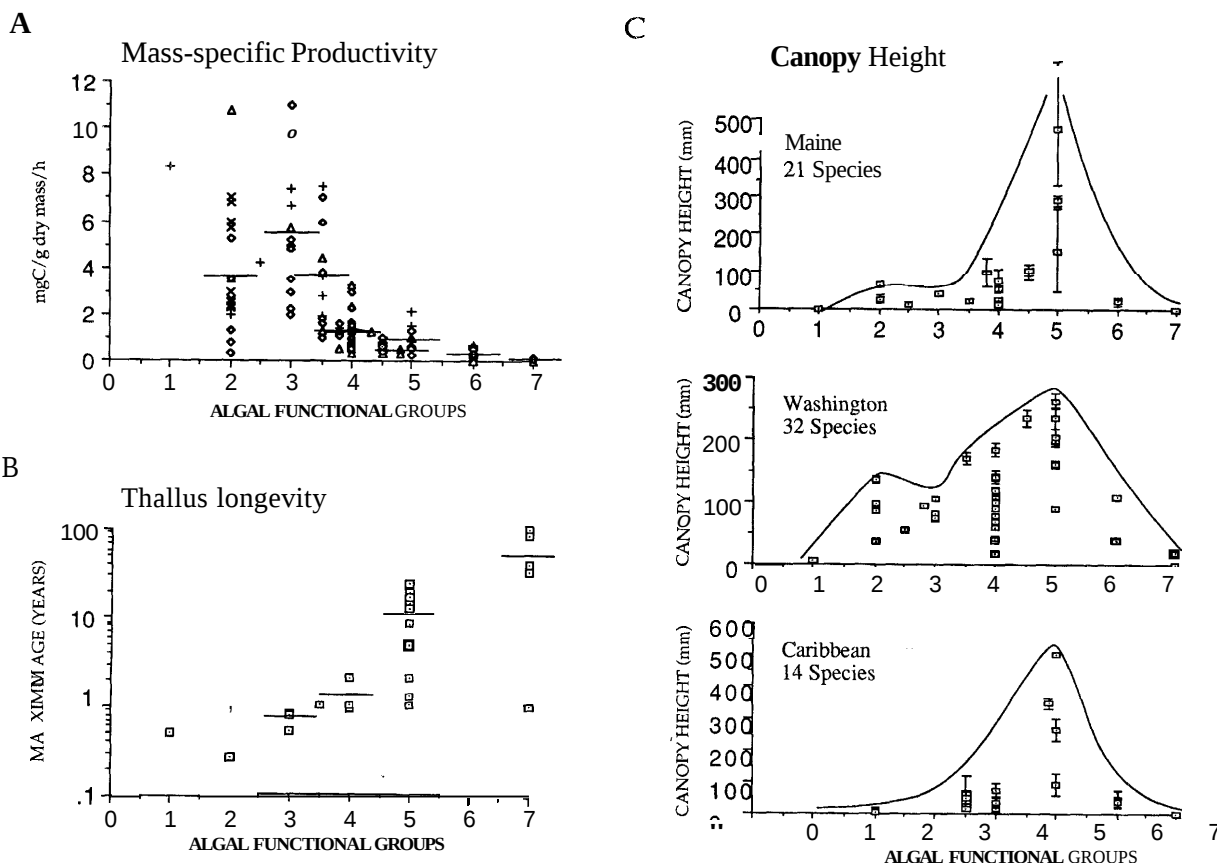


Fig. 3A. Mass-specific productivity of algae from southern California ($\diamond$ Littler and Arnold 1982), the Caribbean (Δ Littler et al. 1983b, X Carpenter 1986), and Hawaii ($+$ Doty 1971). Average productivity values for well studied functional groups are represented by horizontal lines. Numbers for algal functional groups correspond to the numbers in Fig. 1. Note that AG 2 (turf) production may be low due to inadequate agitation (see Carpenter 1985). B. Thallus longevity. Points represent thallus longevity of 27 species based on 25 published studies (Appendix). Average longevity values for well studied functional groups are represented by horizontal lines. C. Canopy heights measured in the field for dominant species in Maine, Washington, and the Caribbean (Discovery Bay, Jamaica). Lines envelop the maximum canopy heights recorded for each algal functional group and points represent average canopy heights per species. Error bars represent standard deviation per species.

respectively. Only habitats with significant urchin abundance (the invertebrate herbivore that grazes with the highest intensity) were scored as having a high disturbance potential.

Our quadrat data for St. Croix were taken in 1982, before the *Diadema antillarum* mass mortality in 1983, and thus urchins were still a significant herbivore. Due to the addition of grazing fishes at tropical sites, the ranking of herbivore-induced disturbance in St. Croix differed from that of Washington or Maine. Just as invertebrates were separated according to their intrinsic differences in grazing intensity, so too were fish groups subdivided. Based on intensity and impact, herbivorous fishes were subdivided into: 1) non-denuding (no net removal of algae from the substratum, Hixon and Brostoff 1983), 2) denuding and 3) excavating (Hatcher 1983, Steneck 1983a, 1988). For our ranking, only bites from denuding and excavating fishes were used since they are unequiv-

ocally agents of disturbance to algae. Fish grazing frequency was measured as bite rates and was determined from visual observations and time-lapse movies taken in 1981 and 1982 (see Steneck 1983a for methods). Invertebrate herbivores at tropical sites were measured identically to those of non-tropical sites but zones that included bite-rates from fishes in addition to significant invertebrate grazing achieve the disturbance potential ranking of "very high".

Results

Intrinsic properties of organisms: characteristics of functional groups

Algal morphology and anatomy (e.g., Fig. 1) correspond to intrinsic properties such as mass-specific productivity

Table 1. Potential impact of herbivore taxa on functional groups of algae (compare references to functional groups identified in Fig. 1). Community structure is most affected by the groups that commonly denude algae. X = Commonly denudes group, X = Commonly consumes group, - = Occasionally consumes group, Blank = Rarely or never consumes group.

Herbivore taxa	Algal functional groups						
	1	2	3	4	5	6	7
Polychaeta ¹	X	X	X				
Malacostraca ²	X	X	X	-	-	-	
Gastropoda							
Rhipidoglossa ³	X	X	X	-	-		
Taenioglossa ⁴	X	X	X	-	-		
Docoglossa ⁵	X	X			X		X
Polyplocophora ⁶	X	X	X	X	X	X	X
Echinoida ⁷	X	X	X	X	X	X	X
Perciformes							
Low intensity ⁸	X	X	X	-	-		
High intensity ⁹	X	X	X	X	X	X	X
% groups commonly denuding	100	67	33	22	22	11	11

¹ Day 1967, Fauchald and Jumars 1979*, Hartman 1968, Woodin 1977, Kohn and White 1977, Steneck 1983b
² Brawley and Adey 1981, Carpenter 1986, Howard 1982, Zimmerman et al. 1979, Hicks 1986, Steneck 1983a,b, Brawley and Fei 1987
³ Graham 1955*, Steneck and Watling 1982*, Steneck 1983a,b, Ward 1966, Ankel 1936
⁴ Lubchenco 1978, Steneck and Watling 1982*, Steneck 1983a,b, Graham 1955
⁵ Nicotri 1977, Steneck and Watling 1982, Steneck 1982, Branch and Branch 1980, Walker 1972, Fletcher 1987
⁶ Steneck and Watling 1982*, Steneck 1983a,b, Graham 1955, Dethier and Duggins 1984
⁷ Carpenter 1981, 1986, Steneck 1983a,b, Lawrence 1975*, Fletcher 1987
⁸ (e.g., Pomacentridae, Acanthuridae) Jones 1968, Hixon and Brostoff 1983, Vine 1974, Russ 1987, Montgomery 1980, Brawley and Adey 1977, Steneck 1983a,b, Lewis 1985
⁹ (e.g., Scaridae) Hatcher 1981, Russ 1984, Steneck 1983a,b, Lewis 1985

*Review articles.

(Fig. 3A), thallus longevity (Fig. 3B, Appendix) and canopy height (Fig. 3C). Canopy height increases with thallus complexity (i.e., tissue differentiation into cortex and medulla, Fig. 1) which also correlates with plant biomass (see Methods above). In general, the thalli of larger erect algae are longer-lived and slower-growing than thalli of small filamentous and microalgal forms. The progressively enlarged cortex with thick cell walls (algal groups “AG” 4–5) and calcification (AG 6 and some AG 7) appear to make macroalgae more resistant to physical and biological disturbances (Steneck and Watling 1982, Littler et al. 1983a, Pennings and Paul 1992). As a result of the size, growth and longevity characteristics, larger forms (see Fig. 3 for AG 4–6) are better at monopolizing light resources than smaller or low-canopy forms (AG 1,2 and 7; reviewed in Carpenter 1990). Evidence for this is seen in studies of algal succession (e.g.

Paine 1977, Emerson and Zedler 1978, Murray and Littler 1978, and Sousa et al. 1981), and in experiments where the removal of larger macrophytes allows the growth of smaller canopy-forming algal groups (e.g., Dayton 1975, Sousa 1979, Lubchenco 1980, Sousa et al. 1981, Ojeda and Santelices 1984, and Duggins and Dethier 1985) or where removal of herbivores results in dominance of larger forms (Paine and Vadas 1969a, Sammarco et al. 1974, Lewis 1986). The close correspondence between functional groupings and ecological characteristics is explored further below.

Functionally different herbivore groups can differentially affect algal groups. Intrinsic properties of herbivores such as bite penetration depths into calcareous crustose algae have been measured as indicating herbivore-induced disturbance intensity (e.g., Steneck 1983b, 1990, Steneck et al. 1991). Table 1 shows herbivore taxa in terms of their capacity to consume and/or denude various algal functional groups. Many grazers entirely remove microalgae, filamentous, and foliose forms, but fewer can denude larger macroalgae and even fewer remove crusts (particularly coralline crusts). Larger expansive and calcified algal forms also appear to suffer less secondary tissue loss (e.g., to wave action following herbivory) than do simpler forms (Padilla 1987) and thus are less likely to be denuded. Community-level impact of different herbivore groups appears to follow denuding capacity. For example, scarids (parrotfishes), which have the deepest bite-depth penetration into calcareous algae, can remove all functional groups of algae. Among the invertebrates, grazing intensity ranges from echinoids, to deep grazing gastropods and finally to shallow grazing gastropods and other low intensity grazers such as polychaetes (Steneck 1983b), and their reported impact follows this pattern (Table 1).

Extrinsic properties of the environment

The ranking of productivity potential of the environment in the well mixed, subtidal environments of Maine and St. Croix corresponded directly to recorded light levels (Table 2). In Maine, the monthly rate of algal biomass production was highly correlated with light intensity (Table 2A: $r=0.98$, $n=7$ stations). A similar pattern was found on a wave-exposed forereef transect in St. Croix, grading from mean low water to a depth of nearly 40 m (Table 2B, Steneck 1983a, Carpenter 1985a). Dry mass productivity under herbivore free conditions at four canyon wall habitats correlated with light ($r=0.89$, $n=4$) and oxygen production recorded using a respirometer ($r=0.94$). Oxygen productivity correlated ($r=0.86$, $n=8$) with light over the entire depth transect from mean low water to 40 m (Table 2B).

Intertidal environments (in Maine and Washington) from mean lower low water to the upper reaches of the intertidal zone encompass another gradient of progressively reduced annual productivity potential (Tables 2A and

Table 2A. Ranking productivity potential of the environment at target habitats in Maine. Habitats are arranged from highest zone to greatest depth. Productivity variance expressed as standard error.

Maine				
Target habitats (sub- and intertidal)	Production g (dry)/m ² /yr	Number of samples	Light (μmol/m ² /s)	Productivity potential
High intertidal zone (+1.6 m)	0.98 (k0.9)	6	ND	LOW
Low intertidal zone (-0.2 m)	5.1 (k1.6)	9	ND	MID
Coastal -1 m depth	152.3 (k17.5)	6	900	HIGH
Coastal -3 m depth	56.0 (k28.6)	6	450	HIGH
Coastal -10 m depth	1.2 (±0.03)	6	90	MID
Coastal -20 m depth	0.2 (±0.2)	6	9	LOW
Coastal -30 m depth	0.7 (±0.01)	6	1	LOW
Offshore -30 m depth	14.0 (k0.9)	4	20	MID
Offshore -45 m depth	0 (±0)	4	7	LOW

Table 2B. Ranking productivity potential of the environment at target habitats in St. Croix. Dry mass productivity variance is expressed as standard error (n = 6).

St. Croix					
Target habitats (sub- and intertidal)	Production g (dry)/m ² /d	Production μgO ₂ /cm ² /h	Light (mol/m ² /d)	No. of samples ¹	Productivity potential
Algal ridge at MLW	ND	2215 (±600)	43	3	HIGH
Algal ridge 0.5 m	ND	1255 (±502)	ND	3	HIGH
Backreef 1 m	ND	553 (±393)	28	3	MID
Forereef 1.5 m	ND	940 (±269)	28	3	HIGH
Forereef 5 m	ND	756 (±159)	23	3	MID
Forereef 10 m	ND	536 (±79)	17	3	MID
Canyon wall 10 m	3.0 (k0.28)	ND	ND	ND	MID
Canyon wall 20 m	1.35 (k0.25)	561 (±39)	11	3	MID
Canyon wall 30 m	0.93 (+1.1)	387 (±86)	6	3	LOW
Canyon wall 40 m	0.79 (±1.8)	213 (±42)	3	3	LOW

¹ Number of coral plates used in respirometer.

Table 2C. Ranking productivity potential of the environment at target habitats in Washington State based on height in the intertidal zone (e.g., “very high” to “very low”) and degree of exposure (see text). All productivity measurements were done under herbivore-free conditions. Productivity variance expressed as standard deviation.

Washington			
Target habitats (intertidal)	Production g (dry)/m ² /mo	Number of samples	Productivity potential
SJI* Very high			V. LOW
TI Very high			v. LOW
SJI High	7.2 (±15.6)	10	LOW
TI High			LOW
SJI Mid	97.8 (±92.4)	20	MID
TI Mid			MID
SJI Low (few herb)	464.0 (k227.0)	10	HIGH
TI Low (herb removed)			HIGH
SJI Low (with herb)			HIGH
TI Low (with molluscs)			HIGH
TI Low (with urchins)			HIGH
SJI Very low (few herb)			HIGH
SJI Very low (with herb)			HIGH

*SJI = San Juan Island. TI = Tatoosh Island.

Table 3A. Ranking disturbance potential in Maine based on grazing frequency (as indicated by herbivore biomass, see text) herbivore biomass and grazing intensity (increasing left to right from shallow grazing molluscs to urchins).

Target habitats	Shallow grazing molluscs ¹	Deep grazing molluscs ²	Urchins ¹	Total herbivore biomass	No. of samples	Disturbance potential
+1.6 m Intertidal	1.2 (± 6.1) ⁴	0	0	1.2	72 ⁵	LOW
0 m Intertidal	56.9 (± 17.8)	0	0	56.9	83	MID
Coastal 1 m depth	0	0.02 (k0.02)	0 ⁶	0.02	34	LOW
Coastal 3 m depth	0	0.2 (k0.2)	229.2 (± 36)	229.4	39	HIGH
Coastal 10 m depth	0	0.2 (k0.02)	189.0 (± 13.73)	189.2	76	HIGH
Coastal 20 m depth	0	0.9 (k0.4)	9.5 (k5.3)	10.4	30	MID
Coastal 30 m depth	0	0	0	0	33	LOW
Offshore 30 m depth ¹	0	0 ⁸	0	0	>30 dives ⁹	LOW
Offshore 45 m depth	0	0	0	0	>10 dives ¹⁰	LOW

¹ Biomass (g(dry)/m²) of herbivores used throughout. Shallow grazing molluscs = *Littorina littorea*. ² *Tecturatestudinalis*, *Tonicella ruber*, *T. marmorea*. ³ *Strongylocentrotus droebachiensis*. ⁴ Except for this value (standard deviation) all variances are expressed as standard error because they are averages of a population of means. ⁵ n = number of m² quadrats. ⁶ Urchins having a biomass of 56.3(± 8.75) (g(dry)/m²) were found in crevices only. This analysis involves plants growing on the upper surfaces of the boulders where there are no urchins. ⁷ The offshore site is Ammen Rock Pinnacle (104 km east of Boothbay Harbor, ME, see Vadas and Steneck 1988). ⁸ A rare (< 1/10m²) limpet species is the sole herbivore. ⁹ Number of scuba dives. ¹⁰ Number of submersible dives by several observers.

Table 3B. Ranking disturbance potential in Washington state (identical method to Table 3A). Target habitats are arranged from highest to lowest elevations in the intertidal zone for our stations on San Juan (SJI) and Tatoosh (TI) Islands in Washington state.

Target habitats	Shallow grazing molluscs ¹	Deep grazing molluscs ²	Urchins ³	Total herbivore biomass	No. samples	Disturbance potential
SJI Very high	2.9 (k4.0)	3.4 (k5.4)	0	6.3	10	LOW
TI Very high	8.0 (k4.9)	0	0	8.0	5	LOW
SJI High	2.7 (± 2.8)	4.3 (k8.3)	0	7.0	18	LOW
TI High	3.9 (k3.4)	7.1 (± 11.4)	0	11.0	14	LOW
SJI Mid	0.5 (k0.1)	4.4 (± 6.4)	0	4.9	23	LOW
SJI Low (few herb)	0.1 (k0.2)	1.1	0	1.2	24	LOW
SJI Very low (few herb)	0	1.2	0	1.2	16	LOW
TI Mid	0.5 (k0.1)	42.1 (± 41.1)	0	42.6	13	MID
TI Low (herb removed)	0	0.4	0	0.4	5	LOW
SJI Low (with herb)	0	42.1 (k48.6)	0	42.1	7	MID
SJI Very low (with herb)	0	76.8 (± 86.3)	0	76.8	11	MID
TI Low (with molluscs)	0.2 (± 0.9)	40.3 (± 56.6)	0	40.5	13	MID
TI Low (with urchins)	0	3.7 ⁴ (k7.3)	2340 (± 1605) ⁵	2344	8	HIGH

¹ Summed biomass (g(dry)/m²) of *Littorina* spp., *Onchidella* sp., *Siphonaria* sp.; ² *Lottia pelta*, *Tectura scutum*, *Tonicella lineata*, *Katharina tunicata*; ³ *Strongylocentrotus purpuratus*; ⁴ *Tonicella lineata*; ⁵ Urchin biomass estimations were based on test diameter to dry mass regression (calculated for *S. droebachiensis*) of: $y = 0.2827 \cdot x^{2.493}$, $r = 0.94$, $n = 30$).

C respectively); here, however, the factor most limiting algal productivity is probably desiccation rather than light or wave action (Castenholz 1961, Dayton 1971, Seapy and Littler 1982, Horn et al. 1983, Cubit 1984). Measured productivity rates under herbivore-free environments in Washington (Table 2C) show the expected inverse relationship between rates of productivity and elevational height in the intertidal zone.

Ranking disturbance potential among target habitats within each biogeographic location involved only the abundance and feeding capability of herbivore groups, not their preferences. In most cases, total biomass and

abundance of most intense herbivores correspond (Tables 3A–C). In Maine, the 3 and 10 m depth zones had both the greatest total herbivore biomass and dominance by urchins, which are capable of the most intensive grazing (i.e., they are capable of taking large and relatively deep bites into the most resistant algae) and thus were ranked as having a high disturbance potential. At the 0 m intertidal habitat, the dominant herbivore is *Littorina littorea* which is a low-intensity agent of disturbance (i.e., does not graze deeply, Steneck 1990) but is found in high numbers. This habitat is ranked identically to the 20 m habitat where herbivore biomass is lower but feeding

Table 3C. Ranking disturbance potential in St. Croix based on invertebrate herbivores (identical to Tables 3A and B) and fish grazing (bite rate) arranged by increasing grazing intensity from left to right (no shallow grazing molluscs were found) in target habitats arranged from shallowest to deepest (see text).

Target habitats	Deep grazing molluscs ¹	Urchins ²	Bite rate fishes ³	Number quadrats ⁴	Sample size ⁵	Disturbance potential
Algal ridge 0 ⁶ m	0	0		20	3	LOW
Algal ridge 0.5 m	0	38.3 (±3.7) ⁷	313 (±311)	10	3	MID
Backreef ⁸ 1 m	0	144.4 (k11.6)	896 (±896)	31	3	HIGH
Forereef 1.5 m	0.03 (±0.01)	137.6 (27.4)	2823 (±850)	13	3	V. HIGH
Forereef 5 m	0.02 (k0.02)	121.3 (±4.5)	1563 (±1381)	20	3	V. HIGH
Forereef 10 m	0	52 (k5.4)	409 (±371)	21	3	MID
Canyon wall ⁹ 10 m	0	4.2 (±1.2)	109 (±51) ¹⁰	19	7	MID
Canyon wall 20 m	0	20.5 (±1.68)	294 (±975)	30	11	MID
Canyon wall 30 m	0	1.0 (±0.32)	235 (±621)	20	7	MID
Canyon wall 40 m	0	0	0	20	8	LOW
Canyon wall ¹¹ 10 m	0	0	0	0	3	LOW
Canyon wall 20 m	0	0	0	0	3	LOW
Canyon wall 30 m	0	0	0	0	3	LOW
Canyon wall 40 m	0	0	0	0	3	LOW

¹ Biomass (g(dry)/m²) of *Acmaea leucopleura*. ² Biomass (g(dry)/m²) of *Diadema antillarum* (data from 1982), *Echinometra lucunter* (primarily restricted to burrows). ³ Bite rates (bites/m²/h) for denuding fishes (*Microspathodon chrysurus*, *Ophioblennius atlanticus*, *Acanthurus bahianus*, *Acanthurus coeruleus*) and excavating fishes (*Scarus croicensis*, *Sparisoma chrysoterpum*, *Sparisoma viride*) (Steneck 1983a, b). Only forereef at 1.5 m had measurable scarid grazing. ⁴ For urchins and molluscs only. ⁵ Visual 5-min counts 1981, 1982, time lapse movies 1982 (visual counts 1982 only Canyon wall stations). ⁶ MLW = Mean Low Water for spring tides. ⁷ Variance expressed as standard error of the mean. ⁸ Reef sites are Teague Bay Reef. ⁹ Canyon sites are Salt River Canyon. ¹⁰ Variance as standard deviation because this value is not derived from a population of means. ¹¹ Plates were suspended from racks away from canyon wall at identical depths as Canyon Wall stations. Herbivory was never observed at any of these racks. They are listed as "0 HERB." in Fig. 4C.

A. MAINE

B. WASHINGTON

C. ST. CROIX

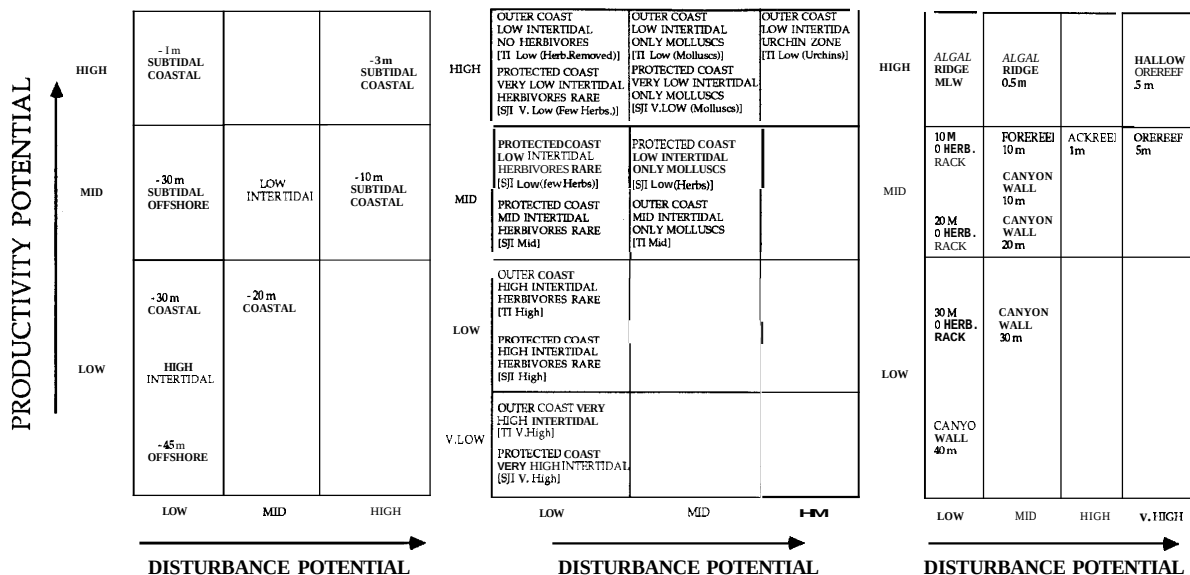


Fig. 4. Target habitats arranged according to productivity and disturbance potentials (based on data in Tables 1 and 2, respectively). A) Maine. Note that offshore sites are more productive at a given depth than coastal sites because of greater water clarity (Vadas and Steneck 1988). B) Washington state. Abbreviations used in Tables 1B and 2B are in brackets. Outer coast sites were assumed to have higher productivity potential per zone because of the stronger wave action and the decreased desiccation stress there (due to fog, spray, and the timing of low tides). C) St. Croix.

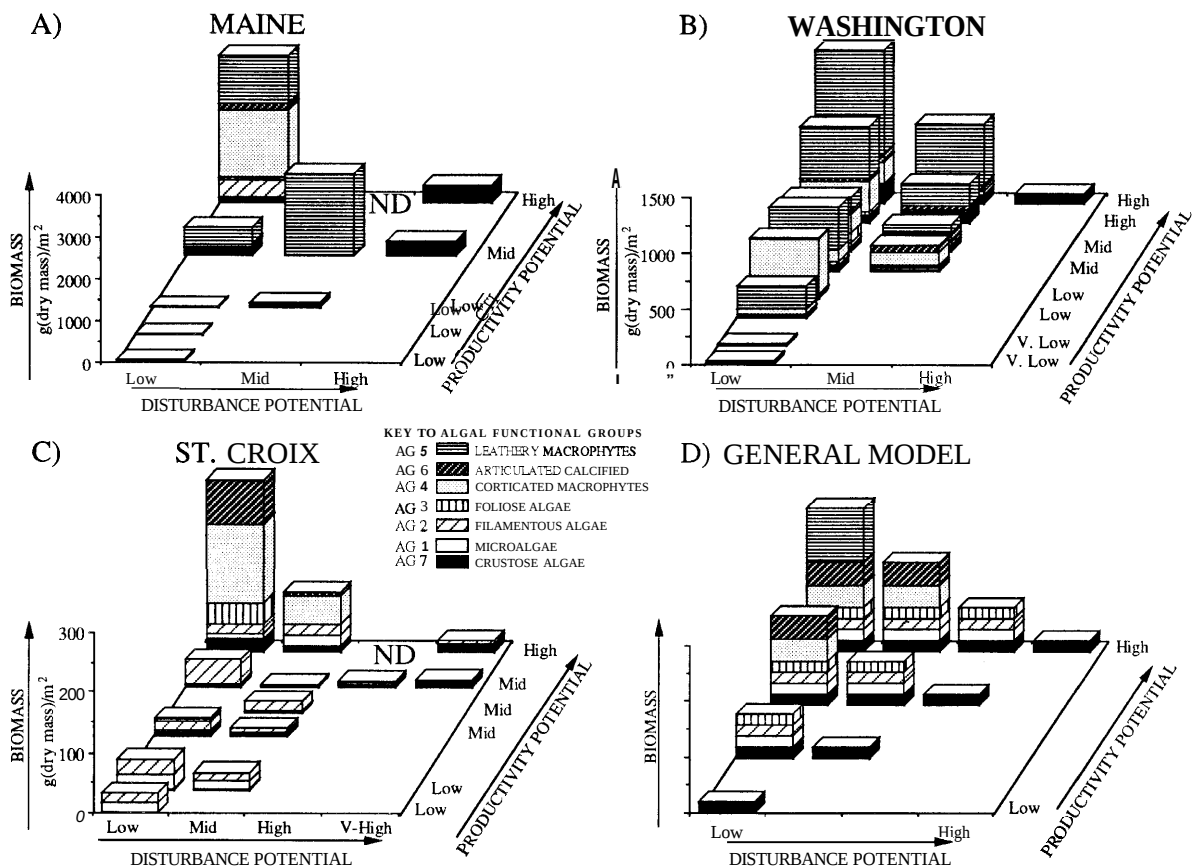


Fig. 5. Model of algal community structure at a functional group level based on environmental structuring parameters of disturbance and productivity potentials. Biomass data were collected for A) Maine, B) St. Croix, C) Washington in target habitats (Fig. 4). All biomass data were gathered at the species level and pooled into functional groups (see text). D) Represents an idealized model derived from patterns in A–C. Algal groups are arranged according to increasing canopy height with the largest forms comprising the upper segments of the stacked histograms. “ND” indicates no data.

capabilities are greater (i.e., urchins vs molluscan counterpart; Steneck 1990). Similar analysis in Washington (Table 3B) of shallow and deep grazing molluscs clearly separates the low herbivore biomass habitats dominated by low intensity grazers from those having a higher biomass of more intense grazers. The highest disturbance potential of the habitats we studied in Washington is in the zone dominated by sea urchins on Tatoosh Island. There, urchins are highly abundant, large, and capable of grazing deeply into all algal groups.

At our tropical sites, integrating the disturbance potential from vertebrate and invertebrate herbivores is relatively easy because urchin abundance and bite rates from fishes are directly correlated over the target habitats (Table 3C, $r = 0.84$, $n = 10$, $P = 0.003$). The lowest levels of herbivory were at the 0 m algal ridge site and the 40 m canyon wall site, whereas both were maximal at the two shallow forereef sites at 1.5 and 5 m water depth. All habitats with an abundance of urchins (i.e., biomass > 100 g/m²) were categorized as either high or very high in

disturbance potential depending upon the herbivore disturbance attributable to fishes. The sites having intermediate invertebrate herbivore biomass also had intermediate levels of fish grazing (0.5 m algal ridge, 10–30 m canyon wall) and thus were categorized as having an intermediate (“mid”) disturbance potential.

Fig. 4 (A–C) summarizes the extrinsic components of the environment as ranked above for each of the surveyed habitats at each of the geographic regions. Productivity potential is summarized from Tables 2 A–C, and disturbance potential from Tables 3A–C.

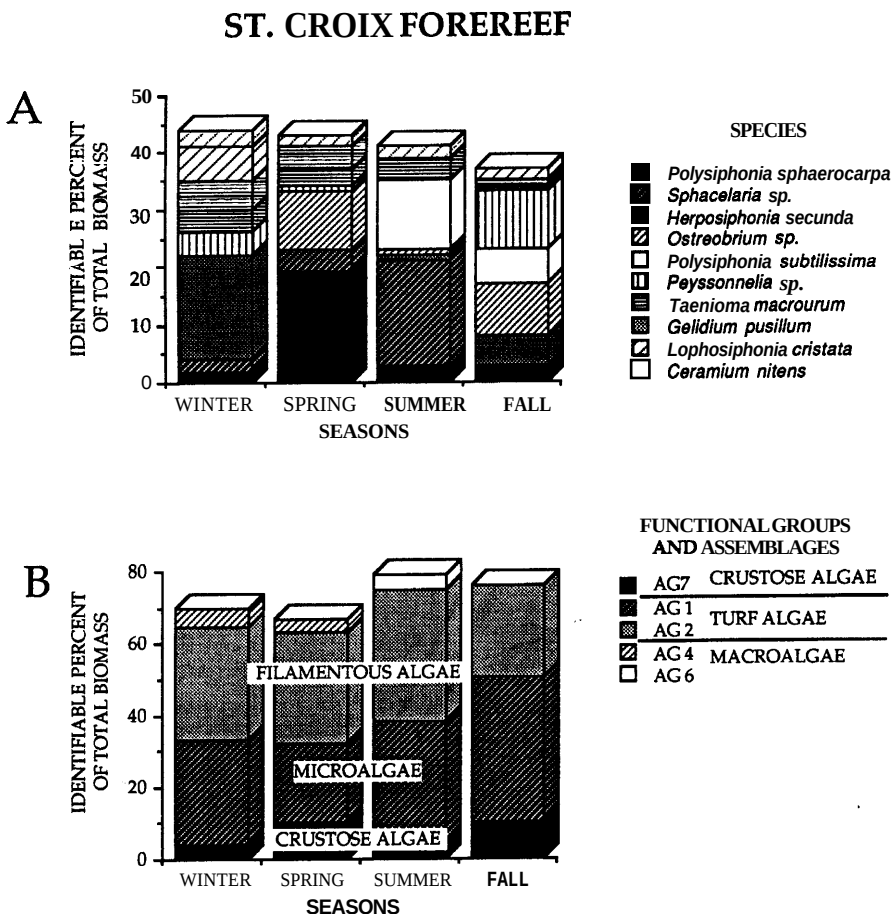
Patterns of algal community structure

Algal assemblages in each region were compared for target habitats (Figs 4A–C). Data on algal biomasses were collected at the species level, then combined into functional groups and plotted on the appropriate coordinate of the disturbance/productivity grid (Figs 5A–C).

Fig. 6. Seasonal stability of the 10 most abundant algal species (A) and functional groups (B) on a fore reef of St. Croix (reanalysis of data in Adey et al. 1981). Differences in the total

percent represented among seasons for species (A) and functional groups (B)

resulted from the different proportions of unidentifiable components when samples were analyzed at species vs functional group levels.



The combined biomass of all species within each functional group was plotted as stacked histograms starting with plants having no canopy such as crustose algae (AG 7) or minute canopies as among the micro- and filamentous algal forms (AG 1 and 2), to the largest canopy forming groups such as the leathery macrophytes, which include kelp (AG 5).

In Maine (Fig. 5A), algal biomass and functional group diversity was lowest in habitats having the lowest productivity potential or highest disturbance potential. Where productivity potential was highest and disturbance potential lowest, algal biomass and functional group diversity were highest, and the community was dominated by large leathery macrophytes (e.g., the kelp *Laminaria longicruris*) and corticated macrophytes (e.g., *Chondrus crispus* and *Mastocarpus stellatus*). Crustose algae dominated zones having the highest disturbance potential where productivity potential was also high, and zones having the lowest productivity potential where disturbance potential was also low. The dominant crustose algae where both environmental parameters were high include the calcified coralline algal species: *Lithothamnion glaciale*, *Clathromorphum circumscriptum* and *Phymatolithon laevigatum*, whereas species dominating where

both were low were the coralline *Leptophytum laeve* and the less abundant fleshy red algal crust *Peyssonnelia rosenvingii* in subtidal and *Verrucaria* spp. in the higher intertidal zones. Due to obvious trophic limitations, no habitat has been found in which the herbivore-induced disturbance potential is high and productivity potential low.

In Washington (Fig. 5B), biomass and functional group diversity again were greatest where disturbance potential was lowest and productivity potential highest. There, leathery macroalgae (e.g., *Hedophyllum sessile*, *Fucus gardneri*) and corticated macrophytes (e.g., *Mastocarpus papillatus*, *Iridaea cornucopiae* and many other red algae) dominated the substrata. At target habitats having the highest productivity and disturbance potentials, crustose algae dominate (predominantly coralline crusts such as *Lithothamnion phymatodeum* and *Pseudolithophyllum whidbeyense*). Where both parameters were low, non-calcified encrusting algae dominate (e.g., lichens and "Petrocelis"). Where the two proposed structuring parameters were at intermediate levels, we found intermediate levels of total algal biomass and slightly reduced functional group diversity.

In St. Croix (Fig. 5C), algal biomass and functional

Table 4. Stability of reef-dwelling algal communities at Discovery Bay, Jamaica from 1978 to 1987. Note small change following Hurricane Allen (1979) versus large change following mass mortality in *Diadema antillarum* (1983). Algae are combined into functional groups and abundances are expressed as average decalcified biomass (g (dry)/m²), n = number of meter square quadrats. Community dominant (i.e., > 50% of biomass) in each zone at each time is printed in boldface.

Backreef (1 m)	1978	S.D.	n	1982	S.D.	n	1987	S.D.	n
Herbivore									
<i>Diadema antillarum</i> (no./m ²)	3.1	5.3	35	3.4	0.03	22	0.4	1.2	37
Algal groups									
Algal turf (AG 1–2)	9.8	4.9	27	7.0	4	14	25.7	13.1	21
Macroalgae (AG 4–6)	233.4	10	27	259.0	34.4	14	265.1	66.7	21
Crustose corallines (AG 7)	0	0	27	15.2	2.8	14	14.1	2.09	5
Sum algal biomass	243.2			281.2			304.9		
Shallow forereef (3 m)	1978	S.D.	n	1982	S.D.	n	1987	S.D.	n
Herbivore									
<i>Diadema antillarum</i> (no./m ²)	8.1	0.7	33	9.1	1.6	25	0.4	0.9	66
Algal groups									
Algal turf (AG 1–2)	10.5	1.3	33	25.6	4.1	3	13.4	9.8	12
Macroalgae (AG 4–6)	0	0	33	0	0	3	46.3	20	12
Crustose corallines (AG 7)	41.7	0.8	33	58.9	5.1	3	11.9	2	12
Sum algal biomass	52.2			84.5			71.6		
Deep forereef (10 m)	1978	S.D.	n	1982	S.D.	n	1987	S.D.	n
Herbivore									
<i>Diadema antillarum</i> (no./m ²)	18.0	5.5	40	13.6	5.4	21	0	0	28
Algal groups									
Algal turf (AG 1–2)	35.6	3.1	10	49.9	28.0	3	11.3	2.4	30
Macroalgae (AG 4–6)	2.4	0.2	10	1.8	0.1	3	400.6	4.4	30
Crustose corallines (AG 7)	26.2	2.6	10	29.4	5.1	3	0.2	0.2	30
Sum algal biomass	64.2			81.1			412.1		

group diversity were greatest by far where disturbance potential was lowest and productivity potential highest. Algal biomass was lowest where productivity potential was high and disturbance potential was “very high”. There, encrusting coralline species such as *Porolithon pachydermum* and *Neogoniolithon* spp. dominated. The extinction depth of tropical marine algae far exceeded the depths to which we could sample, and thus we did not sample where productivity potential was lowest. However, at 40 m on the Salt River Canyon wall in St. Croix, algal biomass and functional group diversity were relatively low. We did not find an appreciable cover of crustose algae as we did at other low productivity potential habitats. This may have been because of the abundance of sediment at our study site (Steneck pers. obs.). The tropical sites were dominated by diminutive turf algae at all but the habitats having mid to low disturbance potential under the highest productivity potential.

Temporal changes in community structure

Sorting out species-level “noise” from significant changes in community structure is a goal of the functional group approach. The composition of algal species changes significantly between seasons in tropical reef systems.

We reanalyzed data on algal species composition from a study conducted in St. Croix by Adey et al. (1981) in which almost none of the dominant species on forereef transects were found from one season to the next (Fig. 6A). However, by reassigning the species to their functional groups (i.e., Fig. 1), a much higher degree of stability was revealed (Fig. 6B). The only change of significance was the addition of macroalgae during the winter and spring. This seasonal shift was evident to those working on this project (R. Steneck pers. obs.) but was not obvious with analyses conducted at the species level (e.g., Fig. 6A).

A long term study of algal abundance and herbivory on Jamaica’s Discovery Bay reef was conducted periodically from 1978 to 1987. During the study, two significant natural events affected the reef: Hurricane Allen in 1979 hit the reef (see Woodley et al. 1981) and the mass mortality in 1983 of the predominant herbivore, *Diadema antillarum* (e.g., Hughes et al. 1987). Only following the mass mortality of sea urchins did community structure shift; algal biomass increased, and dominance shifted from corallines to macroalgae in the shallow forereef, and from minute algal turf to macroalgae in the deep forereef (Table 4). Similar changes were observed throughout the Caribbean following the mass mortality of sea urchins (e.g., in Curacao, Ruyter van Steveninck and Bak 1986;

in St. John, Levitan 1988; and in St. Croix, Carpenter 1985b, 1990). This suggests that a reduction in disturbance potential under constantly high productivity potential will shift community structure from one of algal crust dominance, low biomass, and low functional group diversity to one of macrophyte dominance, significantly higher biomass, and high functional group diversity.

Discussion

Convergent patterns in algal community structure at the functional group level

Similar patterns in algal community structure at the functional group level emerged from all three geographic areas. In each region, the highest biomass and functional group diversity were found in habitats having the lowest disturbance and the highest productivity potentials respectively (Figs 5A–C). The dominant algae (i.e., those with the greatest biomass) under these conditions were species that are relatively large in size and long-lived, such as leathery or corticated macrophytes (AG 5 and 4 respectively in Fig. 1). Where disturbance and productivity potentials were both high or both low, crustose algae usually dominated. In all cases, encrusting coralline algae dominated where those factors were high, but fleshy crusts were found under some conditions where both were low. Fig. 5D summarizes a generalized (and idealized) model of algal biomass dominance and functional group diversity relative to the productivity and disturbance potentials of the environment. Under greater disturbance or reduced productivity potential, the biomass and functional group diversity decrease, and dominance shifts toward groups with lower canopy heights. Under conditions of the highest levels of disturbance or lowest productivity potential, the dominant (and sometimes only) algal form is crustose algae. We offer this approach and general model (Fig. 5D) as a testable model or “templet” *sensu* Southwood (1977) against which other systems can be examined.

Support for the generality of the model is found in the literature. In productive environments, changes in disturbance significantly change the structure of algal communities. Many studies have demonstrated that in productive environments with intense herbivore-induced disturbance (i.e., the upper right corner of Fig. 5D), algal crusts dominate (e.g., Paine and Vadas 1969a, Branch 1975, Lawrence 1975, Menge and Lubchenco 1981, Levings and Garrity 1983, Hay and Gaines 1984, Paine 1984, Duggins and Dethier 1985, Steneck 1986, Fletcher 1987, Fletcher and Underwood 1987, Littler et al. 1991). When the herbivores are removed (moving to the left along the disturbance axis in Fig. 5D), diversity increases and the crusts are masked by larger, canopy-forming macroalgae (Paine and Vadas 1969a, Vine 1974, Dayton 1975, Duggins 1980, Paine 1980, Slocum 1980, Ayling 1981, Sousa et al. 1981, Steneck 1982, Bertness 1984, Carpenter

1985b, 1990, Harrold and Reed 1985, Hay and Taylor 1985, Lewis 1986, Menge et al. 1986, Fletcher 1987, Fletcher and Underwood 1987, Morrison 1988). Areas where herbivores are restricted from foraging, such as reef flats, isolated mangrove roots or heavily wave-exposed sublittoral zones, are often islands of fleshy macroalgae within areas otherwise occupied by crusts, calcified algae, or minute algal turfs (Adey et al. 1977, Hay et al. 1983, Levings and Garrity 1983, Himmelman 1984, Ojeda and Santelices 1984, Lewis 1986, Taylor et al. 1986, Foster 1987). Changes in physically-induced disturbance potential such as an increase in sand scour can shift turf algal communities to coralline dominated communities (Kendrick 1991). Under intermediate levels of grazing, or when grazing or physical disturbance occur intermittently, smaller, shorter-lived (ruderal-weedy) algal forms dominate (i.e., algal turfs AG 1–3: Littler and Arnold 1982, Littler et al. 1983b, Carpenter 1986, Lewis 1986).

Varying productivity potential can also affect algal community structure. In tidepools, removing herbivores from low-intertidal pools (high productivity potential) resulted in domination by leathery macrophytes (Paine and Vadas 1969a), while similar removals in mid-pools led to foliose or corticated macrophytes. In high pools (i.e., low productivity potential), the only change was from one species of crust to another (Dethier 1981a,b). Cubitt (1984) showed that in the high intertidal zone of Oregon, a seasonal increase in productivity potential (due to lowered desiccation stress) combined with little wintertime change in grazing pressure shifts the cover on the rock from largely bare or covered with microalgae in the summer to abundant filamentous and foliose algae in the winter.

Algal functional group dominance along productivity potential gradients correspond to the left axis of Fig. 5D. In the absence of herbivory, there is a consistent, global trend in morphology among benthic marine algae along subtidal gradients in productivity potential (reviewed in Vadas and Steneck 1988) with leathery macrophytes dominating the shallowest areas, corticated macrophytes and foliose algae somewhat deeper, and crustose algae at extinction depths (*sensu* Sears and Cooper 1978). Thus, crustose algae dominate under conditions where both disturbance and productivity potentials are low, such as at great depths or in cryptic environments (Sears and Cooper 1978, Steneck 1978, 1986, Littler et al. 1985, 1986, 1991, Vadas and Steneck 1988). This helps explain why the mass mortality of urchins in the Caribbean had relatively little impact on the dominance of crustose algae in deep cryptic habitats where both productivity and disturbance potentials were very low (i.e., >30 m under plate corals, Jackson and Kaufman 1987, Morrison 1988), but had a major effect in shallow water where both were high before the die off (e.g., Carpenter 1988, Morrison 1988). Stands of large macroalgae require environments with a high productivity potential because they support proportionally more nonphotosynthetic tissue

than do minute turf algae at the other end of the functional group continuum (Littler and Littler 1984). This may be why large leathery macrophytes apparently cannot grow in water as deep as corticated macroalgae or articulated calcified forms (Vadas and Steneck 1988). In contrast, thin (totally pigmented) crustose forms having thalli normal to the direction of incoming light can grow to the greatest depths of the photic zone (Adey and Macintyre 1973, Littler et al. 1985, 1986, Vadas and Steneck 1988). In the Caribbean, *Lobophora variegata*, a corticated erect macroalga in shallow water grows as a prostrate, almost crustose, plant at greater depths (Coen and Tanner 1989). This erect to crustose morphological plasticity may have contributed to the increased abundance of this plant following the mass mortality of *Diadema antillarum* in deep water above extinction depths (Ruyter van Steveninck and Bak 1986). At the community level, Littler et al. (1991) showed that comparisons among shallow habitats in the Indo-Pacific having high productivity potential (i.e., elevated nutrient levels) with low to high levels of herbivore-induced disturbance potential (i.e., grazing activity) shifted to crustose corallines. Such differences in morphology, biomass, diversity and dominance along a gradient in productivity potential are readily visualized in Fig. 5D. Thus, a small shift in the balance between the productivity and the disturbance potentials of the environment can result in a highly visible and predictable shift in the algal assemblage.

Interactions between algal functional groups and structuring processes

Feedback mechanisms between algae and herbivores contribute to the persistence of patterns such as those in Fig. 5D. Some areas dominated by large, canopy forming erect macroalgae (AG 4–6) resist invasion from some invertebrate herbivores by limiting suitable space on which the herbivores can reside and graze (Hay 1981b, Underwood and Jernakoff 1981, Steneck and Watling 1982). As a result, relatively few invertebrate grazers can feed on established macroalgae (Table 1). Such algae also persist because single bites from herbivores are unlikely to remove them, and they can repair themselves by reforming meristematic tissues. When intense-grazing herbivores such as parrotfishes capable of consuming large macroalgae feed, the loss of those algal groups (shift from left to right in Fig. 5D) is often compensated for by an increase in mass-specific productivity (Carpenter 1986). Turfs (AG 1–3) that coexist under high levels of herbivory show rapid replacement, thereby maintaining high levels of local (e.g., limpet-maintained gardens, Branch et al. 1992) or community productivity (Adey and Steneck 1985, Carpenter 1986, Adey and Goertemiller 1987, Williams and Carpenter 1990), and thus maintain or possibly increase the trophic carrying capacity of their environment. However if a further increase in herbivore-induced disturbance shifts the community to dominance

by crusts, then the low nutritional value (Paine and Vadas 1969b) and relatively high resistance to herbivory of that group will lower the trophic carrying capacity of that environment for herbivores. This will limit further increases in herbivore populations. Like clonal terrestrial plants (Bazzaz et al. 1987), crusts are favored where horizontal spread is advantageous relative to vertical growth (i.e., where intense disturbance can remove any vertical growth). Stable coralline-dominated communities existing under conditions of most intense and frequent grazing have been reported world-wide (reviewed by Lawrence 1975, Steneck 1986).

The size, shape and material composition of an alga may control the ability of a grazer to bite the plant, and thus be prime determinants of edibility (e.g., Pennings and Paul 1992). In contrast, chemical deterrents involving palatability usually involve taste (i.e., post-ingestion) and will be important in modifying an herbivore's subsequent foraging behavior if the grazer is capable of visually or chemically recognizing and biting the plant (i.e., it is apparent and edible). Accordingly, the majority of chemical defenses are found among macroalgae (AG 4–6; e.g., Hay et al. 1987, Hay and Fenical 1988, 1992). If an alga with toxins or digestion inhibitors (Tugwell and Branch 1992) is grazed, this constitutes a disturbance to the plant even if the herbivore immediately rejects the tissue consumed (e.g., Targett et al. 1986). If these compounds kill the grazer or result in a behavioral change to avoid the alga, then they are deterrent. Neither our study (Fig. 5) or others have found chemically defended algae dominating zones with high or very high disturbance potentials. Thus there is little evidence that chemical deterrents determine the structure of algal assemblages although they probably control what species within a functional group are found. Nutritional value of algae may also affect the species consumed (Horn and Neighbors 1984, Steinberg 1985), but primarily at within-functional group levels. Such within – versus between – functional group processes may be useful distinctions in studying the structure and function of complex natural communities.

Unifying concepts: marine and terrestrial comparisons

The patterns we have described (Fig. 5D) indicate that algal functional groups exhibit similarities in their distribution and abundance corresponding to two structuring parameters in the environment. A functional group thus comprises the intrinsic characteristics (e.g., morphological and anatomical) that contribute to its ecological success at some point along the continua of environmental productivity and disturbance potentials (e.g., Fig. 4). Terrestrial ecologists have long grouped ecologically or morphologically similar plants (Raunkiaer 1934, Danseureau 1957, Holdridge 1967) but no consistent scheme evolved from their efforts. Although there is general

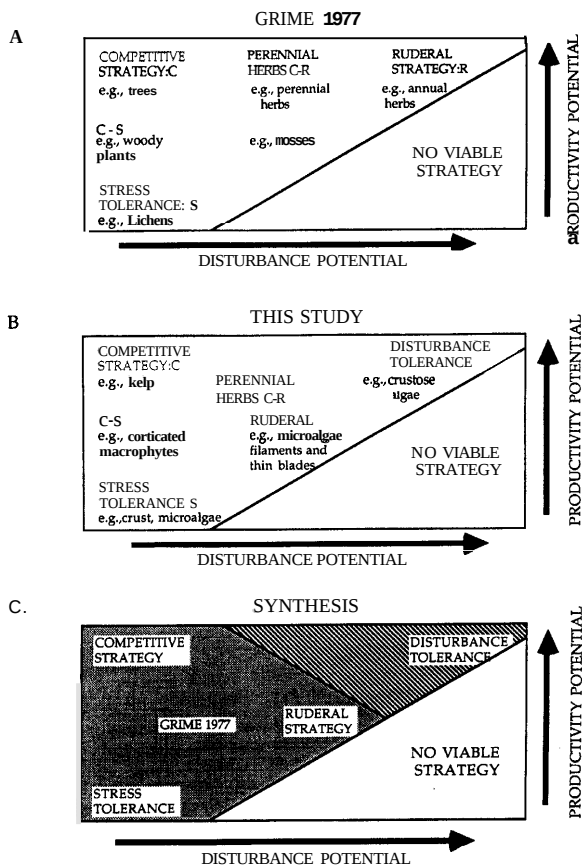


Fig. 7. Generalized model of community dominants that compares Grime's (1977) model (A) with ours (Fig. 5) by using Grime's (1977) terminology and a common orientation of disturbance and productivity potentials of the environment (B, see text and Southwood 1988). The synthesis (C) incorporates disturbance tolerance to Grime's (1977) model.

conceptual agreement concerning the importance of disturbance and productivity potential (often presented as its inverse, "stress" or "adversity") as two of the most important environmental components, there is considerable disagreement about how best to apply these parameters (e.g., see Greenslade 1983, Loehle 1988, Southwood 1988, Taylor et al. 1990, Herms and Mattson 1992). Many studies choose the two variables of productivity and disturbance to create rectangular plots (reviewed by Southwood 1988). However, Grime (1974, 1977, 1981) added "competition" to form a triangular model. This approach has been criticized as tautological because biotic processes such as competition and disturbance are mediated by intrinsic properties of the organisms and thus cannot be used to predict organism dominance (Van der Steen and Scholten 1985). Despite other criticisms of triangular representation of plant "strategies" (e.g., Van der Steen and Scholten 1985, Loehle 1988, Taylor et al. 1990), many marine researchers have applied Grime's models to the study of benthic marine algae (e.g., Shep-

herd 1981, Dayton et al. 1984, Littler and Littler 1984). In Fig. 7A we modified Grime's model taking into account several of these criticisms into a rectangular model based on the productivity and disturbance potentials of the environment (i.e., independent of algae present) as we have defined those terms and in accordance with the habitat tetraplet model of Southwood (1988).

The algal functional groups presented here (Fig. 1), and by Littler and Littler (1980, 1984) show some parallels with terrestrial plant strategies of Grime (Fig. 7A, B). Leathery macrophytes such as kelps correspond to the "Competitive Strategy" of Grime (1981) or the "Growth-Dominated" plants of Herms and Mattson (1992) by being large canopy-forming plants and thus often assumed to be good competitors for light. They are most abundant in productive, relatively undisturbed environments (Fig. 5) and have characteristics such as medium longevity, often structural and/or chemical and anti-herbivore defenses and low tolerance to stress in common with Southwood's (1988) habitat tetraplet model. Similarly, "Stress-Tolerant" (sensu Grime 1981) or "Differentiation-Dominated" (sensu Herms and Mattson 1992) algae include some of the crusts and microalgae, both of which grow in less productive environments. "Ruderal" algae include microalgae, filaments, and foliose algae which, as in their terrestrial counterparts, are short-lived, but colonize and grow rapidly (Littler and Littler 1980, Adey and Goertemiller 1987). They may occupy habitats such as boulders that roll frequently, causing repeated, severe disturbances to the algal assemblage (Sousa 1979, Littler and Littler 1984).

However, marine algae have a fourth distinct and common strategy: Disturbance-Tolerance (Figs 7B, C; Dayton et al. 1984, Littler and Littler 1984, Russell 1986). For example, encrusting coralline algae tolerate disturbances that would severely damage or remove other plants. Disturbance-tolerant plants either resist (by being structurally protected against injury, e.g., Pennings and Paul 1992) or rapidly recover from disturbances. Unlike the Ruderal Strategy of Grime (1981) constant recruitment is not necessary to maintain their dominance. The terrestrial realm also contains examples of genuinely disturbance-tolerant plants, including plants that resist herbivory by being distasteful or inedible (Harper 1969), tolerate it with regrowth (e.g., turf grasses, Mack and Thompson 1982) or thrive under frequent herbivore-induced disturbance (McNaughton 1979). Other plants, such as those of the Fynbos of Southern Africa, routinely tolerate and even require physical disturbance from fire (Bond et al. 1992).

Variations and limitations in approach

Russell (1986) notes that there are problems with any classification of strategies of marine algae (Fig. 7). While functional groups can be placed on such a diagram with some degree of certainty, individual species may be diffi-

cult to classify. He cites examples such as ulvoids which are clearly stress-tolerant and grazer-susceptible, but under some conditions, are good competitors (Lubchenco 1978, Sousa 1979). Although no scheme is perfect, the generality of the model can be seen in the volume of literature (cited above) that it does explain. Some objections can be answered by understanding intraspecific and intra-plant differences in functional characteristics. For example, algae pass through different functional groups as they grow (Steneck and Watling 1982). Therefore macroalgae (AG 4–6) outcompeted by ulvoids (AG 3) were in fact at a spore/sporeling state, and thus more similar to microalgae or filaments in AG 1 and 2 at the time of competition. Phenotypic plasticity also allows species to cross functional groups. Lewis et al. (1987) showed that ecotypic variation can be induced by herbivores; in the presence of frequent fish grazing, a corticated foliose alga (AG 3.5) can become a filamentous form (AG 2). Hanisak et al. (1988) showed that genetically maintained morphological variants of the macroalga *Gracilaria* sp. differ in mass-specific productivity. Similarly, the ploidy level of heteromorphic algae, by definition, determines functional differences related to morphology (Slocum 1980, Dethier 1981b, Steneck and Watling 1982, Littler and Littler 1983, Littler et al. 1987).

Some complex algae may be composed of several different functional modules (sensu Harper 1985). For example a *Sargassum* plant (AG 5) may have a crustose holdfast (—AG 7), a leathery stipe (AG 5) and thin-foliose “leaves” (—AG 3). Littler and Kauker (1984) showed the upright portion of *Corallina officinalis* (AG 6) is more productive and more susceptible to disturbance than the crustose holdfast (AG 7). For a given morphologically complex alga, thallus longevity and mass-specific productivity of their individual modular components probably correspond to the relationships summarized in Fig. 3. Thus one may expect “leaves” of *Sargassum* to be more productive (Kilar et al. 1989) but have a shorter longevity (due to senescence and increased grazer susceptibility) relative to its crustose holdfast. For example, Hay et al. (1987) described amphipod grazing on *Sargassum* as being largely confined to leaves. This provides a new way of considering ecological processes such as recruitment, production, competition and predation by considering each relative to the module of interest. This should complement the modular demography discussed for higher plants by Harper (1977), and for other clonal organisms by Jackson et al. (1985).

Stability at the functional group level

While stability at the species (i.e., population) level is notoriously difficult to define and demonstrate (Connell and Sousa 1983, Connell 1986), stability at the functional group level may be the norm in nature. If levels of productivity potential and disturbance do not change, then algal community structure (relative abundance,

dominance and functional group diversity) should not change, even though species turnover may be high. Thus even though a community having a high disturbance potential is constantly perturbed (in terms of biomass being removed and perhaps of species being driven to local extinction), if that level of perturbation is not altered, the structure of the algal assemblage should remain stable at the functional group level.

Algal communities on reefs provide good examples of stability at the functional group level, despite high rates of disturbance (Hatcher 1983, Carpenter 1986). Shallow forereef zones are characterized as having high levels of herbivory (Ogden and Lobel 1978, Hay 1981c, Hay et al. 1983, Lewis and Wainwright 1985) and low algal biomass (“turfs”, e.g., Carpenter 1986, Littler et al. 1991). Turfs are composed primarily of filamentous and microalgal species and although they are highly diverse with well over 100 species on Caribbean reefs (Adey et al. 1981), only 30 to 50 of these species are common at any time (Adey and Steneck 1985). We found (Fig. 6A) that only a few species persisted or remained abundant from one season to the next but that the community is seasonally relatively stable when examined at a functional group level (Fig. 6B).

Long term stability and evidence for multiple stable points is evident in the structure of forereef communities at Discovery Bay, Jamaica. The reef was described decades ago as having low algal biomass, virtual absence of macroalgae and an abundance of corals (Goreau 1959) which was typical of forereefs throughout the Caribbean (e.g., Randall 1961, Earle 1972, Van den Hoek et al. 1975). Quantitative data from that reef in 1978 and 1982 (Table 4) show that the dominant components changed little over the decades despite intervening hurricanes (see Results). However, the mass mortality of the sea urchin, *Diadema antillarum*, in 1983 significantly reduced the disturbance potential of the shallow forereef (i.e., high productivity potential) environment. The rise to dominance of macroalgae corresponded with the decrease in coral cover (Table 4). The forereef community has remained in this state since, suggesting that multiple stable points (Sutherland 1974) may operate at a functional group level when changes occur in the disturbance potential or productivity potential of the environment. The model (Fig. 5D) predicts that the greatest change in community structure will occur with changes in disturbance potential where productivity potential is high. This may explain why little change was observed in algal community structure in zones having had consistently lower population densities of *Diadema* before the mortality (i.e., lower disturbance potential, such as in the back-reef; Table 4), or having both lower productivity and disturbance potentials such as deep cryptic reef habitats (Jackson and Kaufman 1987, Morrison 1988).

Conclusions

Littler and Littler (1984: 31) note that, by using a functional group approach, it is possible to "... predict community composition from knowledge of disturbance levels in given environments, or the reverse. Further, the approach is applicable anywhere the predominant algal abundances are known without being restricted by phylogenetic group, habitat, or geological era". Our general model (Fig. 5D) provides a simple way to predict algal community composition based on two environmental axes, or conversely, to gain insight about the environmental conditions in an area by examining the algae. Strong patterns emerge in how algae of specific forms relate to the environment because structuring processes (disturbance and productivity potentials) impinge in a form-specific manner. The degree to which our community structure model describes the structure of several disparate marine communities suggests that the relatively few variables we have isolated are fundamentally important. It follows that natural or man-made alterations of one or both of these parameters will cause predictable changes in algal community structure. Thus, while we cannot predict how a given species will respond to a decrease in physiological stress in its environment or to an increase in herbivory over geological time, we can predict how the assemblage of algae will change at the functional group level. Algal functional groups, like all human-imposed aggregations (Orians 1981), have limitations in the precisions of their boundaries and the level of questions they address. Our approach does not deny the utility or necessity of ecological study at the species level, but we conclude that it is useful to examine some community-level questions about structuring processes, diversity, dominance, relative abundance, stability and paleoecology at the level of functional groups.

Acknowledgements – We gratefully acknowledge the help we received from many colleagues with whom we have shared the ideas, especially: the 1978 Coral Reef Ecology class at Discovery Bay Jamaica (who heard the concepts first), W. Adey, R. Carpenter, S. Hacker, M. Hay, J. B. C. Jackson, J. Lubchenco, F. McKinney, D. McNaught, M. Nitecki, R. T. Paine, A. Palma, C. Pfister, J. Porter, S. Stanley, R. L. Vadas, G. Vermeij and L. Watling, G. M. Branch, S. Brawley, S. Dudgeon, D. O. Duggins, S. Hacker, M. Hay, B. Jones, S. Lewis, M. and D. Littler, H. and K. Nielsen, T. Moskovitz, P. Ojeda, C. Pfister, and B. Santelices critiqued drafts of this manuscript. Space and logistical support were provided at the West Indies Laboratory in St. Croix by J. Ogden and R. Dill, Discovery Bay Marine Laboratory in Jamaica by J. Woodley, Darling Marine Center in Maine by L. Watling, Friday Harbor Laboratories in Washington by A. O. D. Willows. Access to field sites at Tatoosh Island, Washington was arranged by R. T. Paine and granted by the Makah Tribal Council and the U.S. Coast Guard. The Nature Conservancy allowed us to work on Yellow Island, and B. and S. Ragen provided access to their shoreline on San Juan Island. P. Mace, K. Paull, K. Irons, and D. Duggins helped in the field in Washington. M. Brittsan, B. Milliken, K. Paull, C. Pfister and S. Stilwell helped in field work and data analysis in Maine. To all we are grateful. This research was primarily funded by grants from the National Science Foundation (OCE 8315136 and OCE 8600262) with additional funding from several sources. Studies

of deep water algae in the Gulf of Maine were funded by a grant from NOAA's National Undersea Research Center at the Univ. of Connecticut. Other research in Maine was funded by UM/ UNH Sea Grant (R/FMD-169, NA86AA-D-SG-047). Research in St. Croix was funded by NOAA/NURC/FDU grants (82–6, 87–5). This is contribution number 269 of the Darling Marine Center.

References

- Adey W. H. and Macintyre, I. G. 1973. Crustose coralline algae: a re-evaluation in the geological sciences. – *Geol. Soc. Am. Bull.* 84: 883–904.
- and Steneck, R. S. 1985. Highly productive eastern Caribbean reefs: synergistic effects of biological, chemical, physical, and geological factors. – In: Reaka, M.L. (ed.), *The ecology of coral reefs*. Vol. 3, No. 1. Symposia series for Undersea Research, NOAA's Undersea Research Program. pp. 163–187.
- and Goertemiller, T. 1987. Coral reef algal turfs: master producers in nutrient poor seas. – *Phycologia* 26: 374–386.
- , Adey, P., Burke, R. and Kaufmann, L. 1977. The Holocene reef systems of eastern Martinique, French West Indies. – *Atoll Res. Bull.* 218: 1–40.
- , Rogers, C. S., Steneck, R. S. and Salesky, N. H. 1981. The South St. Croix reef: a study of reef metabolism as related to environmental factors and an assessment of environmental management. – Rept. to Dept. Conserv. Cult. Affairs, U.S. Virgin Islands. 64 pp.
- Ankel, W. E. 1936. Die Fabsuren von *Helicion* und *Littorina* und die Funktion der Radula. – *Verh. Dtsch. Zool. Ges.* 12: 174–182.
- Ayling, A. M. 1981. The role of biological disturbance in temperate subtidal encrusting communities. – *Ecology* 62: 830–847.
- Bazzaz, F. A., Chiariello, N. R., Coley, P. D. and Pitelka, L. F. 1987. Allocating resources to reproduction and defense. – *Bioscience* 37: 58–67.
- Bertness, M. D. 1984. Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh. – *Ecology* 64: 1794–1807.
- Black, R. 1974. Some biological interactions affecting intertidal populations of the kelp *Egregia laevigata*. – *Mar. Biol.* 28: 189–198.
- Blinks, L. R. 1955. Photosynthesis and productivity of littoral marine algae. – *J. Mar. Res.* 14: 363–373.
- Bond, W. J., Cowling, R. M. and Richards, M. B. 1992. Competition and coexistence. – In: Cowling, R. (ed.), *The ecology of Fynbos: nutrients, fire and diversity*. – Oxford Univ. Press, Oxford, pp. 206–225.
- Bosman, A. L., DuToit, J. T., Hockey, P. A. R. and Branch, G. M. 1986. A field experiment demonstrating the influence of seabird guano on intertidal primary production. – *Estuarine Coastal Shelf Sci.* 23: 283–294.
- Branch, G. M. 1975. Mechanisms reducing intraspecific competition in *Patella* spp.: migration, differentiation and territorial behavior. – *J. Anim. Ecol.* 44: 575–606.
- and Branch, M. L. 1980. Competition between *Cellana tramoserica* (Sowerby) (Gastropoda) and *Patriella exigua* (Lamarck) (Asteroidea), and their influence on algal standing stocks. – *J. Exp. Mar. Biol. Ecol.* 48: 35–49.
- , Harris, J. M., Parkins, C., Bustamente, R. H. and Eekhout, S. 1992. Algal 'gardening' by grazers: a comparison of the ecological effects of territorial fish and limpets. – In: John, D. M., Hawkings, S. J. and Price, J. H. (eds), *Plant-animal interactions in the benthos*. Clarendon Press, Oxford, pp. 405–423.
- Brawley, S. H. and Adey, W. H. 1981. The effect of micrograzers on algal community structure in a coral reef microcosm. – *Mar. Biol.* 61: 167–177.

- and Fei, X. G. 1987. Studies of mesoherbivory in aquaria and in the unbarricaded mariculture farm on the Chinese coast. – J. Phycol. 23: 614–623.
- Carpenter, R. C. 1981. Grazing by *Diadema antillarum* (Philipi) and its effects on the benthic algal community. – J. Mar. Res. 39: 749–765.
- 1985a. Relationships between primary production and irradiance in coral reef algal communities. – Limnol. Oceanogr. 30: 784–793.
- 1985b. Sea urchin mass-mortality: effects on reef algal abundance, species composition and metabolism and other coral reef herbivores. – Proc. Fifth Int. Coral Reef Cong. 4: 53–60.
- 1986. Partitioning herbivory and its effects on coral reef algal communities. – Ecol. Monogr. 56: 345–363.
- 1988. Mass mortality of a Caribbean sea urchin: Immediate effects on community metabolism and other herbivores. – Proc. Natl. Acad. Sci. USA. 85: 511–514.
- 1990. Competition among marine macroalgae: a physiological perspective. – J. Phycol. 26: 6–12.
- Castenholz, R. W. 1961. The effect of grazing on marine littoral diatom populations. – Ecology 42: 783–794.
- Coen, L. D. and Tanner, C. E. 1989. Morphological variation and differential susceptibility to herbivory in the tropical brown alga *Lobophora variegata*. – Mar. Ecol. Prog. Ser. 54: 287–298.
- Connell, J. H. 1986. Variation and persistence of rocky shore populations. – In: Moore, P. G. and Seed, R. (eds), The ecology of rocky coasts. Columbia Univ. Press, New York, pp. 57–69.
- and Sousa, W. P. 1983. On the evidence needed to judge ecological stability or persistence. – Am. Nat. 121: 789–824.
- Cubit, J. D. 1984. Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. – Ecology 65: 1904–1917.
- D'Antonio, C. M. D. 1986. Growth and reproduction of the red alga *Rhodomela larix*. – Can. J. Bot. 64: 1499–1506.
- Dansereau, P. 1957. Biogeography: an ecological perspective. – Ronald Press, New York.
- Day, J. 1967. Polychaeta of southern Africa. Pt. I, Errantia; – Brit. Mus. Nat. Hist.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. – Ecol. Monogr. 41: 351–389.
- 1973. Dispersal, dispersal, and persistence of the annual intertidal alga, *Postelsia palmaeformis* Ruprecht. – Ecology 54: 433–438.
- 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. – Ecol. Monogr. 45: 137–159.
- , Currie, V., Gerrodette, T., Keller, B. D., Rosenthal, R. and Tresca, D. V. 1984. Patch dynamics and stability of some California kelp communities. – Ecol. Monogr. 54: 253–289.
- Dethier, M. N. 1981a. The natural history and community structure of Washington tidepools: disturbance, herbivory and the maintenance of pattern in intertidal microcosms. – Ph.D. Dissertation, Univ. of Washington.
- 1981b. Heteromorphic algal life histories: the seasonal pattern and response to herbivory of the brown crust, *Ralfsia californica*. – Oecologia 49: 333–339.
- and Duggins, D. O. 1984. An “indirect commensalism” between marine herbivores and the importance of competitive hierarchies. – Am. Nat. 124: 205–219.
- DeWreede, R. E. 1984. Growth and age class distribution of *Pterygophora californica* (Phaeophyta). – Mar. Ecol. Prog. Ser. 19: 93–100.
- Doty, M. 1971. The productivity of benthic frondose algae at Waikiki beach 1966–1969. – Univ. Hawaii, Bot. Sci. Paper 22: 1–119.
- Duggins, D. O. 1980. Kelp beds and sea otters: an experimental approach. – Ecology 61: 447–453.
- and Dethier, M. N. 1985. Experimental studies of herbivory and algal competition in a low intertidal habitat. – Oecologia 67: 183–191.
- Earle, S. 1972. The influence of herbivores on the marine plants of Great Lameshur Bay, with an annotated list of plants. – In: Collette, B. B. and Earle, S. A. (eds), Results of the Tektite Program: ecology of coral reef fishes. – Nat. Hist. Mus. L.A. County. Sci. Bull. 14: 17–44.
- Edyvean, R. G. J. and Ford, H. 1984. Population biology of the crustose red alga *Lithophyllum incrustans* Phil. 2. A comparison of populations from three areas of Britain. – Biol. J. Linn. Soc. 23: 353–363.
- Emerson, S. E. and Zedler, J. B. 1978. Recolonization of intertidal algae: an experimental study. – Mar. Biol. 44: 315–324.
- Fauchald, K. and Jumars, P. A. 1979. The diet of worms: a study of polychaete feeding guilds. – Annu. Rev. Oceanogr. Mar. Biol. 17: 193–284.
- Fletcher, W. J. 1987. Interactions among subtidal Australian sea urchins, gastropods, and algae: effects of experimental removals. – Ecol. Monogr. 57: 89–109.
- and Underwood, A. J. 1987. Interspecific competition among subtidal limpets: effect of substratum heterogeneity. – Ecology 68: 385–398.
- Foster, S. A. 1987. The relative impact of grazing by Caribbean coral reef fishes and *Diadema*: effects of habitat and surge. – J. Exp. Mar. Biol. Ecol. 105: 1–20.
- Goff, L. J. and Cole, K. 1976. The biology of *Harveyella mirabilis* (Cryptonemates, Rhodophyta) IV Life history and phenology. – Can. J. Bot. 54: 281–292.
- Goreau, T. F. 1959. The ecology of Jamaican coral reefs I. Species composition and zonation. – Ecology 40: 67–90.
- Graham, A. 1955. Molluscan diets. – Proc. Malac. Soc., Lond. 33: 144–159.
- Greenslade, P. J. M. 1983. Adversity selection and the habitat templet. – Am. Nat. 122: 352–365.
- Grime, J. P. 1974. Vegetation classification by reference to strategies. – Nature 250: 26–31.
- 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. – Am. Nat. 111: 1169–1194.
- 1981. Plant strategies and vegetation processes. – Wiley, New York.
- Hanisak, M. D., Littler, M. M. and Littler, D. S. 1988. Significance of macroalgal polymorphism: intraspecific tests of the functional-form model. – Mar. Biol. 99: 157–165.
- Hansen, J. E. 1977. Ecology and natural history of *Iridaea cordata* (Gigartinales, Rhodophyta). – J. Phycol. 13: 395–402.
- Hardwick-Witman, M. N. 1985. Biological consequences of ice rafting in a New England salt marsh community. – J. Exp. Mar. Biol. Ecol. 87: 283–298.
- Harlin, M. M. 1971. Epiphytic marine algae: interactions with their host. – Ph. D. Dissertation, Univ. of Washington.
- Harper, J. L. 1969. The role of predation in vegetational diversity. – Brookhaven Symp. Biol. 22: 48–62.
- 1977. Population biology of plants. – Academic Press, London.
- 1985. Modules, branches and the capture of resources. – In: Jackson, J. B. C., Buss, L. W. and Cook, R. E. (eds), Population biology and evolution of clonal organisms. Yale Univ. Press, New Haven, CT, pp. 1–34.
- Harrold, C. and Reed, D. C. 1985. Food availability, sea urchin grazing and kelp forest community structure. – Ecology 66: 1160–1169.
- Hartman, O. 1968. Atlas of the Errantiate polychaetous annelids from California. – Allan Hancock Foundation, Los Angeles.
- Hatcher, B. G. 1981. The interaction between grazing organisms and the epilithic algal community of a coral reef: a quantitative assessment. – Proc. 4th. Int. Coral Reef Symp. Manila 2: 515–524.
- 1983. Grazing in coral reef ecosystems. – In: Barnes, D. J.

- (ed.), Perspectives on coral reefs. Aust. Inst. Mar. Sci., Townsville, Australia, pp. 164–179.
- Hawkins, S. H. and Hartnoll, R. G. 1983. Grazing of intertidal algae by marine invertebrates. – *Oceanogr. Mar. Biol. Ann. Rev.* 21: 195–282.
- Hay, C. 1979. Some factors affecting the upper limit of the southern bull kelp, *Duvillea antarctica* Chamisso Hariot on two New Zealand shores. – *J. R. Soc. N. Z.* 9: 279–287.
- Hay, M. E. 1981a. Spatial patterns of grazing intensity on a Caribbean barrier reef herbivory and algal distribution. – *Aquat. Bot.* 11: 97–109.
- 1981b. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. – *Ecology* 62: 739–750.
- 1981c. Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. – *Am. Nat.* 118: 520–540.
- and Gaines, S. D. 1984. Geographic differences in herbivore impact: do Pacific herbivores prevent Caribbean seaweeds from colonizing the Panama Canal? – *Biotropica* 16: 24–30.
- and Taylor, P. R. 1985. Competition between herbivorous fishes and urchins on Caribbean reefs. – *Oecologia* 65: 591–598.
- and Fenical, W. 1988. Marine plant-herbivore interactions: the ecology of chemical defense. – *Annu. Rev. Ecol. Syst.* 19: 111–145.
- and Fenical, W. 1992. Chemical mediation of seaweed-herbivore interactions. – In: John, D. M., Hawkings, S. J. and Price, J. H. (eds), *Plant-animal interactions in the marine benthos*. Clarendon Press, Oxford, pp. 319–337.
- , Coburn, T. and Downing, D. 1983. Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. – *Oecologia* 58: 299–308.
- , Fenical, W. and Gustafson, K. 1987. Chemical defense against diverse coral-reef herbivores. – *Ecology* 68: 1581–1591.
- Harms, D. A. and Mattson, W. J. 1992. The dilemma of plants: to grow or defend. – *Q. Rev. Biol.* 67: 283–335.
- Hicks, G. R. F. 1986. Meiofauna associated with rocky shore algae. – In: Moore, P. G. and Seed, R. (eds), *The ecology of rocky coasts: essays presented to J. R. Lewis*. Columbia Univ. Press, New York, pp. 36–56.
- Himmelman, J. H. 1984. Urchin feeding and distribution in Newfoundland, Eastern Canada. – *Nat. Can.* 111: 337–348.
- Hixon, M. A. and Brostoff, W. N. 1983. Damselfish as keystone predators in reverse: intermediate disturbance and diversity of reef algae. – *Science* 220: 511–513.
- Holdridge, L. R. 1967. Life zone ecology. – Tropical Science Center, San Jose, CA.
- Hom, M. H. and Neighbors M. A. 1984. Protein and nitrogen assimilation as a factor in predicting the seasonal macroalgal diet of the monkeyface prickleback. – *Trans. Am. Fish. Soc.* 113: 388–396.
- , Murray, S. N. and Seapy, R. R. 1983. Seasonal structure of a central California rocky intertidal community in relation to environmental variations. – *Bull. South. Calif. Acad. Sci.* 82: 79–94.
- Howard, A. K. 1982. Impact of feeding activities of epibenthic amphipods on surface-fouling of eelgrass leaves. – *Aquat. Bot.* 14: 91–97.
- Hughes, T. P., Reed, D. C. and Boyle, M. 1987. Herbivory on coral reefs: community structure following mass mortalities of sea urchins. – *J. Exp. Mar. Biol. Ecol.* 113: 39–59.
- Jackson, J. B. C. and Kaufman, L. 1987. *Diadema antillarum* was not a keystone predator in cryptic reef environments. – *Science* 235: 687–689.
- , Buss, L. W. and Cook, R. E. (eds) 1985. *Population biology and evolution of clonal organisms*. – Yale Univ. Press, New Haven, CT.
- Jones, R. S. 1968. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (surgeonfishes). – *Micronesica* 4: 309–361.
- Kain, J. M. 1971. Synopsis of biological data on *Laminaria hyperborea*. – FAO Fish. Synopsis No. 87.
- Kendrick, G. A. 1991. Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: effects of simulated scour, erosion and accretion. – *J. Exp. Mar. Biol. Ecol.* 147: 47–63.
- Keser, M. and Larson, B. 1984. Colonization and growth dynamics of three species of *Fucus*. – *Mar. Ecol. Prog. Ser.* 15: 125–134.
- Khailov, K. M. 1979. Ontogenic trends in morphologic parameters of *Cystoseira barbata* thalli. – *Bot. Mar.* 22: 299–311.
- Kilar, J. A., Littler, M. M. and Littler, D. S. 1989. Functional-morphological relationships in *Sargassum polyceratum* (Phaeophyta): Phenotypic and ontogenetic variability in apparent photosynthesis and dark respiration. – *J. Phycol.* 25: 713–720.
- Klinger, T. and DeWreede, R. E. 1988. Stipe rings, age, and size in populations of *Laminaria setchellii* Silva (Laminariales, Phaeophyta) in British Columbia, Canada. – *Phycologia* 27: 234–240.
- Kohn, A. J. and White, J. K. 1977. Polychaete annelids of an intertidal reef limestone platform at Tanguisson, Guam. – *Micronesica* 13: 199–215.
- Lawrence, J. M. 1975. On the relationships between marine plants and sea urchins. – *Oceanogr. Mar. Biol. Ann. Rev.* 13: 213–286.
- Lebednik, P. A. 1977. The Corallinaceae of northwestern North America. 1. *Clathromorphum* Foslíe emend Adey. – *Syesis* 9: 59–112.
- Leigh, E. G. Jr., Paine, R. T., Quinn, J. F. and Suchanek, T. H. 1987. Wave energy and intertidal productivity. – *Proc. Natl. Acad. Sci., USA*. 84: 1314–1318.
- Levings, S. C. and Garrity, S. D. 1983. Diel and tidal movement of two co-occurring neritid snails: differences in grazing patterns on a tropical rocky shore. – *J. Exp. Mar. Biol. Ecol.* 67: 261–278.
- Levitan, D. R. 1988. Algal-urchin biomass responses following mass mortality of *Diadema antillarum* at Saint John, U.S. Virgin Islands. – *J. Exp. Mar. Biol. Ecol.* 119: 167–178.
- Lewis, S. 1985. Herbivory on coral reefs: algal susceptibility to herbivorous fishes. – *Oecologia* 65: 370–375.
- 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. – *Ecol. Monogr.* 56: 183–200.
- and Wainwright, P. C. 1985. Herbivore abundance and grazing intensity on a Caribbean coral reef. – *J. Exp. Mar. Biol. Ecol.* 87: 215–228.
- , Norris, J. N. and Searles, R. B. 1987. The regulation of morphological plasticity in tropical reef algae by herbivory. – *Ecology* 68: 636–641.
- Littler, M. M. and Littler, D. S. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. – *Am. Nat.* 116: 2544.
- and Arnold, K. E. 1982. Primary productivity of marine macroalgal functional-form groups from southwestern North America. – *J. Phycol.* 18: 307–311.
- and Kauker, B. J. 1984. Heterotrichy and survival strategies in the red alga *Corallina officinalis*. – *Bot. Mar.* 27: 37–44.
- and Littler, D. S. 1984. Relationships between macroalgal functional form groups and substrata stability in subtropical rocky-intertidal system. – *J. Exp. Mar. Biol. Ecol.* 74: 13–34.
- , Taylor P. R. and Littler, D. S. 1983a. Algal resistance to herbivory on a Caribbean Barrier Reef. – *Coral Reefs* 2: 111–118.
- , Martz, D. R. and Littler, D. S. 1983b. Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. – *Mar. Ecol. Prog. Ser.* 11: 129–139.
- , Littler, D. S., Blair, S. M. and Norris, J. N. 1985. Deepest known plant life discovered on an uncharted seamount. – *Science* 227: 57–59.
- , Littler, D. S., Blair, S. M. and Norris, J. N. 1986. Deep-

- water plant communities from an uncharted seamount off San Salvador Island, Bahamas: distribution, abundance, and primary productivity. – *Deep-sea Res.* 33: 881–892.
- , Taylor, P. R. and Littler, D. S. 1987. Functional similarity among isomorphic life history phases of *Polycavernosa debilis* (Rhodophyta, Gracilariaceae). – *J. Phycol.* 23: 501–505.
 - , Littler, D. S. and Titlyanov, E. A. 1991. Comparisons of N- and P-limited productivity between high granitic islands versus low carbonate atolls in the Seychelles Archipelago: a test of the relative-dominance paradigm. – *Coral Reefs* 10: 199–209.
- Loehle, C. 1988. Problems with the Triangular Model for presenting plant strategies. – *Ecology*. 69: 284–286.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. – *Am. Nat.* 112: 23–39.
- 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. – *Ecology* 61: 333–344.
 - and Gaines, S. D. 1981. A unified approach to marine plant-herbivore populations. I. Populations and communities. – *Annu. Rev. Ecol. Syst.* 12:405–437.
- MacArthur, R. H. 1972. *Geographical ecology*. – Harper and Row, New York.
- Mack, R. N. and Thompson, J. N. 1982. Evolution in steppe with few large, hooved mammals. – *Am. Nat.* 119: 757–771.
- MacMillan, C. 1902. Observations on *Pterygophora*. – *Minnesota Bot. Stud.*, ser. 2, 2: 723–741.
- McNaughton, S. J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. – *Am. Nat.* 113: 691–703.
- Menge, B. A. 1972. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. – *Ecol. Monogr.* 42: 25–50.
- and Lubchenco, J. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. – *Ecol. Monogr.* 51: 429–450.
 - , Lubchenco, J., Ashkenas, L. R. and Ramsey, F. 1986. Experimental separation of effects of consumers on sessile prey in the low zone of a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. – *J. Exp. Mar. Biol. Ecol.* 100: 225–269.
- Montgomery, W. L. 1980. The impact of non-selective grazing by the giant blue damselfish, *Microspathodon dorsalis*, on algae communities in the Gulf of California, Mexico. – *Bull. Mar. Sci.* 30: 290–303.
- Morrison, D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. – *Ecology* 69: 1367–1382.
- Mumford, T. F. 1973. Observations on the taxonomy and ecology of some species of *Porphyra* from Washington and Vancouver Island, British Columbia. – Ph. D. dissertation, Univ. of Washington.
- Murray, S. and Littler, M. M. 1978. Patterns of algae succession in a perturbed marine intertidal community. – *J. Phycol.* 14: 506–512.
- Nicotri, M. E. 1977. Grazing effects of four marine intertidal herbivores on the microflora. – *Ecology* 58: 1020–1032.
- Norton, T. A., Hiscock, K. and Kitching, J. A. 1977. The ecology of Lough Ine XX. The *Laminaria* forest at Carrigathorna. – *J. Ecol.* 65: 919–941.
- Ogden, J. C. and Lobel, P. S. 1978. The role of herbivorous fishes and urchins in coral reef communities. – *Evol. Biol. Fish.* 3: 19–63.
- Ojeda, F. P. and Santelices, B. 1984. Invertebrate communities in holdfasts of the kelp *Macrocystis pyrifera* from southern Chile. – *Mar. Ecol. Prog. Ser.* 16: 65–73.
- Orians, G. H. 1981. Aggregations: curse and necessity. – In: *Natural Resources Council 1980. Issues and current studies*, pp. 57–66.
- Padilla, D. K. 1987. The importance of secondary tissue loss: an alternative explanation for potential structural differences in algae. – *Bull. Ecol. Soc. Am.* 68: 382 (Abstr.).
- Paine, R. T. 1977. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. *The Changing Scenes in Natural Sciences, 1776–1976*. – *Acad. Nat. Sci. Special Publ.*, pp. 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. – *J. Anim. Ecol.* 49: 667–685.
 - 1984. Ecological determinism in the competition for space. – *Ecology* 65: 1339–1348.
 - and Vadas, R. L. 1969a. The effect of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. – *Limnol. Oceanogr.* 15: 710–719.
 - and Vadas, R. L. 1969b. Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. – *Mar. Biol.* 4: 11–86.
 - , Slocum, C. J. and Duggins, D. O. 1979. Growth and longevity in the crustose red alga *Petrocelis middendorffii*. – *Mar. Biol.* 51: 185–192.
- Patrick, R. 1970. Benthic stream communities. – *Am. Sci.* 58: 546–549.
- Pennings, S. C. and Paul, V. J. 1992. Effect of plant toughness, calcification and chemistry on herbivory by *Dolabella auricularia*. – *Ecology* 73: 1606–1619.
- Peters, R. H. 1991. *A critique for ecology*. – Cambridge Univ. Press, Cambridge.
- Porter, J. W. 1980. Primary productivity in the sea: reef corals in situ. – In: Falkowski, P. G. (ed.), *Primary productivity in the sea*. Plenum, New York, pp. 403–410.
- Raffaelli, D. G. 1979. The grazer-alga interaction in the intertidal zone on New Zealand rocky shores. – *J. Exp. Mar. Biol. Ecol.* 38: 81–100.
- Randall, J. E. 1961. Overgrazing of algae by herbivorous marine fishes. – *Ecology* 42: 812.
- Raunkiaer, C. 1934. *The life forms of plants and statistical plant geography*. – Clarendon Press, Oxford.
- Reichle, D. E., O'Neill, R. V. and Harris, W. F. 1975. Principles of energy and material exchange in ecosystems. – In: Lowe-McConnell, R. H. (ed.), *Unifying concepts in ecology*. Van Nostrand Reinhold, New York, pp. 27–43.
- Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of Collards (*Brassica oleracea*). – *Ecol. Monogr.* 43: 95–124.
- Round, F. E. 1981. *The ecology of the algae*. – Cambridge Univ. Press, Cambridge.
- Russ, G. R. 1984. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation of mid-shelf and outershelf reefs. – *Mar. Ecol. Prog. Ser.* 20: 35–44.
- 1987. Is rate of removal of algae by grazers reduced inside territories of tropical damselfishes? – *J. Exp. Mar. Biol. Ecol.* 110: 1–17.
- Russell, G. 1986. Variation and natural selection in marine macroalgae. – *Oceanogr. Mar. Biol. Ann. Rev.* 24: 309–377.
- Ruyter van Steveninck, E. D. de and Bak, R. P. M. 1986. Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. – *Mar. Ecol. Prog. Ser.* 34: 87–94.
- Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. – *Am. Nat.* 111: 337–359.
- Sammarco, P. W., Levinton, J. S. and Ogden, J. C. 1974. Grazing and control of coral reef community structure by *Diadema antillarum*. (Echinodermata: Echinoidea): a preliminary study. – *J. Mar. Res.* 32: 47–53.
- Seapy, R. R. and Littler, M. M. 1982. Population and species diversity fluctuations in a rocky intertidal community relative to severe aerial exposure and sediment burial. – *Mar. Biol.* 71: 87–96.
- Sears, J. R. and Cooper, R. A. 1978. Descriptive ecology of

- offshore, deep-water, benthic algae in the temperate western North Atlantic Ocean. – *Mar. Biol.* 44: 309–314.
- Shepherd, S. A. 1981. Ecological strategies in a deep water red algal community. – *Bot. Mar.* 24: 457–463.
- Slocum, C. J. 1980. Differential susceptibility to grazers in two phases of an intertidal alga: advantages of heteromorphic generations. – *J. Exp. Mar. Biol. Ecol.* 46: 99–110.
- Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. – *Ecology* 60: 1225–1239.
- , Schroeter, S. C. and Gaines, S. D. 1981. Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. – *Oecologia* 48: 297–307.
- Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies. – *J. Anim. Ecol.* 46: 337–365.
- 1988. Tactics, strategies and templates. – *Oikos* 52: 3–18.
- Steinberg, P. D. 1985. Feeding preferences of *Tegula funebris* and chemical defenses of marine brown algae. – *Ecol. Monogr.* 55: 333–349.
- Steneck, R. S. 1978. Factors influencing the distribution of crustose coralline algae (Rhodophyta, Corallinales) in the Damariscotta River estuary, Maine. – Masters thesis, Univ. of Maine, Orono, ME.
- 1982. A limpet-coralline alga association: adaptations and defenses between a selective herbivore and its prey. – *Ecology* 63: 507–522.
- 1983a. Quantifying herbivory on coral reefs: just scratching the surface and still biting off more than we can chew. – In: Reaka, M. L. (ed.), *The ecology of deep and shallow coral reefs*. Symposia Series for Undersea Research, Vol. 1. Office of Undersea Research, NOAA, Rockville, MD, pp. 103–112.
- 1983b. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. – *Paleobiology* 9: 44–61.
- 1986. The ecology of coralline algal crusts: consequent patterns and adaptive strategies. – *Annu. Rev. Ecol. Syst.* 17: 273–303.
- 1988. Herbivory on coral reefs: a synthesis. – *Proc. 6th International Coral Reef Symposium, Australia* 1: 37–49.
- 1990. Herbivory and the evolution of nongeniculate coralline algae (Rhodophyta, Corallinales) in the North Atlantic and North Pacific. – In: Garbary, D. and South, R. (eds), *Evolutionary biogeography of the marine algae of the North Atlantic*. NATO ASI Series G 22, pp. 107–129.
- and Watling, L. 1982. Feeding capabilities and limitations of herbivorous molluscs: a functional group approach. – *Mar. Biol.* 68: 299–319.
- , Lutz, R. A. and Cerrato, R. M. 1977. Age and morphometric variation in subtidal populations of mussels. – *Proc. 69th National Shellfish Association Symposium*. Baltimore, MD.
- , Hacker, S. D. and Dethier, M. N. 1991. Mechanism determining competitive dominance between crustose coralline algae: an herbivore-mediated reversal. – *Ecology* 72: 938–950.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. – *Am. Nat.* 108: 859–876.
- Targett, N. M., Targett, T. E., Vrolijk, N. H. and Ogden, J. C. 1986. Effects of macrophyte secondary metabolites on feeding preferences of the herbivorous parrotfish *Sparisoma radians*. – *Mar. Biol.* 92: 141–148.
- Taylor, D. R., Aarssen, L. W. and C. Loehle. 1990. On the relationship between r/K selections and environmental carrying capacity: a new habitat templet for plant life history strategies. – *Oikos* 58: 239–250.
- Taylor, P. R., Littler, M. M. and Littler, D. S. 1986. Escapes from herbivory in relation to the structure of mangrove island macroalgal communities. – *Oecologia* 69: 481–490.
- Tugwell, S. and Branch, G. M. 1992. Do polyphenols in marine algae reduce digestibility? – *Ecology* 73: 205–215.
- Underwood, A. J. 1984a. The vertical distribution and seasonal abundance of intertidal microalgae on a rocky shore in New South Wales. – *J. Exp. Mar. Biol. Ecol.* 78: 199–220.
- 1984b. Vertical and seasonal patterns in competition for microalgae between intertidal gastropods. – *Oecologia* 64: 211–222.
- and Jernakoff, P. 1981. Interactions between algae and grazing gastropods in the structure of a low-shore algal community. – *Oecologia* 48: 221–233.
- Vadas, R. L. and Steneck, R. S. 1988. Patterns of deep water benthic algae in the Gulf of Maine. – *J. Phycol.* 24: 338–346.
- Van den Hoek, C., Cortel-Breeman, A. M. and Wanders, J. B. W. 1975. Algal zonation in the fringing coral reef of Curaçao, Netherlands Antilles, in relation to corals and gorgonians. – *Aquatic. Bot.* 1: 269–308.
- Van der Steen, W. J. and Scholten, M. 1985. Methodological problems in evolutionary biology. IV Stress and stress tolerance, an exercise in definitions. – *Acta Biotheor.* 34: 81–90.
- Vine, P. J. 1974. Effects of algal grazing and aggressive behavior of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral-reef ecology. – *Mar. Biol.* 24: 131–136.
- Walker, A. J. M. 1972. Introduction to the ecology of the Antarctic limpet *Patinigera polaris* at Signy Island, South Orkney Island. – *Br. Antarct. Surv. Bull.* 28: 49–69.
- Ward, J. 1966. Feeding, digestion, and histology of the digestive tract in the keyhole limpet *Fissurella barbadensis* Gmelin. – *Bull. Mar. Sci.* 16: 668–684.
- Widdowson, T. B. 1965. A taxonomic study of the genus *Hedophyllum setchell*. – *Can. J. Bot.* 64: 1499–1506.
- Williams, S. L. and Carpenter, R. C. 1990. Photosynthesis/ photon flux density relationships among components of coral reef turfs. – *J. Phycol.* 26: 36–40.
- Woodin, S. A. 1977. Algal “gardening” behavior by nereid polychaetes: effects on soft-bottom community structure. – *Mar. Biol.* 44: 3942.
- Woodley, J. D., Chomesky, E. A., Clifford, P. A., Jackson, J. B. C., Kaufmann, L. S., Knowlton, N., Lang, J. C., Pearson, M. P., Porter, J. W., Rooney, M. C., Rylaarsdam, K. W., Tunnicliffe, V. J., Wahle, C. M., Wulff, J. L., Curtis, A. S. G., Dallmeyer, M. D., Jupp, B. P., Koehl, M. A. R., Neigel, J. and Sides, E. M. 1981. Hurricane Allen’s impact on Jamaican coral reefs. – *Science* 214: 749–755.
- Zimmerman, R., Gibson, R. and Harrington, J. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. – *Mar. Biol.* 54: 41–47.

Appendix.

Maximum thallus longevities reported for algae. Functional group designation number (i.e., Fig. 1) for each algal species is represented in the column labeled "Algal group"

Reference	Species	Algal group	Max. age (yr)
Patrick 1970	Diatoms	1	0.5
Steneck unpubl.	<i>Ulothrix flacca</i>	2	0.3
Mumford 1973	<i>Porphyra</i> spp.	3	0.8
Harlin 1971	<i>Smithora haiadum</i>	3	0.75
Steneck unpubl.	<i>Enteromorpha</i>	3	0.5
Steneck unpubl.	<i>Halosaccion glandiforme</i>	3	0.5
Hansen 1977	<i>Iridaea splendens</i>	3.5	1
Slocum 1980	<i>Mastocarpus papillatus</i>	4	0.9
Goff and Cole 1976	<i>Odonthalia floccosa</i>	4	1
D'Antonio 1986	<i>Neorhodomela larix</i>	4	2
Steneck unpubl.	<i>Ascophyllum nodosum</i>	5	15
Khailov 1979	<i>Cystoseira barbata</i>	5	18
Hay 1979	<i>Duvillea antarctica</i>	5	9
Black 1974	<i>Egregia laevigata</i>	5	1.25
Connell 1986	<i>Eisenia arborea</i>	5	5
Widdowson 1965	<i>Hedophyllum sessile</i>	5	2
Duggins 1980	<i>Laminaria</i> sp.	5	7
Vadas and Steneck 1988	<i>Laminaria</i> sp.	5	7
Kain 1971	<i>Laminaria hyperborea</i>	5	13
Norton et al. 1977	<i>Laminaria hyperborea</i>	5	9
Klinger and DeWreede 1988	<i>Laminaria setchellii</i>	5	17
Paine Pers. Comm. Oct. 1987	<i>Lessoniopsis littoralis</i>	5	25
Dayton 1973, Paine 1979	<i>Postelsia palmaeformis</i>	5	1
Paine Pers. Comm. Oct. 1987	<i>Pterygophora californica</i>	5	20
MacMillan 1902	<i>Pterygophora californica</i>	5	17
DeWreede 1984	<i>Pterygophora californica</i>	5	9
Steneck et al. 1977	<i>Clathromorphum compactum</i>	7	40
Lebednik 1977	<i>Clathromorphum nereostratum</i>	7	100
Edyvean and Ford 1984	<i>Lithophyllum incrustans</i>	7	34
Paine et al. 1979	"Petrocelis"	7	85
Dethier 1981a,b	"Ralfsia californica"	7	1