A FUNCTIONAL GROUP APPROACH TO THE STRUCTURE OF ALGAL-DOMINATED COMMUNITIES

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

Robert S. Steneck and Megan N. Dethier

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.

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 substantial 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...
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
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:

\[ B_i = R_i + Pn_i - D_i \]

\[ B_i = \text{Biomass of an algal species or functional group (i) that accumulates over some period of time. } i = \text{the specific algal functional group(s) concerned i.e., 1-7 (see Fig. 1). The numeric designation in Fig. 1 is based on the ranking of mass-specific productivity (see Results).} \]

\[ R_i = \text{Rate of recruitment, which is a function of:} \]

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).

\[ Pn_i = \text{Rate of net primary productivity, which is a function of:} \]

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”.

\[ D_i = \text{Rate of herbivore-induced disturbance, which, assuming no refuge, is a function of:} \]

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:

\[ \text{Rate of disturbance (e.g., from herbivores), involving:} \]

Disturbance intensity (amount of biomass lost per event).

\[ \text{Disturbance frequency (events per unit time).} \]

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

Caribbean

Tropical subtidal research was conducted on the Caribbean islands of St. Croix (Teague Bay reef; 17°4'64°37'W and Salt River Canyon 17°48'N, 64°45'W) Jamaica (18°28'N, 77°17'W). Productivity, herbivory algal community structure were measured at three ; and nine depth zones distributed along the north shore St. Croix (0-40 m depths, site details in Steneck 1982). Seasonal comparisons in the structure of algal communities were made at a site on the south shore of St. C (site details in Adey and Steneck 1985). Long-term search transects in Jamaica were established on the wern reef of Discovery Bay (site details in Woodley 1981). Replicated transects were surveyed in 1978, 1 and 1987 at target sites situated in the backreef (1 m), shallow (3 m) and deep (10 m) forereef zones.

General methods

Patterns of distribution and abundance

At each target habitat along subtidal sampling transe haphazardly tossed quadrats (25 cm x 25 cm) were s ped for algal percent cover, canopy height and biom Intertidal sampling used 10 x 10 cm quadrats which v also haphazardly tossed. Herbivores in each quadrat v identified, counted, and measured (length or test di ter). Algal biomass was estimated using a relatively t destructive technique developed at our study site: Maine. The heights of the algal canopies in quadrats v measured by repeatedly inserting a ruler or calibr floating line to the substratum and measuring the lon fronds. Algal percent cover was visually determined, algae were collected within randomly chosen quadrat total biomass and canopy height determinations. The gression of algal biomass and algal canopy height significant (F ratio = 59.1, p < 0.001) for quadrats h a 100% algal cover: y = 134.8 + 7.76x, R² = 0.53, n = where y = dry mass of algal (g) per meter square x = canopy height (mm). This relationship applies species so that only the canopy height of algal mass percent cover data were recorded for the majority of intertidal zone biomass estimates at the Maine and Wington sites.

Biomass was measured directly for all sites in St. C.
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 (Littler and Arnold 1982), the Caribbean (Littler et al. 1983b, 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 unequivocally 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
dence for this is seen in studies of algal succession (Algal groups "A" - 5 and calcification (A" 6 and larger erect algae are longer-lived and slower-growing than 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. Intrinsically 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, Steneck and Watling 1982). The ranking of productivity potential of the environment 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, scads (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).

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

<table>
<thead>
<tr>
<th>Herbivore taxa</th>
<th>Algal functional groups</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Polychaeta</td>
<td>X</td>
</tr>
<tr>
<td>Malacostraca</td>
<td>X</td>
</tr>
<tr>
<td>Gastropoda</td>
<td></td>
</tr>
<tr>
<td>Rhipidiglossa</td>
<td></td>
</tr>
<tr>
<td>Taenioglossa</td>
<td></td>
</tr>
<tr>
<td>Docoglossa</td>
<td></td>
</tr>
<tr>
<td>Polyplocaphora</td>
<td></td>
</tr>
<tr>
<td>Echinoida</td>
<td></td>
</tr>
<tr>
<td>Perciformes</td>
<td></td>
</tr>
</tbody>
</table>

% groups commonly denuding |

|       | 100 | 67  | 33  | 22  | 22  | 11  | 11  |


*Review articles.

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 cayon 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.

<table>
<thead>
<tr>
<th>Maine</th>
<th>Target habitats (sub- and intertidal)</th>
<th>Production g (dry/m^2/yr)</th>
<th>Number of samples</th>
<th>Light (µmol/m^2/s)</th>
<th>Productivity potential</th>
</tr>
</thead>
<tbody>
<tr>
<td>High intertidal zone (+1.6 m)</td>
<td>0.98 (±0.9)</td>
<td>6</td>
<td>ND</td>
<td>LOW</td>
<td></td>
</tr>
<tr>
<td>Low intertidal zone (-0.2 m)</td>
<td>5.1 (±1.6)</td>
<td>9</td>
<td>ND</td>
<td>MID</td>
<td></td>
</tr>
<tr>
<td>Coastal -1 m depth</td>
<td>152.3 (±17.3)</td>
<td>6</td>
<td>900</td>
<td>HIGH</td>
<td></td>
</tr>
<tr>
<td>Coastal -3 m depth</td>
<td>56.0 (±28.6)</td>
<td>6</td>
<td>450</td>
<td>HIGH</td>
<td></td>
</tr>
<tr>
<td>Coastal -10 m depth</td>
<td>1.2 (±0.03)</td>
<td>6</td>
<td>90</td>
<td>MID</td>
<td></td>
</tr>
<tr>
<td>Coastal -20 m depth</td>
<td>0.2 (±0.2)</td>
<td>6</td>
<td>9</td>
<td>LOW</td>
<td></td>
</tr>
<tr>
<td>Coastal -30 m depth</td>
<td>0.7 (±0.01)</td>
<td>6</td>
<td>1</td>
<td>LOW</td>
<td></td>
</tr>
<tr>
<td>Offshore -30 m depth</td>
<td>14.0 (±0.9)</td>
<td>4</td>
<td>20</td>
<td>MID</td>
<td></td>
</tr>
<tr>
<td>Offshore -45 m depth</td>
<td>0 (±0)</td>
<td>4</td>
<td>7</td>
<td>LOW</td>
<td></td>
</tr>
</tbody>
</table>

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).

<table>
<thead>
<tr>
<th>St. Croix</th>
<th>Target habitats (sub- and intertidal)</th>
<th>Production g (dry/m^2/d)</th>
<th>Production µgO_2/cm^2/h</th>
<th>Light (mol/m^2/d)</th>
<th>No. of samples</th>
<th>Productivity potential</th>
</tr>
</thead>
<tbody>
<tr>
<td>Algal ridge at MLW</td>
<td>ND</td>
<td>2215 (±600)</td>
<td>43</td>
<td>3</td>
<td>HIGH</td>
<td></td>
</tr>
<tr>
<td>Algal ridge 0.5 m</td>
<td>ND</td>
<td>1255 (±502)</td>
<td>ND</td>
<td>3</td>
<td>HIGH</td>
<td></td>
</tr>
<tr>
<td>Backreef 1 m</td>
<td>ND</td>
<td>553 (±393)</td>
<td>28</td>
<td>3</td>
<td>MID</td>
<td></td>
</tr>
<tr>
<td>Forereef 1.5 m</td>
<td>ND</td>
<td>940 (±269)</td>
<td>28</td>
<td>3</td>
<td>HIGH</td>
<td></td>
</tr>
<tr>
<td>Forereef 5 m</td>
<td>ND</td>
<td>756 (±159)</td>
<td>23</td>
<td>3</td>
<td>MID</td>
<td></td>
</tr>
<tr>
<td>Forereef 10 m</td>
<td>ND</td>
<td>536 (±79)</td>
<td>17</td>
<td>3</td>
<td>MID</td>
<td></td>
</tr>
<tr>
<td>Canyon wall 10 m</td>
<td>3.0 (±0.28)</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>MID</td>
<td></td>
</tr>
<tr>
<td>Canyon wall 20 m</td>
<td>1.35 (±0.25)</td>
<td>561 (±39)</td>
<td>11</td>
<td>3</td>
<td>MID</td>
<td></td>
</tr>
<tr>
<td>Canyon wall 30 m</td>
<td>0.93 (±0.1)</td>
<td>387 (±86)</td>
<td>6</td>
<td>3</td>
<td>LOW</td>
<td></td>
</tr>
<tr>
<td>Canyon wall 40 m</td>
<td>0.79 (±1.8)</td>
<td>213 (±42)</td>
<td>3</td>
<td>3</td>
<td>LOW</td>
<td></td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th>Washington</th>
<th>Target habitats (intertidal)</th>
<th>Production g (dry/m^2/mo)</th>
<th>Number of samples</th>
<th>Productivity potential</th>
</tr>
</thead>
<tbody>
<tr>
<td>SJII Very high</td>
<td>7.2 (±15.6)</td>
<td>10</td>
<td>V. LOW</td>
<td></td>
</tr>
<tr>
<td>TI Very high</td>
<td>7.2 (±15.6)</td>
<td>10</td>
<td>V. LOW</td>
<td></td>
</tr>
<tr>
<td>SJII High</td>
<td>97.8 (±92.4)</td>
<td>20</td>
<td>LOW</td>
<td></td>
</tr>
<tr>
<td>TI High</td>
<td>97.8 (±92.4)</td>
<td>20</td>
<td>LOW</td>
<td></td>
</tr>
<tr>
<td>SJII Mid</td>
<td>646.0 (±227.0)</td>
<td>10</td>
<td>MID</td>
<td></td>
</tr>
<tr>
<td>TI Mid</td>
<td>646.0 (±227.0)</td>
<td>10</td>
<td>MID</td>
<td></td>
</tr>
<tr>
<td>SJII Low (few herb)</td>
<td>646.0 (±227.0)</td>
<td>10</td>
<td>HIGH</td>
<td></td>
</tr>
<tr>
<td>TI Low (herb removed)</td>
<td>646.0 (±227.0)</td>
<td>10</td>
<td>HIGH</td>
<td></td>
</tr>
<tr>
<td>SJII Low (with herb)</td>
<td>646.0 (±227.0)</td>
<td>10</td>
<td>HIGH</td>
<td></td>
</tr>
<tr>
<td>TI Low (with molluscs)</td>
<td>646.0 (±227.0)</td>
<td>10</td>
<td>HIGH</td>
<td></td>
</tr>
<tr>
<td>SJII Low (with urchins)</td>
<td>646.0 (±227.0)</td>
<td>10</td>
<td>HIGH</td>
<td></td>
</tr>
<tr>
<td>SJII Very low (few herb)</td>
<td>646.0 (±227.0)</td>
<td>10</td>
<td>HIGH</td>
<td></td>
</tr>
<tr>
<td>SJII Very low (with herb)</td>
<td>646.0 (±227.0)</td>
<td>10</td>
<td>HIGH</td>
<td></td>
</tr>
</tbody>
</table>

*SJII = San Juan Island. TI = Tatoosh Island.
A. Ranking disturbance potential in Maine based on grazing frequency (as indicated by herbivore biomass, see text) and grazing intensity (increasing left to right from shallow grazing molluscs to urchins).

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 (SJ) and Tatoosh (TI) Islands in Washington state.

C. respectively; here, however, the factor most limiting algal productivity is probably desiccation rather than light or wave action (Castenholz 1961, Dayton 1971, Scasy 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).

<table>
<thead>
<tr>
<th>Target habitats</th>
<th>Deep grazing molluscs</th>
<th>Urchins</th>
<th>Bite rate fishes</th>
<th>Number quadrats</th>
<th>Sample size</th>
<th>Disturbance potential</th>
</tr>
</thead>
<tbody>
<tr>
<td>Algal ridge 0 m</td>
<td>0</td>
<td>0</td>
<td>313 ±311</td>
<td>20</td>
<td>3</td>
<td>LOW</td>
</tr>
<tr>
<td>Algal ridge 0.5 m</td>
<td>0</td>
<td>38.3 ±3.7</td>
<td>144.4 ±11.6</td>
<td>10</td>
<td>3</td>
<td>MID</td>
</tr>
<tr>
<td>Backreef 1 m</td>
<td>0</td>
<td>144.4 ±11.6</td>
<td>896 ±896</td>
<td>31</td>
<td>3</td>
<td>HIGH</td>
</tr>
<tr>
<td>Fore reef 1.5 m</td>
<td>0.03 ±0.01</td>
<td>137.6 ±7.4</td>
<td>2823 ±850</td>
<td>13</td>
<td>3</td>
<td>V. HIGH</td>
</tr>
<tr>
<td>Fore reef 5 m</td>
<td>0.02 ±0.02</td>
<td>121.3 ±4.5</td>
<td>1563 ±1381</td>
<td>20</td>
<td>3</td>
<td>V. HIGH</td>
</tr>
<tr>
<td>Fore reef 10 m</td>
<td>0</td>
<td>52 ±5.4</td>
<td>409 ±371</td>
<td>21</td>
<td>3</td>
<td>MID</td>
</tr>
<tr>
<td>Canyon wall 10 m</td>
<td>0</td>
<td>4.2 ±1.3</td>
<td>109 ±51</td>
<td>19</td>
<td>7</td>
<td>MID</td>
</tr>
<tr>
<td>Canyon wall 20 m</td>
<td>0</td>
<td>20.5 ±1.68</td>
<td>294 ±975</td>
<td>30</td>
<td>11</td>
<td>MID</td>
</tr>
<tr>
<td>Canyon wall 30 m</td>
<td>0</td>
<td>1.0 ±0.32</td>
<td>235 ±621</td>
<td>20</td>
<td>7</td>
<td>MID</td>
</tr>
<tr>
<td>Canyon wall 40 m</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>20</td>
<td>3</td>
<td>LOW</td>
</tr>
<tr>
<td>Canyon wall 50 m</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>3</td>
<td>LOW</td>
</tr>
<tr>
<td>Canyon wall 60 m</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>3</td>
<td>LOW</td>
</tr>
</tbody>
</table>

1 Biomass (g dry/m²) of Acmaea leucopla. 2 Biomass (g dry/m²) of Diadema antillarum (data from 1982). 3 Echinometra lucunter (primarily restricted to burrows). 4 Bite rates (bites/m²/h) for denuding fishes (Microspathodon chrysops, Ophioblennius atlanticus, Acanthurus bahianus, Acanthus coeruleus) and excavating fishes (Scarus croicensis, Selenocirrus variés, Spermata maculatus) (Steneck 1983a, b). Only fore reef at 1.5 m had measurable scarid grazing. 5 For urchins and molluscs only. 6 Visual 5-min counts 1981, 1982, time lapse movies 1982 (visual counts 1982 only by Canyon wall stations). 7 MLW = Mean Low Water for spring tides. 8 Variance expressed as standard error of the mean. 9 Reef sites are Teague Bay Reef. 10 Canyon sites are Salt River Canyon. 11 Variance as standard deviation because this value is not derived from a population of means. 12 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.

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 2A–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 forereef 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 longicuris) 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 circumscripsum and Phymatolithon laevigatum, whereas species dominating where both were low were the coralline Leptophyllum laeve and the less abundant fleshy red algal crust Peyssonnelia rosenbergii 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
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 (e.g., 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. Steenek 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, Ruytten van Steveninck and Bak 1986;
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.


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). Cubit (1984) showed that in the high intertidal zone of Oregon, a seasonal increase in productivity potential (due to lowered desiccation stress) combined with little winter time 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. Morrisson 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 leafy 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 have thalli normal to the direction of incoming light can grow to the greatest depths of the photic zone (Adley 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 DGDema 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 coralline. 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 (Adley and Steneck 1985, Carpenter 1986, Adley and Goettemuller 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, Dansereau 1957, Holdridge 1967) but no consistent scheme evolved from these efforts. Although there is general
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 templet 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 templet 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 cartilaginous 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 (Ades et al. 1981), only 30 to 50 of these species are common at any time (Ades 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 backreef; 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 ecological era". Our general model (Fig. S5) 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 precision 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.

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References


- 1983. Grazing in coral reef ecosystems. - In: Barnes, D. J.


Holdridge, L. R. 1967. Life zone ecology. – Tropical Science Center, San Jose, CA.


Steneck, R. S. 1978. Factors influencing the distribution of crustose coralline algae (Rhodophyta, Corallinaeaceae) in the Damariscotta River estuary, Maine. - Masters thesis, Univ. of Maine, Orono, ME.
### 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”.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Species</th>
<th>Algal group</th>
<th>Max. age (yr)</th>
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<tr>
<td>Patrick 1970</td>
<td>Diatoms</td>
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<td>Halosaccion glandiforme</td>
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