



## Effects of physical and biological disturbances on algal turfs in Kaneohe Bay, Hawaii

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### Abstract

Disturbance in coral reef environments commonly results in an algal community dominated by highly productive, small filamentous forms and cyanobacteria, collectively known as algal turf. Research on the types of disturbance responsible for this community structure has concentrated mainly on biological disturbance in the form of grazing, although physical and other forms of biological disturbances may be important in many coral reef areas. On the reef flat in Kaneohe Bay, Oahu, Hawaii, algal turfs grow primarily upon coral rubble that tumbles with passing swells. We manipulated the frequency of rubble tumbling in field experiments to mimic the effects of physical disturbance by abrasion and light reduction on algal biomass, canopy height, and community structure. Treatments approximated a gradient of disturbance intensities and durations that occur on the reef flat. Although sea urchins and herbivorous fishes are not widespread and abundant on the reef flat, biological disturbances to algal turf communities in the form of herbivory by small crabs and abrasion by tough macroalgae contributed significantly to the variation in algal turf biomass. Within all experiments increasing disturbance significantly reduced algal biomass and canopy heights and the community structure shifted to more disturbance-tolerant algal forms. This study shows that the chronic physical disturbances from water motion and biological disturbances other than grazing from large herbivores can control algal communities in coral reef environments. © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:* Algal turfs; Coral reef; Disturbance; Hawaii; Herbivores; Hydrodynamics; Macroalgae

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## 1. Introduction

Dramatic examples of physical disturbance are evident in most marine habitats (Paine, 1979; Sousa, 1979; Walsh, 1983; Williams, 1988; Seymour et al., 1989), including coral reefs (Knowlton et al., 1981; Williams, 1984; Edmunds and Witman, 1991; Bythell et al., 1993). Disturbance, defined here as the removal of biomass due to environmental causes (Grime, 1977), can control the structure of algal communities (Paine and Levin, 1981; Connell, 1983; Sousa, 1984; Dayton et al., 1989). On coral reefs, it is well-documented that disturbance by herbivores can control benthic algal community structure (Sammarco et al., 1973; Brock, 1979; Carpenter, 1981, 1986; Sammarco, 1983; Hughes et al., 1985; Lewis and Wainwright, 1985). As grazing intensity increases, algal communities shift from macroalgae to fast-growing algal turfs and eventually to herbivore-resistant algal crusts (Littler et al., 1983; Hackney et al., 1989; Steneck and Dethier, 1994). The high diversity and abundances of herbivores on coral reefs have fostered numerous studies of grazing, but other biological and also physical disturbances should result in similar shifts in algal community structure on coral reefs (Hatcher and Larkum, 1983; Phillips et al., 1997). For example, Foster (1987) indirectly demonstrated the importance of water flow on algal community structure because herbivory was restricted by high water flow. Lieberman et al. (1979, 1984) suggested that algal communities growing on cobbles in coral reef habitats could be controlled by physical disturbance when water motion shifted cobbles on the substratum.

We investigated the effects of physical and biological disturbance on algal turf communities in Kaneohe Bay, Hawaii. Most coral reefs have a disturbance regime that favors an algal turf-dominated community (Hay, 1981; Lewis, 1986; Carpenter, 1990a; McClanahan et al., 1996). The diverse algae within turfs are primarily unicells and small filaments from five major Divisions. Such species regenerate rapidly after disturbance (Littler and Littler, 1980; Hackney et al., 1989), in part because they have very high rates of photosynthesis (Carpenter, 1985; Adey, 1987; Adey and Goertemiller, 1987; Hatcher, 1988). Algal turfs have major ecological functions on coral reefs. They contribute up to 80% of coral reef primary production (Wanders, 1976; Adey and Steneck, 1985) and fix a considerable mass of nitrogen (Williams and Carpenter, 1997; 1998). Algal turfs are grazed by a variety of vertebrate and invertebrate herbivores of importance to local fisheries (Hay, 1984; Russ and Alcala, 1989; McClanahan et al., 1996).

During a study of hydrodynamic control of algal turf metabolism in Kaneohe Bay, Hawaii (Williams and Carpenter, 1998), it became evident that water motion was important in controlling algal turf community structure. Kaneohe Bay is situated on the windward coast of the island of Oahu and its long axis (17 km) is open to large swells. The seaward third of Kaneohe Bay consists of a shallow (2.5 m average depth) reef flat of unstable coral rubble (dead coral fragments) with occasional coral heads ('bommies') providing limited relief. The energy of swells entering the bay is dissipated primarily by waves breaking over the shallowest region of the barrier reef, which is not emergent (Bathen, 1968; Hunter and Evans, 1995). Kaneohe Bay shares these and other features with Pacific reef environments characterized as having a relatively high energy regime (Veron, 1993). The coral rubble is covered by algal turfs and thus the reef flat is a very

productive habitat. We described the factors contributing to the physical disturbance of coral rubble tumbling on the reef flat and then conducted field manipulations of tumbling frequency and periods of light reduction to the algal turfs growing on the coral rubble. We hypothesized that with increasing disturbance, algal biomass and canopy height would be reduced and algal community structure would shift to more disturbance-resistant algal functional forms (turfs and crusts).

Disturbance to algae by water motion in Kaneohe Bay also seemed important because of the apparently low densities of large herbivores on the reef flat. Although diverse grazers affect algal communities on reefs (Borowitzka, 1981; Hay, 1985; Steneck, 1988), larger grazers such as fishes and sea urchins typically have the greatest influence (Ogden and Lobel, 1978; Van Den Hoek et al., 1978; Lewis and Wainwright, 1985; Foster, 1987; McClanahan et al., 1994; Chabanet et al., 1997). When larger herbivores are not abundant, mesoherbivores that forage less extensively, e.g. small fishes (blennies, damselfishes) and crabs, become relatively more important in controlling algal communities (Brawley and Adey, 1977; Potts, 1977; Lassuy, 1980; Lobel, 1980; Montgomery, 1980; Coen, 1988a,b). Only a few studies have considered the effects of microherbivores such as amphipods, gastropods, and polychaetes that graze small areas ( $\sim 1\text{--}100\text{ cm}^2$ ) due to their limited mobility and reduced size (Brawley and Adey, 1981; Carpenter, 1986). We also investigated the effects of herbivory and abrasion by macroalgae on algal turf biomass, canopy height, and community structure on the reef flat.

## 2. Methods

Four experimental sites (approximately  $25 \times 25\text{ m}$ ) were established on the reef flat. These sites were located approximately 200 m south of Kapapa Island and were approximately 50 m from the reef crest, with distances between sites ranging from 56 to 81 m (Site 1: N21°28'05" W157°47'40", Site 2: N21°28'06" W157°47'36", Site 3: N21°28'05" W157°47'35", Site 4: N21°28'06" W157°47'34"). Sites were chosen for their similarities in substratum type, apparent current velocity regimes, depth, and distance from the reef crest.

### 2.1. Distribution of substratum types and algal communities

Prior to selection of experimental sites, sampling was conducted along 100-m transects to characterize substratum types and algal community distribution across the Kaneohe Bay reef flat. Algal functional form (macroalgae, turf, or crust), substratum type, and algal turf canopy height were recorded at 835 random points (25 random points in every 3 m, averaged to one value  $3\text{ m}^{-1}$ ) along a 100-m transect at each of three sites on the reef flat. Although the rubble field was the dominant substratum on the reef flat, logistics prevented sampling more than 1 transect there; two transects were located on consolidated pavement. Transects were laid perpendicular to the reef crest. At the pavement dominated site, one transect was placed near the reef crest (approximately

100 m from the breaking waves) and the other began approximately 100 m shoreward from the end of the first transect.

## 2.2. Rubble tumbling and water flow

When rubble tumbles in flowing water, attached algae are abraded or dislodged and light is reduced on the underside of rubble pieces (Sousa, 1979). The tumbling rate of coral rubble thus should provide an index of physical disturbance to algal turfs in Kaneohe Bay.

Ambient tumbling rates of coral rubble were quantified in situ approximately 10 m shoreward of the four experimental sites in order to not disturb the simultaneous experimental manipulations. During summer 1995 and January 1996, 60 rubble pieces of the median size class (median length of long axis: 8 cm,  $n = 613$ ) were collected from the reef flat. After drying and bleaching, each piece was numbered on one side, and a dot was painted on the other side. Rubble was soaked in seawater for 24 h, then returned to the reef flat with the numbered side up. Marked rubble was monitored daily and ‘tumbled’ pieces (those with the dot facing up) were recorded and replaced (dot side down). At all four experimental sites, natural tumbling rates of the loose rubble pieces in the high and ambient tumbling treatments were recorded similarly to estimate site-specific tumbling rates ( $n = 80 \text{ site}^{-1}$ ). This technique yielded a conservative estimate of tumbling rates because multiple tumbles were not determined. Tumbling frequency ( $\#$  of tumbles  $\text{day}^{-1}$ ) was calculated daily for a 14-day period and then tumbling rates per day were averaged to yield a mean tumbling rate. Differences in tumbling rates between sites were analyzed using a one-way ANOVA. The tumbling frequencies provided the treatment levels in the manipulative experiments below.

Rubble tumbling rates were regressed against concurrent daily mean, daily mean maximum and daily maximum water flow speeds over the reef flat. An electromagnetic current meter (Model S4, InterOcean Inc., San Diego, CA) was deployed 0.5 m above the substratum where it logged flow speed and direction one minute out of every hour (sampling at 2 Hz). Data were downloaded every 7 days. To characterize water flow patterns over the reef flat, water flow speeds were measured in five areas across the reef flat (approximately 500 m apart and 50 m from the reef crest) and the current meters remained at each area for 4–6 weeks. Rubble tumbling rates were regressed against water flow speeds that were recorded concurrently from adjacent sites.

To assess potential differences in water flow speeds among the four sites of the experiments, we logged water flow speeds continuously for 1 h with another electromagnetic current meter (Marsh-McBirney, Model 511, Frederick, MD) deployed 0.3 m above the substratum. Flow at each of the sites was measured twice at approximately the same time of day (10:00–14:00 h) at the same tidal stage.

## 2.3. Prevalence of biological disturbance in Kaneohe Bay

### 2.3.1. Abundances of macroherbivores

Sea urchins occurring on the reef flat primarily belong to the genera *Echinothrix* and *Echinometra*. *Echinometra oblonga* and *Echinometra mathaei* typically reside within crevices they excavate in consolidated coral substratum where they subsist mainly on

drift algae and algae accumulated in the crevices (Russo, 1977; Grünbaum et al., 1978). Abundances of *Echinometra* species and mean crevice size were estimated in areas of coral pavement in 1 m<sup>2</sup> quadrats ( $n = 25$ ) at random points along a 100-m transect.

*Echinothrix diadema* inhabits crevices and grooves in coral heads and rarely is found on the rubble matrix. All *Echinothrix* on 30 coral heads in and around the experimental sites on the reef flat were counted in the summers of 1995 and 1996 and densities m<sup>-2</sup> were calculated based on the planar area of a coral head (estimated as an ellipse).

Swimming transects were conducted (as per Carpenter, 1990b; Aronson et al., 1994) to estimate abundances of common herbivorous fishes. Two individuals swam along a compass heading (at an approximate rate of 0.15 m s<sup>-1</sup>) between the four experimental sites and counted juvenile and adult parrotfish (Scaridae), surgeonfish (Acanthuridae) and bottom-dwelling blennies (Blennidae) encountered within 2 m of the transect (fishes identified according to Hoover, 1993). Distances between sites ranged from 56 to 81 m and census counts were normalized to 100-m transect lengths. Censuses were conducted between 10:00 and 14:00 h local-time when horizontal visibility was at least 5 m and were repeated once in the same day. The mean for each transect per day was calculated by averaging counts from the two observers per transect and then the two replicates of each transect.

Because herbivorous fishes and *Echinothrix* were closely associated with the few coral heads found on the reef flat, the relative amount of coral head coverage versus sand and rubble was quantified. Transects (100 m,  $n = 14$ ) were laid along the reef flat substratum at various angles from each of the four experimental sites and the length of the transect that intercepted coral heads versus sand or rubble substratum was recorded.

In the rubble field, we observed numerous small (<3 cm carapace width) crabs feeding on algal turfs. Herbivorous crab densities in the coral rubble fields were estimated by haphazardly placing a 27-cm diameter coring cylinder at four sites ( $n = 22$  site<sup>-1</sup>) and recording the number and species of crabs found among the enclosed coral rubble.

### 2.3.2. *Sargassum* density, height and biomass

To assess the potential for disturbance from macroalgae, individual thalli of *Sargassum* species at the four experimental sites were counted in 0.25-m<sup>2</sup> quadrats ( $n = 5$  site<sup>-1</sup>) placed haphazardly within each site during July 1995 and January 1996. Individuals from two of the experimental sites were collected randomly and dried at 90°C for 24 h and weighed. To estimate the extent of a 'sweep' zone, we selected the closest *Sargassum* individual to each of 25 random points along each of four transects (10 m long) and measured the longest branch on each individual. All transects were oriented perpendicular to the reef crest and separated by approximately 250 m.

## 2.4. Experimental manipulations of disturbance to algal turfs

### 2.4.1. Physical disturbance

#### 2.4.1.1. Experimental manipulations of tumbling frequency

We experimentally quantified the effects of disturbance due to tumbling coral rubble in a multifactorial design where algal turfs growing on rubble were subjected to three

levels of experimental tumbling frequency: no tumbling, ambient tumbling rates (as controls), and high tumbling (four times the ambient tumbling rate). Pieces of the median size class were selected haphazardly from the reef flat so that rubble shape would be representative of ambient rubble, which is roughly flat and elliptical. In the no tumbling treatment, four dried and bleached rubble pieces were fastened with cable ties to a 40-cm long  $\times$  5-cm diameter PVC pipe cut in half longitudinally. Pipes were weighted with steel reinforcing rod and positioned in the substratum parallel to the reef crest so that the affixed rubble pieces were flush with the surrounding rubble field. Rubble pieces in the ambient tumbling and high tumbling treatments were dried and bleached. After bleaching, each rubble piece was numbered on one side and a dot painted on the other side. Rubble was soaked in seawater for 24 h, then returned individually to the reef flat with the numbered side up. Once returned to the reef flat, rubble in the ambient tumbling treatment was unmanipulated. For the high tumbling rate treatment, we manually rolled each marked rubble piece two complete turns in succession once every week, returning each rubble piece to its original orientation. The high tumbling rate approximated tumbling rates during storms (see Results) and mimicked the abrasive effect of tumbling.

We conducted a preliminary experiment (4 weeks) at sites 2 and 3 ( $n = 16$  experimental units/treatment) and a longer (8 week) experiment at all four sites ( $n = 40$ ) to compare site-specific effects. We also deployed experiments lasting several months during intervals between field trips. These unattended experiments were restricted to two tumbling treatment levels (no tumbling and ambient) at sites 2 and 3 on the reef flat. Rubble in the no tumbling treatment were affixed as described above and ambient tumbling pieces were selected haphazardly from each site. Eight PVC pipes (four rubble pieces/pipe) were left at each of the two sites for 18 weeks during both the fall (Aug 1995–Jan 1996) and spring (Jan 1996–Jul 1996) seasons.

Ash-free dry mass, algal turf canopy height, and community structure were assessed in each of five, random 1-cm<sup>2</sup> subsamples on each rubble piece. Ash-free dry mass (AFDM) was measured as the difference between mass after drying in an oven at 90°C for 24 h and after combusting in a muffle furnace at 550°C for 6 h. Biomass data were analyzed using a two-way ANOVA with both treatment and site as fixed factors. Canopy height was measured to the nearest mm with a ruler before attached algae in each cm<sup>2</sup> were scraped (1 mm into the substratum to include endolithic forms). Canopy height data were analyzed using an extension of the Friedman's test that allows for multiple observations in each treatment as described in Conover (1971). The functional form of each subsample was assigned to one of five classifications and each classification was given an ordinal (1 through 5): crust (1), crust/turf (2), turf (3), macroalgae/turf (4), or macroalgae (5) and analyzed using ANOVA. Functional form histograms were constructed to verify that the means used in the ANOVA approximated a normal distribution (for brevity, only the summer 1995 experiment is presented). As with previous studies (Steneck and Watling, 1982; Steneck and Dethier, 1994), algal functional forms are based on anatomical and morphological features that potentially correspond to different photosynthetic rates and abilities to resist disturbance. Prostrate, possibly calcified forms were identified as crusts; simple, filamentous forms were turfs, and upright, more complex (e.g. branching or foliose extensions, thicker thalli) forms were macroalgae.

Turfs can grow from crustose forms and some macroalgae take on a turf-like appearance when disturbed. We assigned a functional form classification based on what covered the majority of the surface area in each subsample. In all tumbling experiments, the experimental unit was the mean of the measured response variable calculated for each pipe ( $n = 4$  rubble pieces with subsamples averaged per piece). To ensure a balanced design, loose rubble pieces in the high and ambient tumbling treatments were pooled into means of four randomly selected rubble pieces. Algal species growing on rubble were identified to the lowest taxonomic level possible.

Functional form data were analyzed using ANOVA (functional form categories were changed to numeric values, e.g. crust = 1, crust/turf = 2, turf = 3, etc.), but we also have presented functional form data in histograms to show that the means used in the ANOVA approximated a normal distribution (for brevity, only the summer 1995 experiment is presented).

#### 2.4.1.2. *Experimental manipulations of light reduction*

In addition to being abraded, algae might become light-limited for periods long enough for algal senescence when a piece of rubble is overturned. Irregularities in the shape of rubble lead to an orientation commonly with a 'top' side covered with turfs and a bottom side with sparser turfs and more algal crusts. Hypothetically, the longer the time before the rubble is righted to its normal position, the more deleterious the effects on the top-side turfs. To test this hypothesis, we conducted a multifactorial experiment with four treatment levels (interval spent on the underside) at sites 2 and 3 on the reef flat.

Four pieces of rubble were assigned randomly among 4 treatment levels and affixed to a PVC pipe ( $n = 38$  site<sup>-1</sup>) with a stainless steel nut, bolt, and washer. Pipes with rubble were embedded on the reef flat as described previously. We manually turned the treatment rubble pieces at 7, 14, and 21 days (0.14, 0.07, and 0.05 tumbles day<sup>-1</sup>, respectively), and resecured them to the PVC pipe. The control remained affixed for the length of the experiment. The three treatment tumbling rates in this experiment approximated the mean, minimum, and maximum tumbling rates determined in the field (see Results). At the end of 2 months, 1-cm<sup>2</sup> subsamples ( $n = 3$ ) were taken from the top-side of each rubble piece, and AFDM, canopy height, and algal functional form were estimated. Biomass, canopy height, and functional form data at each site were analyzed separately using a randomized complete block (= pipe) ANOVA (Sokal and Rohlf, 1995). Unplanned contrasts were conducted among treatment means to elucidate the potential importance of individual treatments. Frequency histograms for the functional form data were constructed.

In the laboratory, we measured the light potentially available to algae living on the underside of coral rubble. A Kodak Ektagraphic projector (Model AF, Rochester, NY) provided the light source. A piece of rubble was placed 1–3 mm away from a thermopile detector for photosynthetically active radiation (3.8 mm diameter sensor, Model 2M, Dexter Research Center, Inc., Dexter, MI) positioned normal to the light source. Three photon flux densities (1144, 1347, and 1495  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) were used with each of three rubble pieces. These photon flux densities were within the range of ambient light levels measured over the reef flat on a sunny day (1000–1600  $\mu\text{mol}$

photons  $\text{m}^{-2} \text{s}^{-1}$ ). Light was measured under five haphazardly chosen areas of each rubble piece and a mean photon flux density under all rubble pieces for each light level was calculated. To measure the reduction in indirect light by coral rubble pieces, the angle between the light source and light meter was modified to approximately 0, 20, and 45°.

#### 2.4.2. Biological disturbance

##### 2.4.2.1. Experimental manipulations of crab herbivory on algal turfs

To avoid the inevitable problems of caging on the high-energy reef flat, the effects of crabs grazing on algal turfs were quantified in a unifactorial laboratory experiment with three densities of crabs (ambient, twice ambient, and a no crab control). A twice ambient density treatment was included to approximate the upper range of crab densities in the field (see Results). Four aquaria (37.8 l, each containing six pieces of rubble and 1 kg of sand) were assigned randomly to each of the three treatments. All aquaria had flowing seawater and were in an outdoor rack that received morning sun. The three most abundant crab species were hand-collected from the field, identified in the laboratory, and placed randomly in tanks. Because of size differences among crabs, carapace width was used instead of crab number to standardize treatment levels. After 1 month, algal ash-free dry mass (AFDM) and canopy height were measured and functional form (crust, turf, macroalgae) was recorded for 1  $\text{cm}^2$  subsamples ( $n = 3$ ) on each rubble piece. The average value from the six rubble pieces in each aquarium was used as the experimental unit for statistical analysis. The heteroscedasticity in the canopy height data could not be corrected by transformation and thus, these results were analyzed using non-parametric tests.

##### 2.4.2.2. Experimental manipulations of *Sargassum* sweeping on algal turfs

Coral rubble pieces of the median size (median length of long axis: 8 cm) were collected from the reef flat. Two rubble pieces were attached with cable ties to each of 16 PVC pipes (40 cm  $\times$  3.5 cm diameter, cut longitudinally) for each treatment at two sites on the reef flat. A *Sargassum* thallus (length of longest branch: 15 cm) was attached to the PVC pipe equidistant between the two rubble pieces with underwater epoxy putty (Z-spar, KOP-COAT, Los Angeles, CA). No *Sargassum* was attached to control pipes. Pipes were embedded within the substratum with the long axis of the pipe in parallel with the dominant axis of water flow. At the end of the 2 months, the longest branch of each thallus and the corresponding area of potential contact on each rubble piece were measured. Random subsamples ( $n = 3$ ) on each rubble piece were assessed for AFDM, canopy height and functional form. The mean for the two rubble pieces per pipe was used as the experimental unit ( $n$ ) for statistical analysis. Biomass data were analyzed using a two-way ANOVA with both treatment and site as fixed factors. Canopy height data were analyzed using an extension of the Friedman's test that allows for multiple observations in each treatment as described in Conover (1971). Functional form were analyzed using ANOVA and data presented in histograms.



### 3. Results

#### 3.1. Substratum and algal distribution

Greater than 70% of the total reef flat area consisted of coral rubble fields while less than 30% was consolidated pavement (pers. observ.). Coral rubble composed on average  $68 \pm 4\%$  (S.E.) of the substratum in coral rubble fields (Fig. 1) but only  $8 \pm 2\%$  (S.E.) in pavement dominated areas (for brevity, only one transect is shown). Coral cover consisted of isolated and heavily eroded ‘bommies’ of the major corals *Montipora flabellata*, *Pocillopora meandrina*, and *Porites lobata*. These isolated bommies provided limited refuge for herbivorous fishes and sea urchins, which seemed to limit their effects on algal turfs on the reef flat (see below).

Algal turfs were the dominant functional form on the reef flat, representing a mean of  $71 \pm 3\%$  (S.E.) on coral rubble fields and  $52 \pm 2\%$  (S.E.) in pavement dominated areas (Fig. 2). Algal taxa on experimental rubble were representative of algal turfs from the reef flat (Table 1). Upright macroalgae (species of *Dictyota*, *Dictyopteris*, *Sargassum*, *Turbinaria*) grew on larger pieces of rubble. *Sargassum* species are found commonly in coral reef areas (DeWreede, 1976; Ang, 1985; Price, 1989; Martin-Smith, 1994) and were the most abundant large macroalga on the reef flat in Kaneohe Bay.

#### 3.2. Rubble tumbling rates

Tumbling rates (mean  $\pm$  S.E.) on the reef flat were similar in summer of 1995

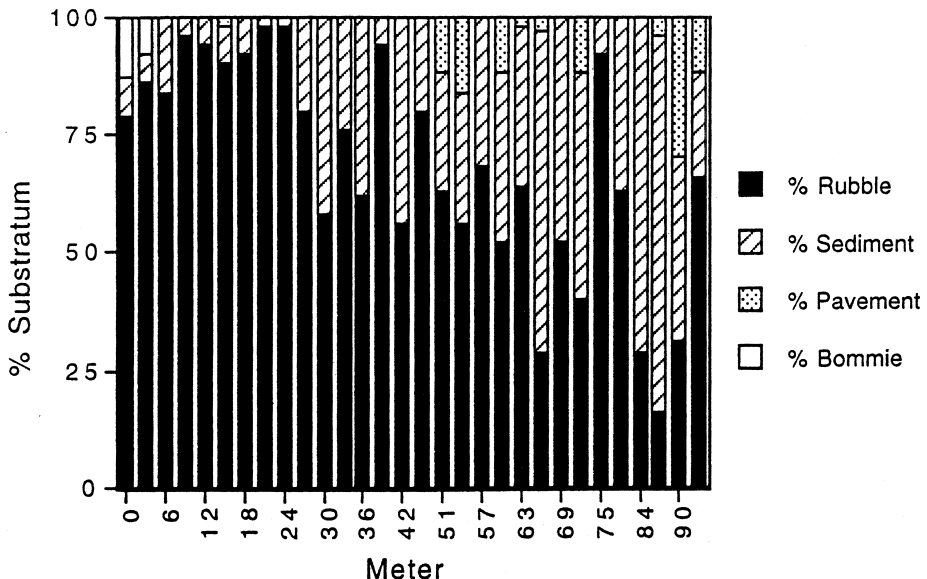


Fig. 1. Distribution of major substratum types on Kaneohe Bay reef flat (June 1994, 25 points in every 3 m along a 100-m transect on rubble field, 0 m = shoreward end of transect).

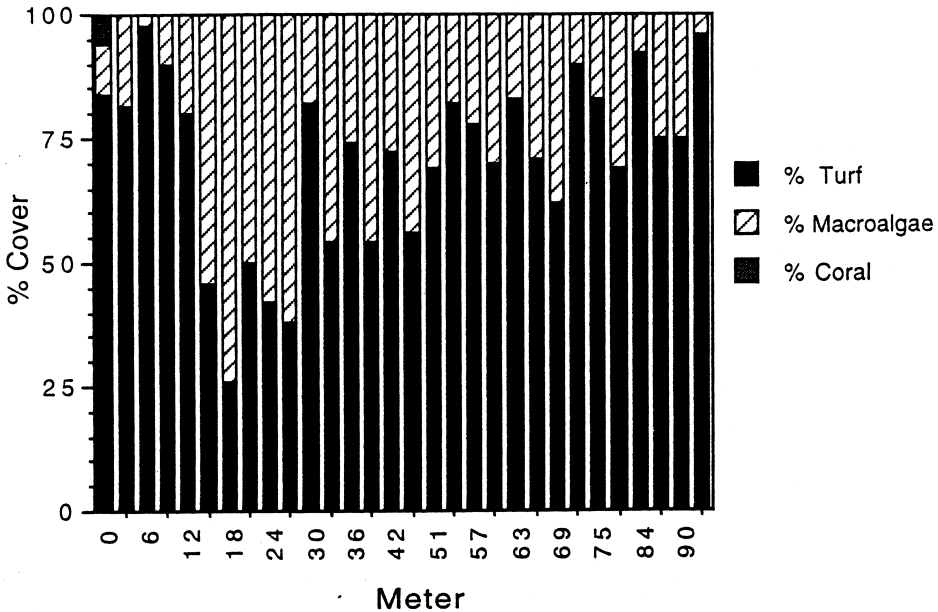


Fig. 2. Community structure on Kaneohe Bay reef flat (June 1994, 25 points every 3 m along a 100-m transect on rubble field, 0 m = shoreward end of transect).

( $0.06 \pm 0.01$  tumbles  $\text{day}^{-1}$ ) and January of 1996 ( $0.07 \pm 0.02$  tumbles  $\text{day}^{-1}$ ), but varied significantly among sites during the summer of 1995 (one-way ANOVA,  $df = 3$ ,  $316 F = 4.458$ ,  $P < 0.005$ ; site 1 =  $0.04 \pm 0.01$ , sites 2–4 were the same at  $0.07 \pm 0.01$ ). Tumbling rates were correlated significantly and positively with daily mean ( $r^2 = 0.386$ ;  $df = 1, 31$ ;  $P < 0.0001$ ), daily mean maximum ( $r^2 = 0.391$ ;  $df = 1, 31$ ;  $P < 0.0001$ ) and daily maximum flow speeds, but the daily maximum flow speed best explained the variance in tumbling rates ( $r^2 = 0.468$ , Fig. 3). The daily mean maximum flow speed (mean  $\pm$  S.E.) for Kaneohe Bay reef flat ( $0.688 \pm 0.016 \text{ m s}^{-1}$ ) was approximately three times as high as daily mean flow speeds ( $0.234 \pm 0.004 \text{ m s}^{-1}$ ) (Fig. 4). Water flow speeds were very similar at the four experimental sites (overall mean =  $0.186 \pm 0.008 \text{ m s}^{-1}$ ). Measured water flow speeds were consistently above the minimum of  $0.160 \text{ m s}^{-1}$  (extrapolated from regressions) required to tumble ambient-sized coral rubble.

### 3.3. Prevalence of biological disturbance in Kaneohe Bay

#### 3.3.1. Abundances of macroherbivores

In general, censuses of sea urchins and fishes confirmed our impressions that macroherbivores were restricted in occurrence and low in density on the Kaneohe Bay reef flat.

*Echinometra mathaei*, *E. oblonga*, and *Echinothrix diadema* were distributed patchily on hard substrata such as pavement or bommies on the Kaneohe Bay barrier reef flat.

Table 1  
Algal taxa within turf growing on the reef flat in Kaneohe Bay

<b>Cyanophyta</b>	<b>Rhodophyta</b>
<i>Arthrospira</i> sp.	<i>Acanthophora spicifera</i> *
Cocoid cyanobacteria	<i>Amphiroa</i> sp.*
<i>Lyngbya</i> sp.	<i>Centroceras clavulatum</i>
<i>Oscillatoria</i> sp.	<i>Ceramium</i> sp.
	<i>Champia</i> sp.
<b>Chlorophyta</b>	<i>Coelothrix irregularis</i> *
<i>Acetabularia mobii</i> *	<i>Corallina</i> sp.
<i>Caulerpa lentillifera</i> *	<i>Desmia hornemannii</i>
<i>C. webbiana</i> *	<i>Gelidium</i> sp.*
<i>Cladophora</i> sp.*	<i>Gelidiales</i> spp.
<i>Codium arabicum</i>	<i>Gracilaria</i> sp.*
<i>Dictyosphaeria</i> sp.*	<i>Griffithsia</i> sp.
<i>Enteromorpha</i> sp.*	<i>Herposiphonia</i> sp.
<i>Ernodesmis verticillata</i> *	<i>Hypnea chordacea</i> *
<i>Neomeris annulata</i>	<i>Jania</i> sp.*
<i>Udotea abbreviata</i> *	<i>Laurencia</i> sp.*
<i>Valonia</i> sp.*	<i>Laurencia succisa</i>
	<i>Liagora</i> sp.*
<b>Chrysophyta</b>	<i>Martensia fragilis</i>
Bacillariophyceae	<i>Peyssonellia rubra</i>
	<i>Polysiphonia</i> sp.
	<i>Pterocladia</i> sp.*
	<i>Taenioma</i> sp.
<b>Phaeophyta</b>	
<i>Colpomenia sinuosa</i> *	
<i>Dictyota friabilis</i> *	
<i>Ectocarpus indicus</i>	
<i>Hapalospongidion</i> sp.	
<i>Lobophora variegata</i> *	
<i>Mesospora</i> sp.	
<i>Padina</i> sp.*	
<i>Sargassum echinocarpum</i> *	
<i>S. polyphyllum</i> *	
<i>Sphacelaria furcigera</i>	
<i>Turbinara ornata</i> *	

\* Macroalgal species growing as turf.

*Echinometra* species were restricted to coral pavement, while *Echinothrix diadema* were common on and under bommies. We rarely saw *Echinothrix* away from coral head cover during the day or in early evening (20:00–21:00 h) but during the night they grazed an approximately 1-m radius zone away from bommies. In coral rubble fields, sea urchins were found only on large pieces of rubble or bommies.

Densities of sea urchins generally were similar for all species. *Echinometra oblonga* had densities of  $2 \pm 0.1$  individuals  $m^{-2}$  (mean  $\pm$  S.E.), and *E. mathaei* of  $3 \pm 0.1$  individuals  $m^{-2}$ . *Echinothrix diadema* densities on bommies were  $2 \pm 0.1$  individuals  $m^{-2}$  in both summer 1995 and 1996.

The dominant herbivorous fishes observed on the Kaneohe Bay reef flat were

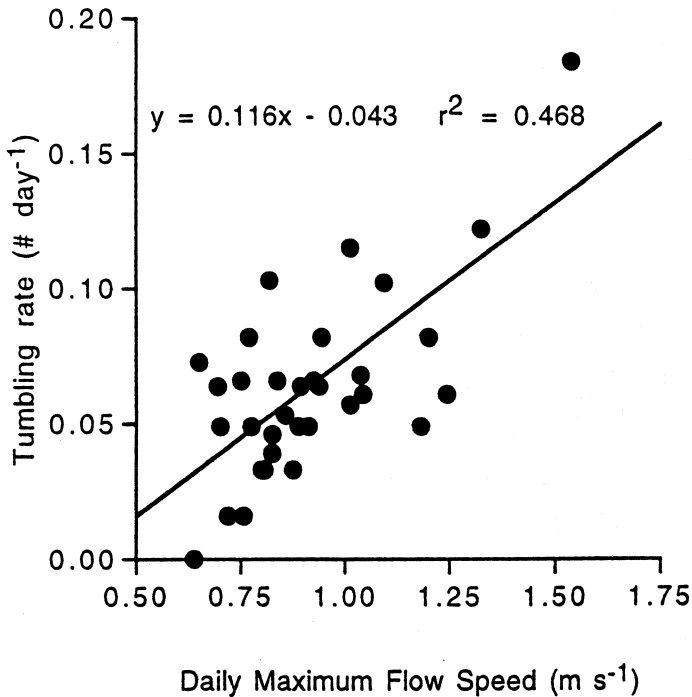


Fig. 3. Coral rubble tumbling rates (# tumbles day<sup>-1</sup>) as a function of daily maximum water flow speed.

parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) (Table 2). Acanthurids were most numerous, ranging from 64 to 78% of average total counts. Less than 2% of all fish counted (36/2294) were adult scarids. Most of the fishes counted (60%) were found on or within 0.5 m of bommies. Because bommies occupied only 5% of total substratum, effects of herbivorous fishes grazing away from bommies is probably limited.

Three species of herbivorous crabs (*Chlorodopsis areolata*, *Lophozozymus intonsus*, and *Thalamita edwardsi*, identified from Edmondson, 1946) were common on the reef flat where we observed them grazing algal turfs. The mean ( $\pm$ S.E.) of all censuses across four sites in 1995 was  $14 \pm 0.7$  individuals m<sup>-2</sup> and  $10 \pm 0.6$  individuals m<sup>-2</sup> for the two sites in 1996. All three species occurred in roughly equal numbers. All species were roughly the same size; average crab carapace width was  $1.0 \pm 0.2$  cm ( $\pm$ S.E.,  $n = 21$ ).

### 3.3.2. Abundances of *Sargassum* spp.

*Sargassum echinocarpum* and *S. polyphyllum* grew commonly on the Kaneohe Bay reef flat. *Sargassum* densities differed significantly between the four sites in both summer 1995 and January 1996 (Table 3); site 4 consistently had an order of magnitude lower density of *Sargassum* compared to the other three sites. *Sargassum* biomass did not differ between site 2 and site 3 in either summer 1995 or January 1996.

The mean canopy height ( $\pm$ S.E.) for *Sargassum* individuals was  $10.9 \pm 0.6$  cm (Table

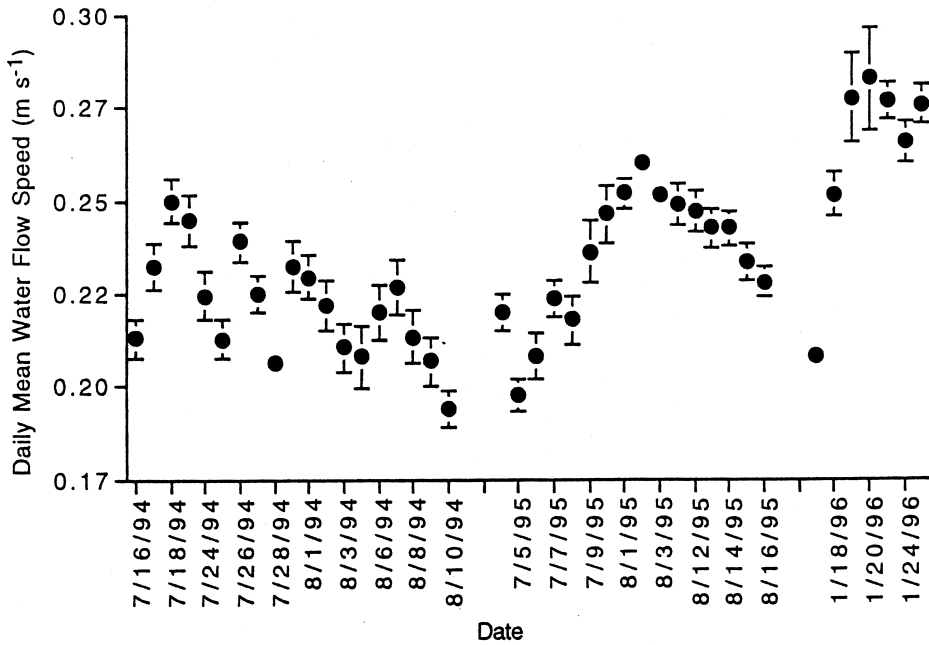


Fig. 4. Daily mean water flow speeds ( $\pm$ S.E.) on Kaneohe Bay reef flat recorded by InterOcean S4 current meter (sampling at 2 Hz).

4). *Sargassum* grew taller on stable pavement than on unstable coral rubble, suggesting that physical disturbances (rubble tumbling) also might affect macroalgae.

Table 2

Species of fishes counted in swimming transect censuses across the reef flat in Kaneohe Bay, Oahu (Hoover (1993) used for identification)

#### Acanthurids

*Acanthurus blochii*

*A. leucopareius*

*A. nigroris*

*A. olivaceus*

*A. triostegus*

*A. xanthopterus*

#### Blennies

*Cirripectes vanderbilti*

*Istiblennius zebra*

#### Scarids

*Calotomus carolinus*

*Scarus perspicillatus*

*S. psittacus*

*S. rubroviolaceus*

Table 3

Mean ( $n = 5$ ) number of *Sargassum*  $m^{-2}$  (S.E.) at each of the four experimental sites

	Summer 1995	January 1996
Site 1	50 (11.0)	16 (4.5)
Site 2	76 (12.4)	32 (8.9)
Site 3	61 (31.5)	22 (7.3)
Site 4	6 (1.0)	0 (0.0)
Mean	48 (20.4)	17 (7.8)
Overall mean	33 (9.5)	

### 3.4. Experimental manipulations of disturbance to algal turfs

#### 3.4.1. Physical disturbance

##### 3.4.1.1. Effects of tumbling on algal turf biomass, canopy height, and community structure

The ambient tumbling treatment reduced algal turf biomass by  $>17\%$  in all experiments (Figs. 5 and 6) and the high tumbling treatment also reduced algal biomass in half of the experiments. Shorter-term experiments (4 and 8 weeks in duration) reflected patterns that were accentuated in longer-term experiments (18 and 48 weeks). Algal biomass at the two sites in the preliminary experiment (4 weeks, June 1995) was reduced significantly by 33 and 56% in the ambient and high tumbling treatments relative to the no tumbling treatment ( $df = 2, 18, F = 29.034, P < 0.0001$ ). In the 8-week experiment during summer 1995, tumbling treatments significantly reduced algal biomass but orthogonal decomposition revealed no difference between the high and ambient tumbling treatment effects (Table 5). Algal biomass also was reduced in the long-term tumbling experiments (Table 6; winter 1995:  $df = 1, 20, F = 5.193, P = 0.034$ ; spring 1996:  $df = 1, 7, F = 6.999, P = 0.033$ ) except at site 3 in the winter experiment where tumbling had no significant effect (interaction term:  $df = 1, 20, F = 5.405, P = 0.031$ ). One pipe/site placed in the rubble field in August of 1995, by accident, was not recovered in January 1996 and remained on the reef flat until July 1996. The algal biomass on ambient tumbling rubble was reduced by 40% compared to the ‘year-long’ no tumbling rubble from these two pipes.

Increased disturbance also significantly reduced algal turf canopy height in the 8-week tumbling experiment in summer 1995 (Friedman’s statistic = 398.6,  $df = 2, P < 0.0001$ , Fig. 7) and both long-term tumbling experiments (winter 1995: Friedman’s statistic =

Table 4

Mean height (cm) of *Sargassum* (S.E.,  $n = 25$  site $^{-1}$ ) and substratum type for each of four haphazard sites on the reef flat

Substratum	Mean
Pavement/sand/rubble	13.0 (0.9)
Pavement	14.0 (1.1)
Rubble	7.7 (0.6)
Rubble	8.9 (0.5)

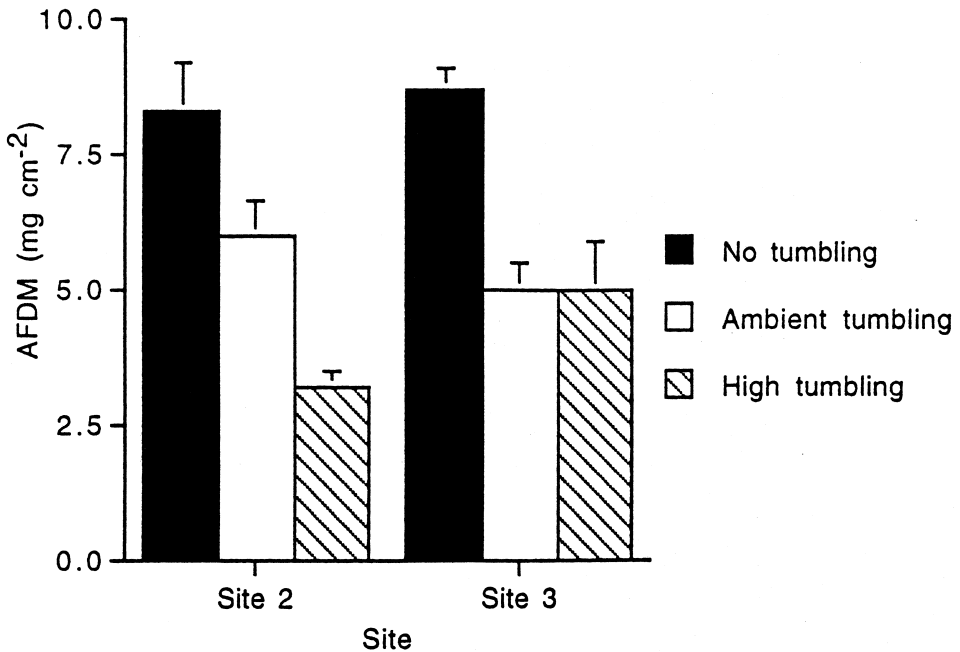


Fig. 5. Algal turf ash-free dry mass (AFDM) as a function of rubble tumbling in the preliminary experiment (June 1995). Ambient  $\approx 0.5$  tumbles week<sup>-1</sup>, high tumbling = 2 tumbles week<sup>-1</sup>. Mean + 1 S.E. ( $n = 4$ ).

160.8,  $df = 1$ ,  $P < 0.001$ ; spring 1996: Friedman's statistic = 33.9,  $df = 1$ ,  $P < 0.001$ ; Table 6).

Rubble tumbling also resulted in a significantly different algal community structure. Increased disturbance significantly shifted the community structure toward algal turfs and crusts from algal turfs and sparse macroalgae in the 8-week experiment during summer 1995 and a significant site effect also was detected (treatment effect:  $df = 2$ , 89,  $F = 12.691$ ,  $P < 0.0001$ ; site effect:  $df = 3$ , 89,  $F = 25.549$ ,  $P < 0.0001$ , Fig. 8). A significant community structure shift occurred in the spring 1996 experiment ( $df = 1$ , 9  $F = 2.9644$ ,  $P = 0.0004$ ) but no effect was detected in the winter 1995 experiment ( $df = 1$ , 20,  $F = 3.8374$ ,  $P = 0.0642$ ).

#### 3.4.1.2. Effects of overturning on algal turf biomass, canopy height, and community structure

Algal turf biomass was reduced significantly during the time spent on the underside of overturned rubble before being righted (Fig. 9). Although biomass reduction varied similarly with treatment between sites, site 2 had a significant block (pipe) effect ( $df = 27$ , 78,  $F = 2.6952$ ,  $P < 0.0001$ ). Consequently, we could not discern true treatment effects from block effects and will not present site 2 data for any of the response variables. At site 3, biomass on the top-sides of rubble was reduced by 12% in the 1-week treatment (turned once per week, faced down a total of 5 weeks), 22% in the 2-week treatment (turned once every 2 weeks, faced down a total of 6 weeks) and 19%

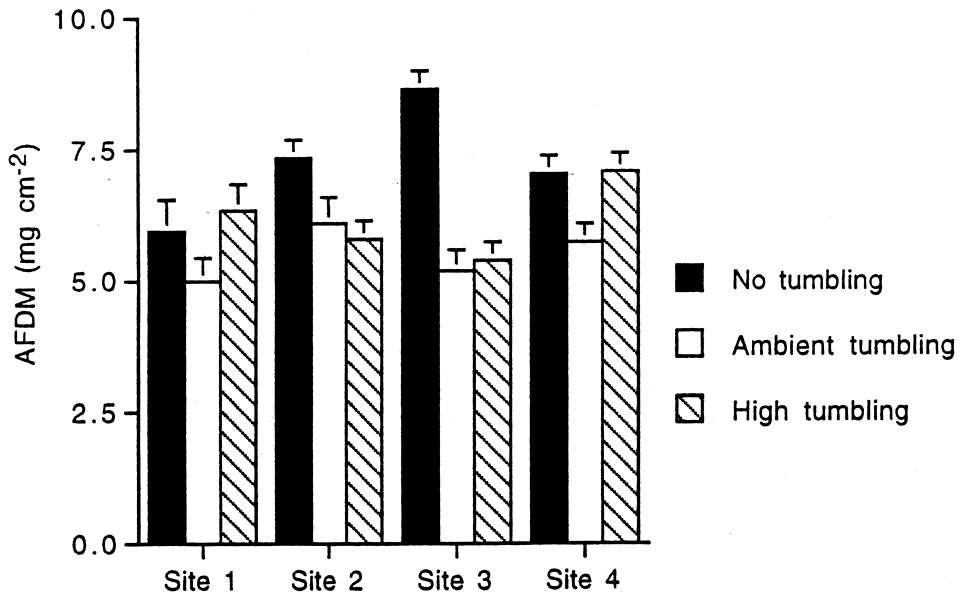


Fig. 6. Algal turf ash-free dry mass (AFDM) as a function of tumbling frequency at four sites on the reef flat during the summer of 1995. Ambient  $\approx 0.5$  tumbles week<sup>-1</sup>, high tumbling = 2 tumbles week<sup>-1</sup>. Mean + 1 S.E. ( $n = 10$ ).

in 3-week treatment (turned once every 3 weeks, faced down a total of 6 weeks) when compared to the no reduction treatment (never turned, faced up all 10 weeks, Table 7). Also at site 3, canopy height significantly increased with length of time spent overturned (Table 8, Fig. 10); shaded turfs grew long but very sparse filaments. Algal turfs and crusts became more prevalent as the period of being overturned increased (Table 9, Fig. 11). Post hoc contrasts revealed that  $> 70\%$  of the variance in total treatment effect for biomass and canopy height was due to the reduction of light. A second contrast revealed a significant difference between the 1-week versus the 2- and 3-week treatments. The percent of the total variance contributed by the 1-week treatment was  $\sim 25$  vs.  $\sim 5\%$  for the 2- and 3-week treatments. These contrasts indicate that the period of overturning contributes relatively little to the total effect of being overturned and shaded.

Table 5

Results of a two-way ANOVA for ash-free dry mass of algal turf ( $\text{mg cm}^{-2}$ ) for the summer 1995 tumbling experiment (includes orthogonal decomposition for tumbling treatments)

Source of variation	df	MS	F value	P value
Tumbling treatment	2	26.9206	14.8736	$< 0.0001$
No tumbling vs. ambient	1	51.1806	30.7961	$< 0.0001$
Ambient tumbling vs. high	1	6.5276	3.6327	0.0619
Site	3	3.4555	1.9085	0.1338
Interaction	6	7.2969	4.0302	0.0013
Error	91	164.7620	1.8106	



Table 6  
Tumbling treatment means for ash-free dry mass and algal canopy height (values are means (S.E.))

Tumbling experiment	AFDM (mg cm <sup>-2</sup> )	Algal canopy height (mm)
Long-term winter (Aug 95–Jan 96)		
Site 2		
No tumbling	14.7 (0.8)	0.8 (0.3)
Ambient tumbling	10.2 (1.0)	0.2 (0.5)
Site 3		
No tumbling	12.5 (0.7)	0.8 (0.3)
Ambient tumbling	12.4 (1.4)	0.3 (0.3)
Long-term spring (Jan 96–June 96)		
Site 2		
No tumbling	15.2 (1.8)	1.1 (0.2)
Ambient tumbling	10.5 (0.7)	0.2 (0.5)
Site 3		
No tumbling	14.8 (1.0)	0.6 (0.3)
Ambient tumbling	11.9 (3.0)	0.6 (0.2)
Year-long (Aug 95–July 96)		
No tumbling	18.4 (0.1)	1.0 (0.2)
Ambient tumbling	11.1 (0.7)	0.4 (0.5)

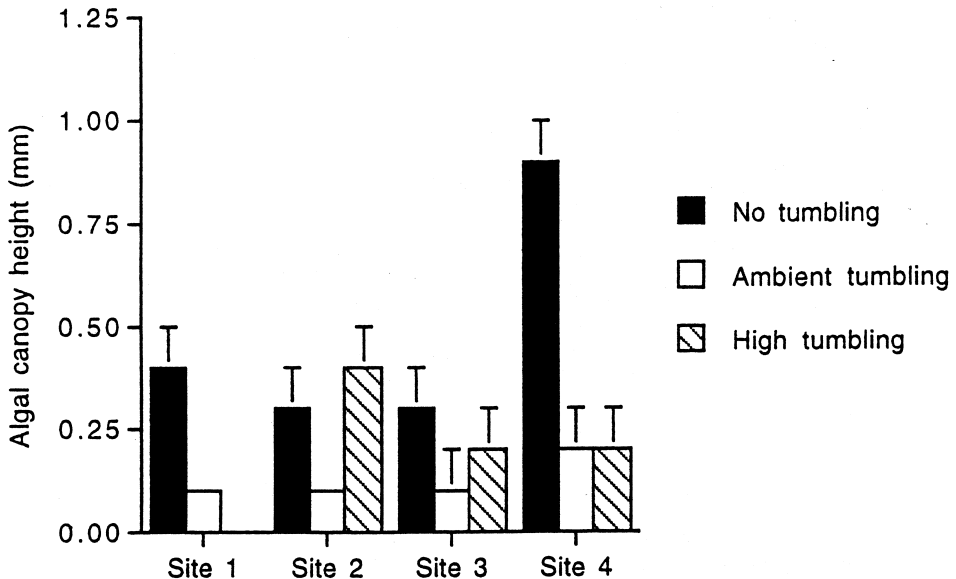


Fig. 7. Algal canopy height (mm) as a function of tumbling treatment in the summer 1995 experiment at four sites on the reef flat. Mean + 1 S.E. ( $n = 10$ ).

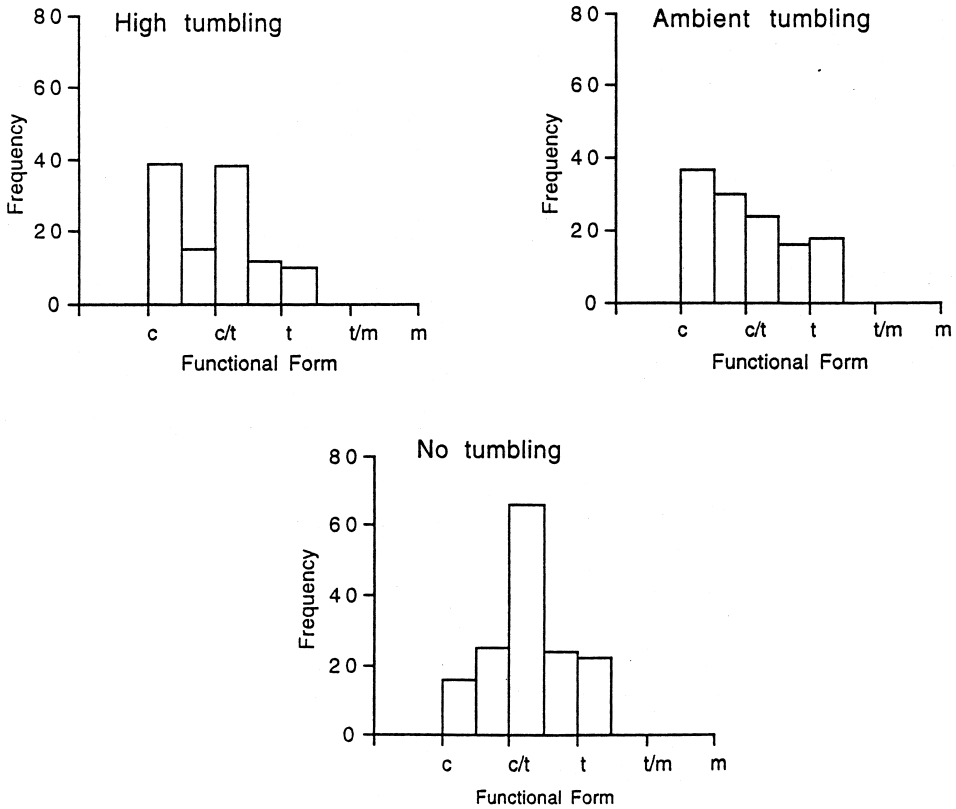


Fig. 8. Frequency histograms for functional form data in the summer 1995 tumbling experiment treatments. Intermediate categories resulted from using an ordinal classification in analyses. (c = crust, c/t = crust/turf, t = turf, t/m = turf/macroalgae, m = macroalgae;  $n = 120$ ).

Algae on the underside of rubble pieces experienced only indirect light. In laboratory trials, the available light averaged 375 and 899  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  when measured at a 45 and 20° angle relative to the light source respectively. No reflected light was detected with the sensor oriented perpendicular to the light source. With a rubble piece placed over the light source, light on the underside of rubble was reduced to  $5.0 \pm 0.5$  (S.E.)  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  in all trials. Although light reflected off adjacent rubble pieces in the field might increase these values somewhat, these measured photon flux densities were well below saturating photon flux densities ( $I_k$ ) for algal turf photosynthesis (780–1000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  for the intact community (Carpenter, 1985) and 153  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  for endolithic forms (Williams and Carpenter, 1990)).

### 3.4.2. Biological disturbance

#### 3.4.2.1. Experimental manipulations of crab herbivory on algal turfs

Crabs significantly reduced algal turf biomass by 21.8 and 27.0%, respectively, in the ambient and twice ambient density treatments compared to the no crab control (one-way

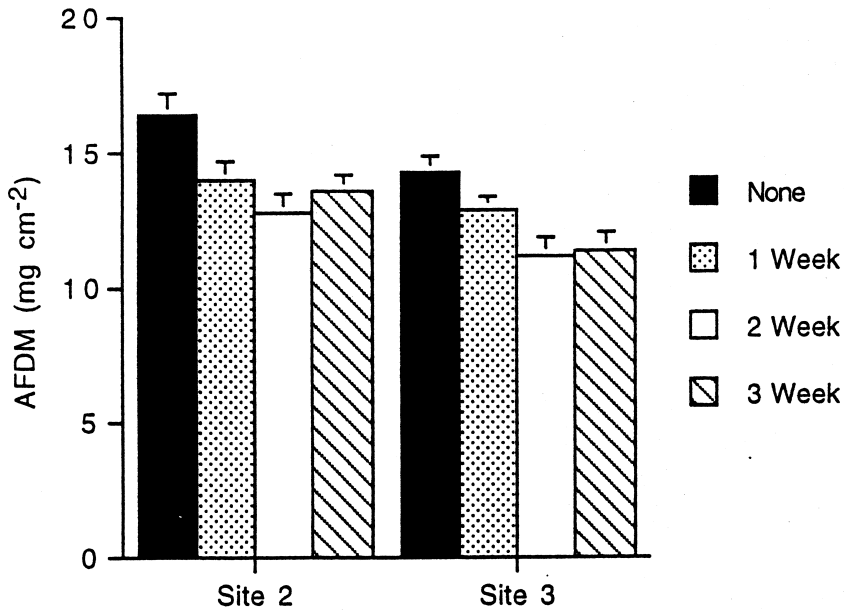


Fig. 9. Algal turf ash-free dry mass (AFDM) as a function of periods of light reduction (overturning) at two sites on the reef flat. Mean + 1 S.E. ( $n = 28$ ).

Table 7

Results of a randomized complete block ANOVA for ash-free dry mass ( $\text{mg cm}^{-2}$ ) of algal turf for site 3 in the overturning (light reduction) experiment including contrasts among means

Source of variation	df	MS	F value	P value
Block (pipe)	27	9.7138	1.1172	0.3437
Treatment	3	56.9836	6.5554	0.0010
No reduction vs. other treatments	1	119.7381	13.7738	<0.0001
1 week vs. 2 week and 3 week	1	48.8074	5.6142	0.0200
2 week vs. 3 week	1	0.6011	0.0691	0.7934
Error	79	8.6947	–	–

Table 8

Results of a randomized complete block ANOVA for canopy height (mm) of algal turf for site 3 for the overturning (light reduction) experiment including contrasts among means

Source of variation	df	MS	F value	P value
Block (pipe)	27	0.3973	1.3104	0.1795
Treatment	3	9.7642	10.7441	<0.0001
No reduction vs. other treatments	1	7.1691	23.6678	<0.0001
1 week vs. 2 week and 3 week	1	1.9659	6.4887	0.0137
2 week vs. 3 week	1	0.7162	2.3625	0.1283
Error	79	23.9317	–	–

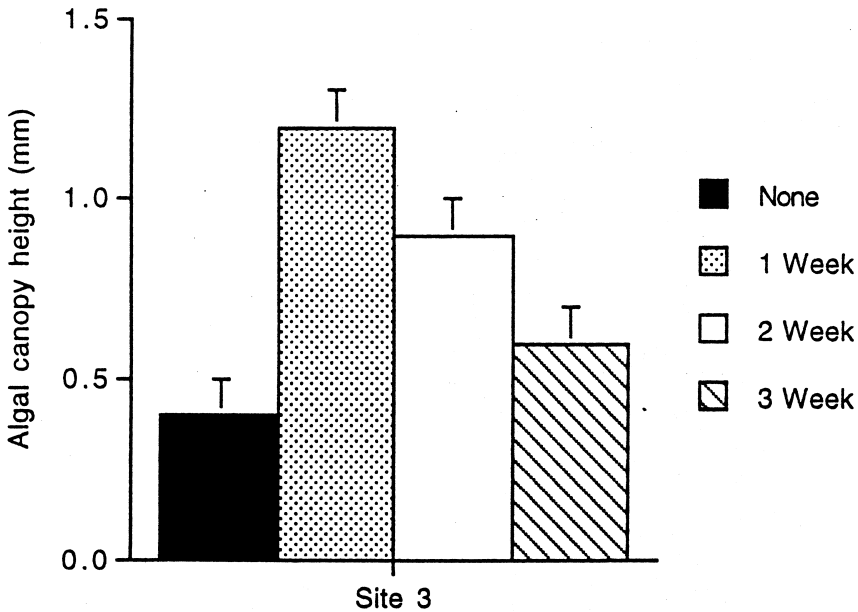


Fig. 10. Algal canopy height (mm) as a function of periods of overturning at site 3 on the reef flat. Mean + 1 S.E. ( $n = 28$ ).

ANOVA,  $df = 2, 9$ ,  $F = 6.9164$ ,  $P = 0.0152$ , Fig. 12). Algal turf canopy height also was reduced significantly by crab herbivory (Kruskal–Wallis  $H = 6.269$ ,  $df = 2$ ,  $P = 0.044$ ); without crabs, the canopy height was 16- and 2.5-times taller than in the twice ambient and ambient treatments, respectively (Fig. 13).

#### 3.4.2.2. Experimental manipulations of *Sargassum* sweeping on algal turfs

*Sargassum* sweeping significantly reduced algal turf biomass in the field (two-way ANOVA  $df = 1, 49$ ,  $F = 21.2745$ ,  $P < 0.0001$ ). Biomass was 28.1% lower for the swept rubble than the controls at both sites (Fig. 14). Algal canopy height was reduced

Table 9

Results of a randomized complete block ANOVA for functional form of algae for site 3 in the overturning (light reduction) experiment including contrasts among means

Source of variation	df	MS	F value	P value
Block (pipe)	27	0.2914	1.0136	0.4627
Treatment	3	0.8271	2.8802	0.0416
No reduction vs. other treatments	1	2.3743	8.2639	0.0050
1 week vs. 2 week and 3 week	1	0.0178	0.0585	0.8114
2 week vs. 3 week	1	0.0961	0.3352	0.5654
Error	79	22.9809	–	–

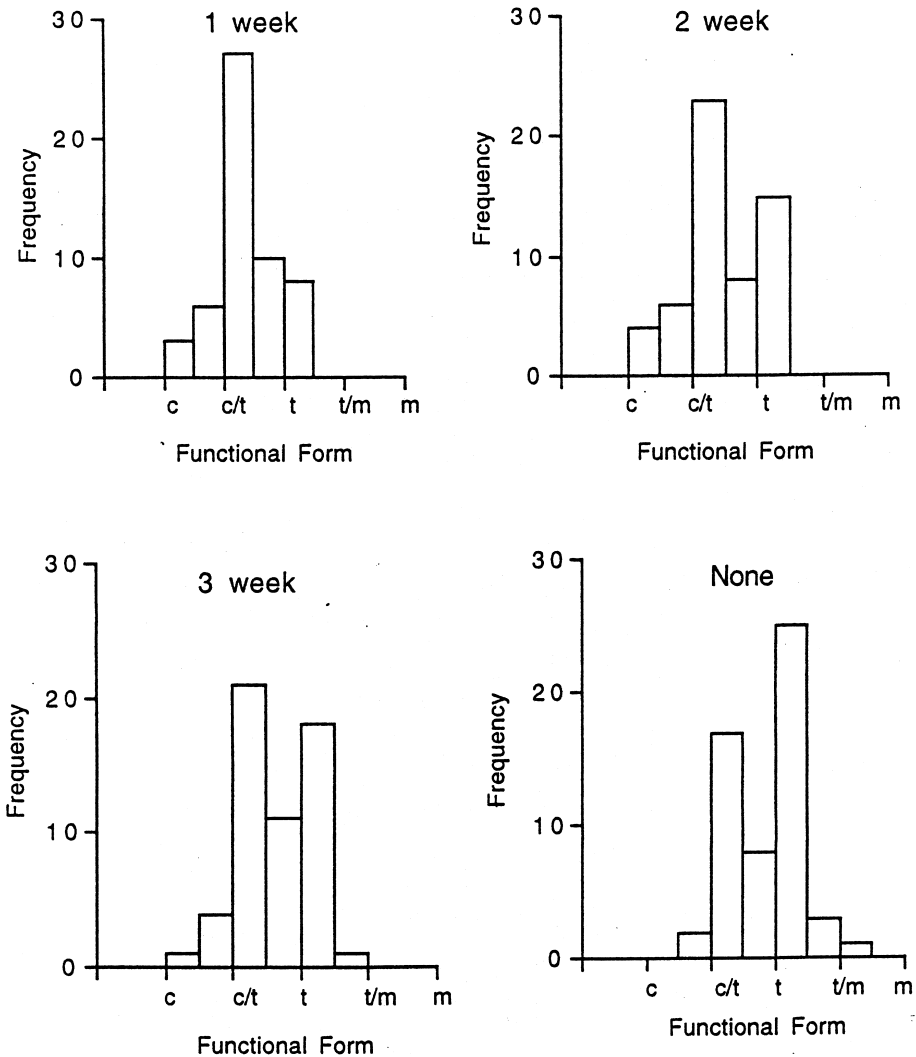


Fig. 11. Frequency histograms for functional form data in the overturning treatments. Intermediate categories resulted from using an ordinal classification in analyses (c = crust, c/t = crust/turf, t = turf, t/m = turf/macroalgae, m = macroalgae;  $n = 56$ ).

significantly by greater than 50% in the swept treatment when compared to the control (Fig. 15) (Friedman's statistic = 154.8,  $df = 1$ ,  $P < 0.001$ ). Algal community structure shifted significantly from mainly algal turfs and sparse macroalgae toward algal turfs and crusts with increased disturbance (two-way ANOVA  $df = 1$ , 49,  $F = 24.4117$ ,  $P < 0.0001$ , Fig. 16). In *Sargassum*-swept treatments, *Sphacelaria furcigera* was the dominate algal turf species. The crust, *Peyssonnelia rubra*, was abraded visibly on many rubble pieces.

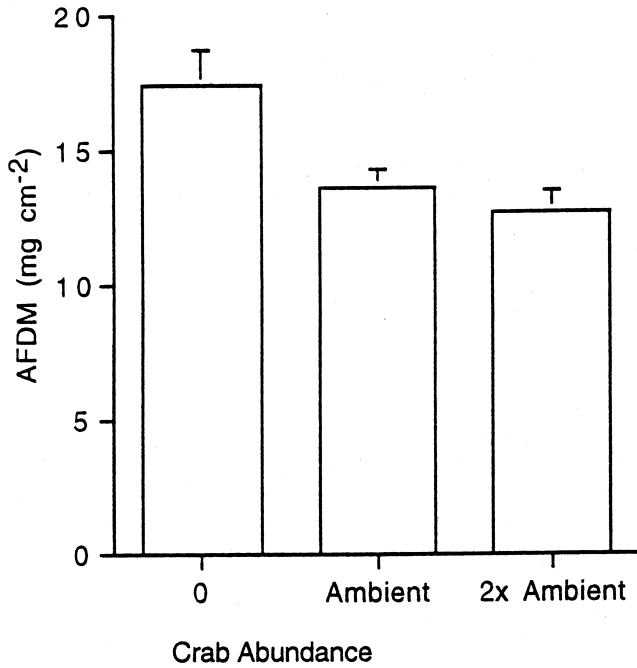


Fig. 12. Algal ash-free dry mass (AFDM) as a function of crab abundance. Mean + 1 S.E. ( $n = 4$ ).

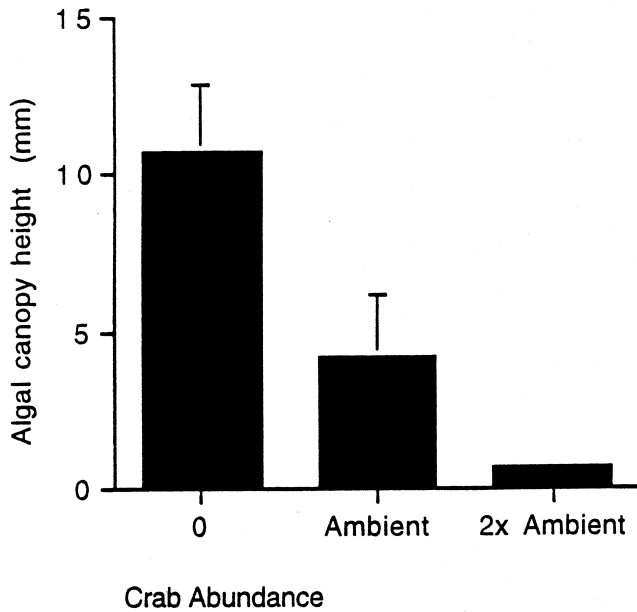


Fig. 13. Algal canopy height (mm) as a function of crab abundance. Mean + 1 S.E. ( $n = 4$ ).

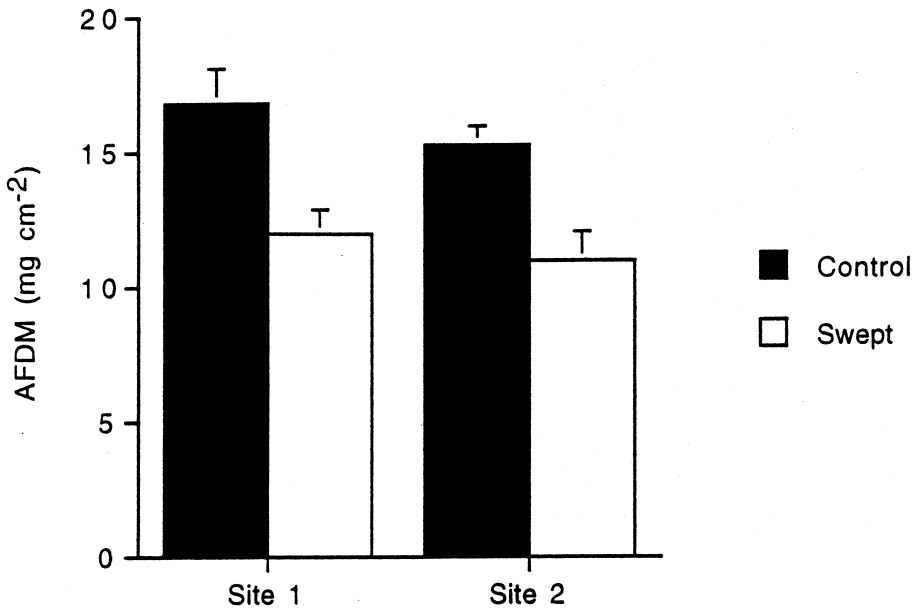


Fig. 14. Algal turf ash-free dry mass (AFDM) as a function of *Sargassum* sweeping at two sites on the reef flat. Mean + 1 S.E. ( $n = 14$ ).

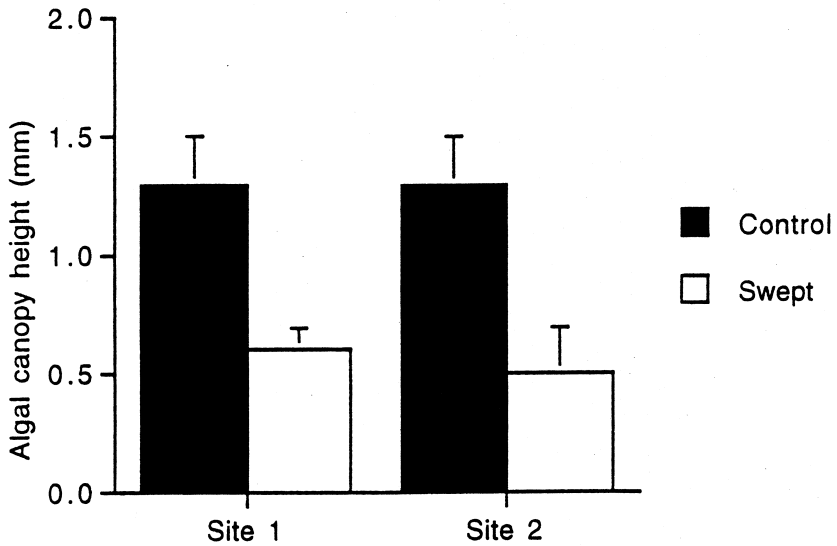


Fig. 15. Algal canopy height (mm) as a function of *Sargassum* sweeping at two sites on the reef flat. Mean + 1 S.E. ( $n = 13$ ).

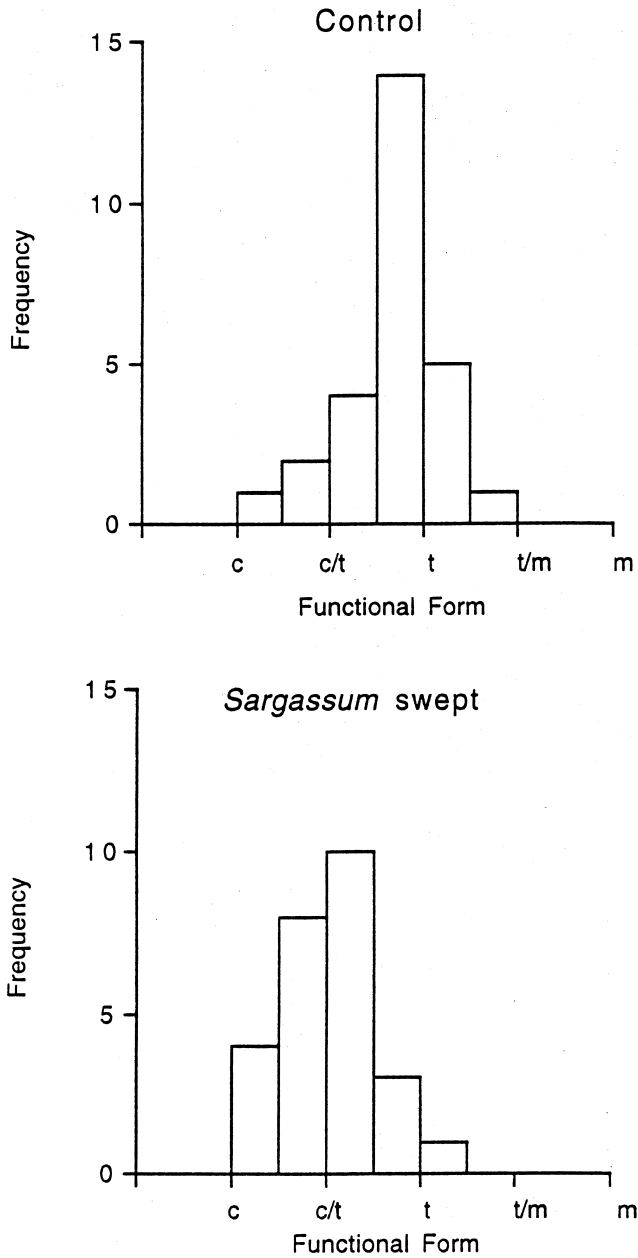


Fig. 16. Frequency histograms for *Sargassum* sweeping treatments. Intermediate categories resulted from using an ordinal classification in analyses (c = crust, c/t = crust/turf, t = turf, t/m = turf/macroalgae, m = macroalgae; n = 28).



#### 4. Discussion

Disturbance in the form of grazing exerts major control over algal community structure and biomass on coral reefs (Ogden and Lobel, 1978; Galzin, 1987; Morrison, 1988; Zeller, 1988; Carpenter, 1990a,b; McClanahan et al., 1996). We have shown here that chronic physical disturbance and rarely-considered biological disturbances also can control algal community structure and reduce biomass to levels equivalent to those under herbivory on coral reefs. In our study, chronic physical disturbance caused by rubble tumbling reduced algal biomass by up to 40% through abrasion and light reduction, decreased algal canopy height, and helped maintain an algal community dominated by turfs over most areas of the reef flat. These results suggest that more frequent, less intense disturbances associated with average water flow conditions (Connell, 1978; Grigg, 1983; Phillips et al., 1997) deserve as much attention as the effects of intense, infrequent disturbances such as hurricanes (Porter and Meier, 1992; Letourneur et al., 1993; Rogers, 1993; Chabanet et al., 1995).

One limitation to the tumbling experiments (and the light reduction experiment) is that the reduction of nutrient advection associated with reduced water flow-rates was not controlled for in these experiments. Algal turf photosynthetic rates and nitrogen fixation rates increase with higher water flow speeds (Carpenter et al., 1991; Williams and Carpenter, 1998). The algae hypothetically affected most by reduced water flow-rates were those growing on the undersides of the treatment rubble which rarely were overturned, e.g. in the light reduction experiment. However, the measured 99.99% reduction in light by rubble pieces suggests that light was the most limiting factor for the attached algal turfs. Although undoubtedly nutrients are regenerated from the benthos under the rubble, too little is known about relative supply rates and nutrient limitation of algal turfs to speculate about the importance of this as an uncontrolled treatment effect, other than to note that algal biomass was limited on the undersides of rubble.

Abrasion and cover by sand is probably an important physical disturbance that we could not quantify. Sand directly affects algal biomass through burial, light reduction, and abrasion during bedload transport (Rogers, 1990; Kendrick, 1991; Trowbridge, 1996). Sediment deposition and movement also can contribute to controlling community structure (Rogers, 1990; Airoidi et al., 1996). In this study, the variability in algal biomass in the high tumbling treatment could be due to confounding artifacts of the manipulation (manually tumbling rubble two times a week). The effects of high tumbling on algal biomass may have been mediated by alleviating shading from excessive sand that was covering attached algae. Also, the manipulated high tumbling treatment did not replicate the periods of light reduction that would occur with this tumbling frequency.

As expected from initial observations, the influence of larger herbivores seems to be reduced on the Kaneohe Bay reef flat. Densities of sea urchins and herbivorous fishes (Table 10) were low compared to other coral reef flats. For example, densities of *Echinothrix diadema* on Kaneohe Bay reef flat were as low as densities of *Diadema antillarum* after the 1983/1984 mass mortality in St. Croix (Carpenter, 1990a). Human fishing pressure has been shown to limit the effects of fish grazing in coral reef environments (Levitan, 1992; Richmond, 1993; Hughes, 1994; Maragos and Cook, 1995; Roberts, 1995; McClanahan, 1997), and we observed people spearfishing on the

Table 10  
Herbivorous fish abundances on coral reefs censused with replicate visual belt transects (mean (S.E.) normalized to 100-m<sup>3</sup> transects)

Location	Date	Scarids			Acanthuids	Total	Citation
		Juvenile	Adult	Total			
Australia							Choat and Bellwood (1985)
Lizard Island ( <i>n</i> = 20)	September 1982	–	–	14	21	35	
Panama ( <i>n</i> = 8)	June 1982	–	–	10 (0)	13 (0)	23	Lewis and Wainwright (1985)
Panama ( <i>n</i> = 50)	April 1982	–	–	13 (0)	20 (0)	23	Lewis (1986)
Panama ( <i>n</i> = 8)	June 1982	–	–	10 (0)	13 (0)	23	
Moorea, French Polynesia ( <i>n</i> = 8)		–	–	18 (1)	61 (2)	79	Galzin (1987)
Belize ( <i>n</i> = 4)	June 1985	–	–	16	19	35	Macintyre et al. (1987)
Panama ( <i>n</i> = 3)	October 1978	–	–	?	23 (16)	23 +	Robertson (1988)
Virgin Islands ( <i>n</i> = 4)	June 1985	87 (8)	18 (3)	105	32 (1)	137	Carpenter (1990b)
Virgin Islands ( <i>n</i> = 4)	September 1985	–	28 (5)	154	27 (1)	183	
Kenya ( <i>n</i> = 6)	February 1992	–	–	9 (2)	1 (0)	10	McClanahan et al. (1994)
Australia							Caley (1995)
Lizard Island ( <i>n</i> = 5)	June 1990	5	0	5	1	6	
One Tree Island ( <i>n</i> = 5)	June 1990	33	3	37	0	37	
Kenya ( <i>n</i> = 6)	December 1994	–	–	7	75	82	McClanahan et al. (1994)
Oahu, HI ( <i>n</i> = 7)	June 1995	4 (2)	0 (0)	4	7 (2)	11	This study
Oahu, HI ( <i>n</i> = 10)	January 1996	5 (2)	0 (0)	5	9 (2)	14	
Oahu, HI ( <i>n</i> = 7)	June 1996	2 (1)	0 (0)	2	7 (2)	9	

reef flat almost daily. Fishing pressure may contribute to the low densities and small sizes of herbivorous fishes on the Kaneohe Bay reef flat. Scarids and other large fishes might migrate from the reef flat to reside immediately seaward of the reef crest where we observed many adults in slightly deeper water. Reef flat environments typically have low densities of acanthurids and scarids presumably due to poor post-settlement survival (Russ, 1984). In addition to apparent fishing pressures, herbivory is restricted because the Kaneohe Bay reef flat provides little substratum relief for larger, mobile herbivores. Species richness and diversity of herbivorous fish assemblages increase with the architectural complexity of the substratum (Galzin et al., 1994; Chabanet et al., 1997). There are relatively few bommies to provide refuge and increased foraging area to sea urchins and fishes, and the frequent movement of coral rubble apparently restricts sea urchins to the less common stable pavements and bommies (Russo, 1977).

In the absence of major herbivory from sea urchins and fishes, small crabs are the dominant grazers of algal turfs on the reef flat. Small crabs reduced algal turf biomass and canopy height in the laboratory experiment where predators were absent and the rubble did not tumble. Under these conditions, grazing pressure should have been elevated relative to the field, and the loss of biomass to crabs in the field should be less than the 22% difference in the laboratory experiment.

Instead of herbivory, the major biological disturbance to the algal turfs is abrasion by erect and tough macroalgae. In the area around them, *Sargassum* thalli maintain an algal community dominated by turfs and reduce turf biomass by > 28%. We estimated that sweeping could affect every cm of substratum on the reef flat based on the mean thallus height as the sweep radius and the overall mean density of *Sargassum* on the reef flat. Although this overestimates the total area disturbed because the thalli are not regularly distributed and do not sweep a uniform circle around their holdfast, abrasion of algal turf biomass by *Sargassum* can be widespread. Disturbance to algal turfs by *Sargassum* and other macroalgae varies directly with water flow speeds and periods of oscillation over the reef flat. Also, the sweep radius of a seaweed over algal turfs is determined by its height, which is set by seasonal recruitment and growth patterns balanced against drag-induced thallus breakage and apparently also by the tumbling of coral rubble (Table 3). We have assumed that mechanical damage is the apparent mechanism of interference. However, other mechanisms might be operating. *Sargassum* from Hawaii is known to contain low concentrations of polyphenolic compounds (Targett et al. 1995). If released from the vesicles that contain them, polyphenolics might have anti-algal properties (Ragan and Glombitza, 1986). That acknowledged, Ragan and Glombitza (1986) concluded that the evidence for the ecological relevance of polyphenolic release from brown seaweeds was weak.

Algal turf communities on the Kaneohe Bay reef flat are maintained, and their biomass is controlled, by numerous disturbances. We experimentally quantified that biological disturbances, primarily abrasion by *Sargassum* thalli, result in a reduction of algal turf biomass by almost a third. Physical disturbances, e.g. reduction of light and biomass removal as coral rubble tumbles, can reduce biomass in experiments by 40%. That chronic physical disturbances are as important to coral reef communities as biological disturbances has not been documented previously by coral reef ecologists. Both physical and biological factors influencing coral reef ecology should be considered concurrently in future experiments.

## 5. Conclusions

Our studies demonstrate that water flow regimes ultimately are very important in setting the frequency of chronic disturbances to algal turfs and thus influencing algal community structure on coral reefs. Water flow regimes directly control physical disturbances when algal turfs are abraded and periodically buried as rubble substratum tumbles in waves and currents, and indirectly influence biological disturbance intensity and frequency. Water motion sweeps seaweeds over algal turfs and restricts the foraging behavior of herbivores. The importance of water flow regimes on coral reefs to date has been documented primarily for individual organisms and their feeding and metabolism (Jokiel, 1978; Andrews et al., 1988; Patterson and Sebens, 1989; Patterson et al., 1991; Helmuth and Sebens, 1993; Genin et al., 1994; Lesser et al., 1994; Fabricius et al., 1995; Williams and Carpenter, 1998). Our findings add to the growing recognition that hydrodynamics are of primary importance in coral reef ecosystems as a whole (Atkinson, 1988, 1992; Andrews and Pickard, 1990; Patterson et al., 1991). For example, water flow regulates the high rates of net primary production and nitrogen fixation in algal turfs (Carpenter et al., 1991; Williams and Carpenter, 1998). Metabolic rates are negatively correlated with boundary layer thickness over the turfs, and boundary layer thickness is reduced as ambient water flow speeds increase and algal canopy heights decrease (Carpenter and Williams, 1993; Williams and Carpenter, 1997, 1998). Physical disturbance and biological disturbance in the form of herbivory (Carpenter, 1986; Williams and Carpenter, 1997) lead to significant reductions in algal canopy height. In addition, water flow indirectly influences the ability of herbivores to crop algal canopies by limiting foraging activity (Lieberman et al., 1979; Foster, 1987). The importance of physical factors in regulating many aspects of coral reef ecosystem function represents a major shift from the paradigm of tight biological control (Odum and Odum, 1955; Muscatine and Porter, 1977; Smith, 1988; Sorokin, 1990). It should come as no surprise that coral reefs thrive in areas of high water flow (Grigg, 1983; Adey and Goertemiller, 1987; Darwin, 1988 (reissue); Hamner and Wolanski, 1988; Hatcher, 1990; Atkinson, 1992).

We predict that physical disturbances will increase in relative importance in marine communities under global change scenarios as storms, overfishing, and anthropogenic effects increase (Massel and Done, 1993; Richmond, 1993; Wilkinson, 1993; McClanahan et al., 1994; McClanahan, 1995; Stone et al., 1996). Where physical disturbance becomes more important, the trophic structure of the coral reef will change as primary production is removed before it can be eaten and as herbivore foraging is reduced. Ecologists need to understand the specific effects of physical disturbances on communities and the relationship between physical forcing functions and disturbance intensity and frequency (Miller, 1982; Karlson and Hurd, 1993). The latter is very poorly understood at present. Until progress is made, it will be difficult to predict the set of conditions under which a community will change in response to disturbance, and to detect the relative importance of physical versus biological disturbances. As one step, our study demonstrates the relationship between water flow regimes and the frequency of both physical and biological disturbance to their effects on algal turfs.

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## References

- Adey, W., 1987. Food production in low-nutrient seas. *BioScience* 37, 340–348.
- Adey, W., Steneck, R.S., 1985. Highly productive eastern Caribbean reefs: Synergistic effects of biological and chemical, physical, and geological factors. In: Reaka, M.L. (Ed.), *The Ecology of Coral Reefs Symposia Series For Undersea Research*, NOAA, Rockville, pp. 163–187.
- Adey, W., Goertemiller, T., 1987. Coral reef algal turfs: master producers in nutrient poor seas. *Phycologia* 26, 374–386.
- Airoidi, L., Fabiano, M., Cinelli, F., 1996. Sediment deposition and movement over a turf assemblage in a shallow rocky coastal area of the Ligurian Sea. *Mar. Ecol. Prog. Ser.* 133, 241–251.
- Andrews, J.C., Pickard, G.L., 1990. The physical oceanography of coral reef systems. In: Dubinsky, Z. (Ed.), *Coral Reefs*, Elsevier, Amsterdam, pp. 11–48.
- Andrews, J.C., Gay, S., Sammarco, P.W., 1988. Influence of circulation on self-seeding patterns at Helix Reef-Great Barrier Reef. In: *Proc. 6th Int. Coral Reef Symp.*, Australia, Vol. 2, pp. 469–474.
- Ang, P.O., 1985. Phenology of *Sargassum siliquosum* J. Ag. and *S. paniculatum* J. Ag. (Sargassaceae, Phaeophyta) in the reef flat of Balibago (Calatagan, Philippines). In: *Proc. 5th Int. Coral Reef Cong.*, Tahiti, Vol. 5, pp. 51–57.
- Aronson, R.B., Edmunds, P.J., Precht, W.F., Swanson, D.W., Levitan, D.R., 1994. Large-scale long-term monitoring of Caribbean coral reefs: simple, quick, inexpensive techniques. *Atoll Res. Bull.* 247, 1–19.
- Atkinson, M.J., 1988. Are coral reefs nutrient-limited? In: *Proc. 6th Int. Coral Reef Symp.*, Vol. 1, pp. 157–165.
- Atkinson, M.J., 1992. Productivity of Enewetak Atoll reef flats predicted from mass transfer relationships. *Cont. Shelf Res.* 12, 799–807.
- Bathen, K.H. (Ed.), 1968. A descriptive study of the physical oceanography of Kaneohe Bay, Hawaii, University of Hawaii Institute of Marine Biology, Technical Report 14.
- Borowitzka, M.A., 1981. Algae and grazing in coral reef ecosystems. *Endeavour* 5, 99–106.
- Brawley, S.H., Adey, W.H., 1977. Territorial behavior of threespot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. *Environ. Biol. Fish.* 2, 45–51.
- Brawley, S.H., Adey, W.H., 1981. The effect of micrograzers on algal community structure in a coral reef microcosm. *Mar. Biol.* 61, 167–177.
- Brock, R.E., 1979. An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. *Mar. Biol.* 51, 381–388.
- Bythell, J.C., Bythell, M., Gladfelter, E.H., 1993. Initial results of a longterm coral reef monitoring program: impact of Hurricane Hugo at Buck Island Reef National Monument, St. Croix, US Virgin Islands. *J. Exp. Mar. Biol. Ecol.* 172, 171–183.
- Caley, M.J., 1995. Community dynamics of tropical reef fishes: local patterns between latitudes. *Mar. Ecol. Prog. Ser.* 129, 7–18.

- Carpenter, R.C., 1981. Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. J. Mar. Res. 39, 749–785.
- Carpenter, R.C., 1985. Relationships between primary production and irradiance in coral reef algal communities. Limnol. Oceanogr. 30, 784–793.
- Carpenter, R.C., 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecol. Monogr. 56, 345–363.
- Carpenter, R.C., 1990a. Mass mortality of *Diadema antillarum*. I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. Mar. Biol. 104, 67–77.
- Carpenter, R.C., 1990b. Mass mortality of *Diadema antillarum*. II. Effects on population densities and grazing intensity of parrotfishes and surgeonfishes. Mar. Biol. 104, 79–86.
- Carpenter, R.C., Williams, S.L., 1993. Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment. Limnol. Oceanogr. 38, 687–694.
- Carpenter, R.C., Hackney, J.M., Adey, W.H., 1991. Measurements of primary productivity and nitrogenase activity of coral reef algae in a chamber incorporating oscillatory flow. Limnol. Oceanogr. 36, 40–49.
- Chabanet, P., Dufour, V., Galzin, R., 1995. Disturbance impact on reef fish communities in Reunion Island (Indian Ocean). J. Exp. Mar. Biol. Ecol. 188, 29–48.
- Chabanet, P., Ralambondrainy, H., Amanieu, M., Faure, G., Galzin, R., 1997. Relationships between coral reef substrata and fish. Coral Reefs 16, 93–102.
- Choat, J.H., Bellwood, D.R., 1985. Interactions amongst herbivorous fishes on a coral reef: influence of spatial variation. Mar. Biol. 89, 221–234.
- Coen, L.D., 1988a. Herbivory by Caribbean majid crabs: feeding ecology and plant susceptibility. J. Exp. Mar. Biol. Ecol. 122, 257–276.
- Coen, L.D., 1988b. Herbivory by crabs and the control of algal epibionts on Caribbean host corals. Oecologia 75, 198–203.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.
- Connell, J.H., 1983. Disturbance and patch dynamics of reef corals. In: Proc. Inaug. Great Barr. Reef. Conf. pp. 179–189.
- Conover, W.J., 1971. Practical Nonparametric Statistics, Wiley, New York.
- Darwin, C.R., 1988. The Voyage of the Beagle. In: Keynes, R.D. (Ed.), Diary of the Voyage of the H.M.S. Beagle, Cambridge University Press, Cambridge, pp. 413–419.
- Dayton, P.K., Seymour, R.J., Parnell, P.E., Tegner, M.J., 1989. Unusual marine erosion in San Diego county from a single storm. Estuar. Coast. Shelf Sci. 29, 151–160.
- DeWreede, R.E., 1976. The phenology of three species of *Sargassum* (Sargassaceae, Phaeophyta) in Hawaii. Phycologia 15, 175–183.
- Edmondson, C.H., 1946. Reef and Shore Fauna of Hawaii, Bernice P. Bishop Museum, Honolulu, HI.
- Edmunds, P.J., Witman, J.D., 1991. Effect of Hurricane Hugo on the primary framework of a reef along the south shore of St. John, US Virgin Islands. Mar. Ecol. Prog. Ser. 78, 201–204.
- Fabricius, K.E., Genin, A., Benayahu, Y., 1995. Flow-dependent herbivory and growth in zooxanthellae-free soft corals. Limnol. Oceanogr. 40, 1290–1301.
- Foster, S.A., 1987. The relative impacts of grazing by Caribbean coral reef fishes and *Diadema*: Effects of habitat and surge. J. Exp. Mar. Biol. Ecol. 105, 1–20.
- Galzin, R., 1987. Structure of fish communities of French Polynesian coral reefs. II. Temporal scales. Mar. Ecol. Prog. Ser. 41, 137–145.
- Galzin, R., Planes, S., Dufour, V., Salvat, B., 1994. Variation in diversity of coral reef fish between French Polynesian atolls. Coral Reefs 13, 175–180.
- Genin, A., Karp, L., Miroz, A., 1994. Effects of low on competitive superiority in scleractinian corals. Limnol. Oceanogr. 39, 913–924.
- Grigg, R.W., 1983. Community structure, succession and development of coral reefs in Hawaii. Mar. Ecol. Prog. Ser. 11, 1–14.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111, 1169–1194.
- Grünbaum, H., Bergman, G., Abbott, D.P., Ogden, J.C., 1978. Intraspecific agonistic behavior in the rock-boring sea urchin *Echinometra lucunter* (L.) (Echinodermata: Echinoidea). Bull. Mar. Sci. 28, 181–188.

- Hackney, J.M., Carpenter, R.C., Adey, W.H., 1989. Characteristic adaptations to grazing among algal turfs on a Caribbean reef. *Phycologia* 28, 109–119.
- Hammer, W.M., Wolanski, E., 1988. Hydrodynamic forcing functions and biological processes on coral reefs: a status review. In: Proc. 6th Int. Coral Reef Cong., Vol. 1, pp. 103–113.
- Hatcher, B.G., 1988. Coral reef primary productivity: a beggar's banquet. *Trends Ecol. Evol.* 3, 106–111.
- Hatcher, B.G., 1990. Coral reef primary productivity: A hierarchy of pattern and process. *Trends Ecol. Evol.* 5, 149–155.
- Hatcher, B.G., Larkum, A.W.D., 1983. An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. *J. Exp. Mar. Biol. Ecol.* 69, 61–84.
- Hay, M.E., 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* 62, 739–750.
- Hay, M.E., 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* 65, 446–454.
- Hay, M.E., 1985. Spatial patterns of herbivore impact and their importance in maintaining algal species richness. In: Proc. 5th Int. Coral Reef Cong., Tahiti, Vol. 4, pp. 29–34.
- Helmuth, B., Sebens, K., 1993. The influence of colony morphology and orientation to flow by the scleractinian coral *Agaricia agaricites* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* 165, 251–278.
- Hoover, J.P., 1993. *Hawaii's Fishes: A Guide For Snorkelers, Divers and Aquarists*, Mutual Publishing, Honolulu.
- Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1552.
- Hughes, T.P., Keller, B.D., Jackson, J.B.C., Boyle, M.J., 1985. Mass mortality of the echinoid *Diadema antillarum* Philippi in Jamaica. *Bull. Mar. Sci.* 36, 377–384.
- Hunter, C.L., Evans, C.V., 1995. Coral reefs in Kaneohe Bay, Hawaii: two centuries of western influence and two decades of data. *Bull. Mar. Sci.* 57, 501–515.
- Jokiel, P.L., 1978. Effects of water motion on reef corals. *J. Exp. Mar. Biol. Ecol.* 35, 87–97.
- Karlson, R.H., Hurd, L.E., 1993. Disturbance, coral reef communities, and changing ecological paradigms. *Coral Reefs* 12, 117–125.
- Kendrick, G.A., 1991. Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: effect of simulated sand scour, erosion and accretion. *J. Exp. Mar. Biol. Ecol.* 147, 47–63.
- Knowlton, N., Lang, J.C., Rooney, M.C., Clifford, P., 1981. Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. *Nature* 294, 251–252.
- Lassuy, D.R., 1980. Effects of "farming" behavior by *Eupomacentrus lividus* and *Hemiglyphidodon plagiometopon* on algal community structure. *Bull. Mar. Sci.* 30, 304–312.
- Lesser, M.P., Weiss, V.M., Patterson, M.R., Jokiel, P.L., 1994. Effects of morphology and water motion on carbon delivery and productivity in the reef coral, *Pocillopora damicornis* (Linnaeus): Diffusion barriers, inorganic carbon limitation, and biochemical plasticity. *J. Exp. Mar. Biol. Ecol.* 178, 153–179.
- Letourneur, Y., Harmelin-Vivien, M., Galzin, R., 1993. Impact of Hurricane Firinga on fish community structure on fringing reefs of Reunion Island, S.W. Indian Ocean. *Environ. Biol. Fish.* 37, 109–120.
- Levitan, D.R., 1992. Community structure in times past: Influence of human fishing pressure on algal–urchin interactions. *Ecology* 73, 1597–1605.
- Lewis, S.M., 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol. Monogr.* 56, 183–200.
- Lewis, S.M., Wainwright, P.C., 1985. Herbivore abundance and grazing intensity on a Caribbean coral reef. *J. Exp. Mar. Biol. Ecol.* 87, 215–228.
- Lieberman, M., John, D.M., Lieberman, D., 1979. Ecology of subtidal algae on seasonally devastated cobble substrates off Ghana. *Ecology* 60, 1151–1161.
- Lieberman, M., John, D.M., Lieberman, D., 1984. Factors influencing algal species assemblages on reef and cobble substrata off Ghana. *J. Exp. Mar. Biol. Ecol.* 75, 129–143.
- Littler, M.M., 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, 25–44.
- Littler, M.M., Taylor, P.R., Littler, D.S., 1983. Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* 2, 111–118.

- Lobel, P.S., 1980. Herbivory by damselfishes and their role in coral reef community ecology. *Bull. Mar. Sci.* 30, 273–289.
- Macintyre, I.G., Graus, R.R., Reinthal, P.N., Littler, M.M., Littler, D.S., 1987. The Barrier Reef sediment apron: Tobacco Reef, Belize. *Coral Reefs* 6, 1–12.
- Maragos, J.E., Cook, Jr. C.W., 1995. The 1991–1992 rapid ecological assessment of Palau's coral reefs. *Coral Reefs* 14, 237–252.
- Martin-Smith, K.M., 1994. Short-term dynamics of tropical macroalgal epifauna: patterns and processes in recolonisation of *Sargassum fissifolium*. *Mar. Ecol. Prog. Ser.* 110, 177–185.
- Massel, S.R., Done, T.J., 1993. Effects of cyclone waves on massive coral assemblages on the Great Barrier Reef: meteorology, hydrodynamics and demography. *Coral Reefs* 12, 153–166.
- McClanahan, T.R., 1995. A coral reef ecosystem–fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. *Ecol. Model.* 80, 1–19.
- McClanahan, T.R., 1997. Primary succession of coral reef algae: differing patterns on fished versus unfished reefs. *J. Exp. Mar. Biol. Ecol.* 218, 77–102.
- McClanahan, T.R., Nugues, M., Mwachirey, S., 1994. Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: the role of reef management. *J. Exp. Mar. Biol. Ecol.* 184, 237–254.
- McClanahan, T.R., Kamukuru, A.T., Muthiga, N.A., Yebeo, M.G., Obura, D., 1996. Effect of sea urchin reductions on algae, coral, and fish populations. *Conserv. Biol.* 1, 136–154.
- Miller, T.E., 1982. Community diversity and interactions between the size and frequency of disturbance. *Am. Nat.* 120, 533–536.
- Montgomery, W.L., 1980. The impact of non-selective grazing by the giant blue damselfish, *Microspathodon dorsalis*, on algal 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.
- Muscatine, L., Porter, J.W., 1977. Reef corals: mutualistic symbioses adapted to nutrient-poor environments. *BioScience* 27, 454–460.
- Odum, H.T., Odum, E.P., 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monogr.* 25, 291–320.
- Ogden, J.C., Lobel, P.S., 1978. The role of herbivorous fishes and urchins in coral reef communities. *Environ. Biol. Fish.* 3, 49–63.
- Paine, R.T., 1979. Disaster, catastrophe, and local persistence of the sea palm, *Postelsia palmaeformis*. *Science* 205, 685–687.
- Paine, R.T., Levin, S.A., 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.* 51, 145–178.
- Patterson, M.R., Sebens, K.P., 1989. Forced convection modulates gas exchange in cnidarians. *Proc. Natl. Acad. Sci. USA* 86, 8833–8836.
- Patterson, M.R., Sebens, K.P., Olson, R.R., 1991. In situ measurements of flow effects on primary production and dark respiration in reef corals. *Limnol. Oceanogr.* 36, 936–948.
- Phillips, J.C., Kendrick, G.A., Lavery, P.S., 1997. A test of a functional group approach to detecting shift in macroalgal communities along a disturbance gradient. *Mar. Ecol. Prog. Ser.* 153, 125–138.
- Porter, J.W., Meier, O.W., 1992. Quantification of loss and change in Floridian reef coral populations. *Am. Zool.* 32, 625–640.
- Potts, D.C., 1977. Suppression of coral populations by filamentous algae within damselfish territories. *J. Exp. Mar. Biol. Ecol.* 28, 207–216.
- Price, I.R., 1989. Seaweed phenology in a tropical Australian locality (Townsville, North Queensland). *Bot. Mar.* 32, 399–406.
- Ragan, M.A., Glombitza, K.-W., 1986. Phlorotannins, brown algal polyphenols. *Prog. Phycol. Res.* 4, 129–241.
- Richmond, R.H., 1993. Coral reefs: present problems and future concerns resulting from anthropogenic disturbance. *Am. Zool.* 33, 524–536.
- Roberts, C.M., 1995. Effects of fishing on the ecosystem structure of coral reefs. *Conserv. Biol.* 9, 988–995.
- Robertson, D.R., 1988. Abundances of surgeonfishes on patch-reefs in Caribbean Panamá: due to settlement, or post-settlement events? *Mar. Biol.* 97, 495–501.



- Rogers, C.S., 1990. Responses of coral reefs and reef organisms to sedimentation. *Mar. Ecol. Prog. Ser.* 62, 185–202.
- Rogers, C.S., 1993. Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited. *Coral Reefs* 12, 127–137.
- Russ, G., 1984. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar. Ecol. Prog. Ser.* 20, 23–34.
- Russ, G.R., Alcala, A.C., 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. *Mar. Ecol. Prog. Ser.* 56, 13–27.
- Russo, A.R., 1977. Water flow and the distribution and abundance of echinoids (Genus *Echinometra*) on an Hawaiian reef. *Aust. J. Mar. Freshwater Res.* 28, 693–702.
- Sammarco, P.W., 1983. Effects of fish grazing and damselfish territoriality on coral reef algae. I. Algal community structure. *Mar. Ecol. Prog. Ser.* 13, 1–14.
- Sammarco, P.W., Levinton, J.S., Ogden, J.C., 1973. Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. *J. Mar. Res.* 32, 47–53.
- Seymour, R.J., Tegner, M.J., Dayton, P.K., Parnell, P.E., 1989. Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in southern California. *Estuar. Coast. Shelf Sci.* 28, 277–292.
- Smith, S.V., 1988. Mass balance in coral-reef-dominated areas. In: Jansson, B.-O. (Ed.), *Lecture Notes On Coastal and Estuarine Studies: Coastal-offshore Ecosystem Interactions*, Springer, Berlin, pp. 209–226.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*, W.H. Freeman, New York.
- Sorokin, Y.I., 1990. Aspects of trophic relations, productivity and energy balance in coral reef ecosystems. In: Dubinsky, Z. (Ed.), *Coral Reefs*, Elsevier, Amsterdam, pp. 401–410.
- Sousa, W.P., 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol. Monogr.* 49, 227–254.
- Sousa, W.P., 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15, 353–391.
- Steneck, R.S., 1988. Herbivory on coral reefs: a synthesis. In: *Proc. 6th Int. Coral Reef Symp.*, Australia, Vol. 1, pp. 37–49.
- Steneck, R.S., Watling, L., 1982. Feeding capabilities and limitation of herbivorous molluscs: A functional group approach. *Mar. Biol.* 68, 299–319.
- Steneck, R.S., Dethier, M.N., 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* 69, 476–498.
- Stone, L., Eilam, E., Abelson, A., Ilan, M., 1996. Modeling coral reef biodiversity and habitat destruction. *Mar. Ecol. Prog. Ser.* 134, 299–302.
- Targett, N.M., Boettcher, A.A., Targett, T.E., Vrolijk, N.H., 1995. Tropical marine herbivore assimilation of phenolic-rich plants. *Oecologia* 103, 170–179.
- Trowbridge, C.D., 1996. Demography and phenology of the intertidal green alga *Codium setchellii*: the enigma of local scarcity on sand-influenced rocky shores. *Mar. Biol.* 127, 341–351.
- Van Den Hoek, C., Breeman, A.M., Bak, R.P.M., Van Buurt, G., 1978. The distribution of algae, corals and gorgonians in relation to depth, light attenuation, water movement, and grazing pressure in the fringing coral reef of Curaçao, Netherlands Antilles. *Aquat. Bot.* 5, 1–46.
- Veron, J.E.N., 1993. *Corals of Australia and the Indopacific*, University of Hawaii, Honolulu.
- Walsh, W.J., 1983. Stability of a coral reef fish community following a catastrophic storm. *Coral Reefs* 2, 49–63.
- Wanders, J.B.W., 1976. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles). I. Primary productivity in the coral reef. *Aquat. Bot.* 2, 235–270.
- Wilkinson, C.R., 1993. Coral reefs of the world are facing widespread devastation: can we prevent this through sustainable management practices. In: *Proc. 7th Int. Coral Reef Symp.*, Vol. 1, pp. 11–21.
- Williams, A.H., 1984. The effects of Hurricane Allen on back reef populations of Discovery Bay, Jamaica. *J. Exp. Mar. Biol. Ecol.* 75, 233–243.
- Williams, S.L., 1988. Disturbance and recovery of a deep-water Caribbean seagrass bed. *Mar. Ecol. Prog. Ser.* 42, 63–71.
- Williams, S.L., Carpenter, R.C., 1990. Photosynthesis/ photon flux density relationships among components of coral reef algal turfs. *J. Phycol.* 26, 36–40.
- Williams, S.L., Carpenter, R.C., 1997. Grazing effects on nitrogen fixation in coral reef algal turfs. *Mar. Biol.* 130, 223–231.

- Williams, S.L., Carpenter, R.C., 1998. Effects of unidirectional and oscillatory water flow on nitrogen fixation (acetylene reduction) in coral reef algal turfs, Kaneohe Bay, Hawaii. *J. Exp. Mar. Biol. Ecol.* 226, 293–316.
- Zeller, D.C., 1988. Short-term effects of territoriality of a tropical damselfish and experimental exclusion of large fishes on invertebrates in algal turfs. *Mar. Ecol. Prog. Ser.* 44, 85–93.