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# Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs

T.R. McClanahan

*The Wildlife Conservation Society, Coral Reef Conservation Project, P.O. Box 99470, Mombasa, Kenya*

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## Abstract

Experimental coral plates were placed on four coral reefs to determine the effect that sea urchin and herbivorous fish grazing, and river sediments have on successional changes in algae. Algal functional-group composition, standing crop and chlorophyll concentrations were made eight times over a 450 day period. Despite large differences in the species composition of the grazing community, algal development and composition were distinct depending on whether the dominant grazers were sea urchins or herbivorous fishes. In the two reefs dominated by sea urchin grazers, the plates were colonized by filamentous algal turfs and the full succession was complete in less than 50 days. Algal wet weight and functional group composition were stable over the entire period despite strong seasonality in environmental conditions. In contrast, coral plates established on reefs dominated by herbivorous fishes did not complete their successional development for about 120 days, passed through more successional stages, and when fully developed had a greater diversity of functional groups, standing crop and chlorophyll concentrations. Seasonal changes on the plates were also more pronounced in the fish-dominated reefs and the highest standing crops were found during the southeast monsoon when solar radiation is low, and waters are cool and low in nitrogen. River discharge onto one of the fish-dominated sites reversed the algal succession from dominance by crustose coralline algae to filamentous turfs rather than accelerating the succession towards brown macroalgae—the expected climax. Metabolic effects of fish grazers can modify the effects of environmental conditions on algal community structure and succession. Beyond simply cropping algae, grazers can influence sedimentation and nutrient concentrations and ratios, which makes the specific mechanisms responsible for these observations difficult to determine. Grazing habits that increase nutrient concentrations, sedimentation and disturbance appear to arrest succession in the turf stage. A general conceptual model of successional development under different grazer functional groups is presented.

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## 1. Introduction

Disturbances are common in the coral-reef environment and include numerous abiotic and biotic factors (Pearson, 1981; Karlson and Hurd, 1993; Rogers, 1993). Important

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abiotic disturbances include waves, currents, tides and cyclones and hurricanes that can kill living organisms, break apart the calcium carbonate substrate and provide space for subsequent colonizing organisms (Grigg and Maragos, 1974; Connell, 1978; Pearson, 1981; Smith, 1988; Yap and Gomez, 1988; see papers in Hughes, 1993). Predation is also an important source of disturbance (Sousa, 1979; Carpenter, 1981; Wellington, 1982; Hay et al., 1983; Hay and Taylor, 1985; Hay, 1986; Moran, 1986; Morrison, 1988; McClanahan and Shafir, 1990; Hixon, 1991) that may influence the succession of species through the prey selection, metabolic requirements, and the various feeding behaviors of the predatory species (Paine, 1966; Wellington, 1982; Hixon and Brostoff, 1983; Carpenter, 1986; Scott and Russ, 1987; McClanahan, 1992; McClanahan et al., 1994). The earliest colonizing algae found on recently opened reef space are frequently fast-growing filamentous green and blue-green algae which form an ‘algal turf’ that is followed in the successional development by other algae such as calcareous (i.e. *Halimeda*), crustose coralline (i.e. *Porolithon*) and fleshy brown algae (i.e. *Padina, Sargassum* and *Dictyota*) (Tsuda and Kami, 1973; Adey and Vassar, 1975; Lewis, 1986; Hughes et al., 1987; Carpenter, 1990a; Steneck and Dethier, 1994) and sessile reef invertebrates such as soft and hard corals (Pearson, 1981; Colgan, 1987; Yap and Gomez, 1988; Hughes, 1994; Tanner et al., 1994). The successional sequence or pathways of algae and invertebrates and the role that abiotic and biotic factors play in mediating (such as facilitating or inhibiting), switching the direction or arresting the succession of species after disturbances are only recently being understood (Littler and Littler, 1980; Hay, 1986; Rogers, 1993; Hay, 1994; Steneck and Dethier, 1994; McClanahan, 1995a). Descriptive and experimental studies that compare successional development in different oceanic regions and under different abiotic and biotic conditions are needed to help determine the generality of ecological responses to disturbances.

Herbivory is a biotic disturbance in coral reefs that has received considerable attention because it is now considered to have a major direct and indirect influence on the abundance and species and functional composition of algae (Carpenter, 1981; Hatcher, 1983; Hay et al., 1983; Hixon and Brostoff, 1983; Sammarco, 1983; Carpenter, 1986; Hay, 1986; Morrison, 1988; Carpenter, 1990a; Steneck and Dethier, 1994), seagrass (McClanahan et al., 1994) and corals (Wellington, 1982; Lewis, 1986; Hughes, 1994; McClanahan et al., 1996), and productivity (Brawley and Adey, 1977; Wilkinson and Sammarco, 1983; Carpenter, 1986; Klumpp and McKinnon, 1989), nutrient concentrations and ratios (Wilkinson and Sammarco, 1983; Williams and Carpenter, 1988), and the erosion of reef substrates attributable to reef grazers (Birkeland, 1988). Algal standing stock often determines net production and is frequently affected by herbivores abundance and, therefore, net production can be more limited by herbivory more than by light, nutrient or water-flow limitations (Larkum, 1983; Carpenter, 1986, 1988; Klumpp and McKinnon, 1992). Herbivore abundance and composition can also be influenced by human fishing activities (Hay, 1984; McClanahan et al., 1994, 1996) and, therefore, humans indirectly influence reef ecological structure and processes through influencing reef herbivores (McClanahan and Shafir, 1990; Hughes, 1994; McClanahan, 1995a).

Accumulating evidence suggests that many heavily fished Caribbean and East African shallow reefs become dominated by sea urchin grazers as their predators and competitors are reduced through fishing activities (Hay, 1984; McClanahan and Shafir, 1990; Hughes, 1994; McClanahan, 1994, 1995a,b,c; Watson and Ormond, 1994). This switch in the dominance of the grazer guild can greatly influence the ecology of these reefs because the feeding characteristics of grazers often differ (reviewed by McClanahan, 1992). In order to understand the full consequences of heavy fishing and to increase the predictability of a recently developed simulation model of shallow coral reefs (McClanahan, 1995a) it is necessary to develop a better understanding of the algal successional process as influenced by reef grazers. Further, most comparative experimental herbivory studies of fish versus sea urchin grazing have been completed in the Caribbean and comparable studies from the Indian and Pacific Oceans are few (McClanahan et al., 1994, 1996).

This study was conducted in order to develop further our understanding of algal succession and the role that urchins and fish play in mediating succession. I present findings from successional studies on bare coral plate substratum over an ~450 day period in four different back-reef lagoons. Measurements included algal weights (wet, dry and decalcified), chlorophyll concentrations, algal and functional group composition (i.e. turf, coralline, calcareous and fleshy brown algae). Sites were selected such that 2 reefs were dominated by sea urchin grazers (mostly *Diadema savignyi* and *Echinometra mathaei*) and 2 by fish grazers (i.e. many species in the Acanthuridae, Scaridae, Pomacentridae and Siganidae families). One reef site (Malindi) with herbivorous fish dominance is also disturbed annually by river discharge that colors reef waters brown for about 1–2 months, reduces light penetration, and adds sediments and associated nutrients to the reef substratum (Brakel, 1984; van Katwijk et al., 1993; McClanahan and Obura, 1997). The other fish-dominated site (Watamu) acted as a control for this seasonal river-discharge disturbance.

Predictions for this experiment, based on resource competition theory (Tilman, 1982, 1988; McClanahan, 1992), are that successional development of reef algae will differ between the herbivorous fish and sea urchin grazing treatment sites in that sea urchin grazed sites will have: (1) an algal community in an arrested succession with low algae and chlorophyll concentrations, (2) a greater dominance of early successional turf-forming algae, and (3) a low algal calcium carbonate content. The prediction for the river-discharge disturbance treatment is that the disturbance will increase the abundance of fast-growing turf and fleshy algae cover.

## 2. Methods

### 2.1. Seasonal patterns and study sites

Kenya's southern coastline is paralleled by a fringing reef that contains species-rich coral communities on its lagoonal and leeward edges (Hamilton and Brakel, 1984; McClanahan and Mutere, 1994). The coast (longitude = 3–4°S) experiences predictable seasonal patterns in its oceanographic conditions but no cyclones or hurricanes (McClanahan, 1988). The April–July monsoon rain is the strongest and most predictable of the two seasonal rainfall periods and is associated with thick cloud cover, heavy rains, strong winds, large waves and fast currents. Winds and waves reach their peak intensity in July and sunny and calmer conditions often begin by late August. At the coast, the October–November monsoon is weaker and is often drier, warmer, and has less predictable rainfall than the earlier monsoon. During some years it is often indistinguishable from background conditions, while in rare years it can nearly equal the intensity of the earlier monsoon. In inland highland areas this second monsoon rain is a little later, more intense and predictable and, therefore, the discharge from inland rivers have a second distinct and predictable peak in November (McClanahan and Obura, 1997). Sunlight intensity is lowest in July and peaks in March.

The studies were conducted in coral and algae-dominated areas in back-reef lagoons. Lagoons differed in their protection from fishing but were similar in being protected from strong waves, having a substrate of calcium carbonate and being shallow at low tides ($<1.5$ m deep where Kenya has a 4 m tidal range). The two studied lagoons protected from fishing were in the Malindi and Watamu Marine National Parks (MNP) which have received protection from resource removal for over 20 years. In Malindi the research was performed in a shallow lagoon in a platform reef (North Reef) separated from the fringing reef by a narrow channel. This reef experiences a pulse of land-derived sediments during December when river discharge and the seasonally reversing monsoon-driven currents send discharge over this reefs (Brakel, 1984). By late January the water clarity increases but resuspension of sediments can occur for a few months after the peak. The Watamu reef does not experience this river discharge and sediments but does receive ‘green water’ from a tidal creek (Mida Creek) about 1.5 km from the site. The two fished sites, Vipingo and Diani, are south of these sites and along with the above two protected sites have been described faunistically in some detail (McClanahan and Shafir, 1990; McClanahan, 1994; McClanahan and Mutere, 1994).

Study sites were visited 8 times during midday low tides over a 450 day period. During each of these times the shallow-water ($\sim 20$ cm deep) light (Licor 189 Quantum Radiometer with a LI-192SA underwater quantum sensor) and temperature (thermistor) were measured. During one sampling interval water samples were collected for nitrates and phosphates analysis (Strickland and Parsons, 1972).

### 2.2. Description of the grazer communities

Sea urchins and herbivorous fishes were sampled twice during this time period (December 1993 and 1994), for the purposes of estimating their wet weights. Herbivorous fish were counted by a single observer in 3–5 replicate belt transects (5 m × 100 m) per site in which the families of each observed individual was recorded and individual body lengths were estimated to the nearest 10 cm. Because of the large differences in fish abundance, the observer adjusted the time spent counting fish such that sites with a high density of fish were sampled slower ($\sim 15$ min per pass of the transect) than those with a low fish density (10 min per transect). Fish wet weights were estimated using the fish length–weight relationships for fish families given by McClanahan et al. (1996) and the weights of individuals in each family were summed to estimate the wet weight on a kg/ha basis. During a third sampling period, the fish were sampled using the Discrete Group Sampling (DGS) method where the Acanthuridae, Scaridae and Pomacentridae were sampled as separate groups (Greene and Alevizon, 1989; McClanahan, 1994) and identified to the species level (Smith and Heemstra, 1986). This method is used to determine species composition while the previous method is used to estimate wet weights. Sea urchins were identified, counted in 10 $m^2$ plots and wet weight estimates by multiplying average numbers by average wet weights per species. The two species in the genus *Echinothrix* were not distinguished beyond the genus but *E. diadema* comprised around 90% of the observations.

### 2.3. Description of benthic community structure

Line transects were haphazardly placed at around 5–10 m intervals and transects ranged across an approximately 70 m of reef. Algal and attached benthic communities were twice sampled by twelve to eighteen 10 m line transects per sampling period (December 1993 and 1994) per site (McClanahan and Shafir, 1990) where the linear transect length of various benthic categories was measured to the nearest cm. The canopy algae (tallest species) under the transect line greater than 3 cm in width were described as either: (1) filamentous turf (ranging from heavily grazed or sediment-disturbed turfs to thicker damselfish territories), (2) calcareous (= *Halimeda*), (3) encrusting and branching coralline (i.e. *Porolithon, Amphiroa, Jania*), and (4) fleshy brown algae (i.e. *Padina, Sargassum, Dictyota*). Algae were further identified at the genus level for the fleshy reds and browns and branching corallines using the nomenclature of Moorjani and Simpson (1988). In instances where the substratums' surface was mottled with different algal categories an estimate of the amount of area attributable to each category was made and the transect line distance was apportioned accordingly. Algae with canopy widths less than 3 cm were ignored because they were rare and sometimes difficult to identify in the field.

### 2.4. Plate cover, algal weights and chlorophyll measurements

Experimental plates were placed on the reefs during August 1993. This is just after the seasonal peak in wave energy and is probably a time when bare substratum is most likely to occur due to physical disturbances. Twenty to 30 plates were haphazardly established in each site by placing them into shallow ($<3$ cm deep) naturally occurring depressions in the reef. These depressions stopped the plates from moving and overturning with currents and tides. Coral plates were ~2 cm cross-sections of small massive *Porites* heads (mostly *P. lutea* with diameters $<25$ cm and average plate size was 145±45 (±S.D.) $cm^2$, $n = 114$ plates). Plates had two flat surfaces but edges were irregularly shaped. Individual plates were usually at least 1 m apart and all plates ranged over a distance of around 20–100 m in each site. Chosen sites appeared to be typical of the larger reef areas.

Plates were visited 8 times during the ~450-day experiment. In each site 8–9 haphazardly selected plates were examined, the algal community was described, and all algae within a 5 cm × 5 cm area (~17% of the surface area) were scraped off using a razor blade. We scraped areas that seemed typical of the whole plate. It was seldom possible to determine the areas of the plates that were previously scraped but these areas were avoided if noticed. Samples were immediately stored on ice or frozen until weight and chlorophyll analyses could be completed. Algal weight measurements included wet, dry (dried in an oven at ~60°C for >1 day), and decalcified (using a dilute HCl solution) estimates. The quantity of calcium carbonate in samples was estimated by subtracting the dry decalcified weight from the dry weight. Chlorophyll a, b and c concentrations were estimated from the spectrophotometric determination of samples. Samples were ground and chlorophyll extracted with 90% acetone. Chlorophyll concentrations were estimated with the equations provided by Strickland and Parsons (1972). The ratio of chlorophyll c to chlorophyll a was calculated as this ratio is suggested to be a measure of the successional development of the algal community because pigment diversity often increases with successional time (Margalef, 1968).

Description of the algal community was achieved by visually estimating the percent cover on each plate (to the nearest 5%) that could be attributed to categories of: (1) bare calcium carbonate substrate, (2) algal turf, (3) calcareous algae, (4) encrusting coralline algae, and (5) fleshy algae (mostly brown algae but some red algae as well). Greater than 95% of the total plate cover could be attributed to the above categories. Algal groups were most often distributed monospecifically or in a few distinct patches which made it easy to estimate cover to the 5% level. Calcareous algae often grew from the edges of the plates, and, therefore, estimates of the cover on these plates included the area of the plate themselves plus the additional planar surface area created by the calcareous algae. An estimate of group diversity on the experimental plates was calculated with a modification of Simpson's Index where $D = 1 - \Sigma(n_i / N_t)^2$ where $n_i$ is the cover attributable to each specific group and $N_t$ is the total cover of all estimated groups.

## 3. Results

### 3.1. Physio-chemical conditions of the reefs

As expected Malindi had the highest nutrient and sedimentation concentrations. There were statistically significant differences among the 4 study sites in terms of light, temperature, nitrates and phosphates (Table 1). Differences were, however, not large and differences were not associated with the management status of the reefs. Phosphates were nearly twice as high in Malindi as the other three sites.

### 3.2. Grazer and algal communities

The four studied sites exhibit large differences in the species composition of grazers and for differences between fished and unfished reefs (Table 2 Table 3). The protected reefs are typified by numerous grazing fishes with a total wet weight between 500 (Watamu) and 700 (Malindi) kg/ha while sea urchin abundance was less than 10 kg/ha. In contrast, grazing fish abundance in the unprotected reefs was less than 20 kg/ha while sea urchin abundance varied between 2700 (Vipingo) and 8600 (Diani) kg/ha. Differences between protected and unprotected reefs for all groups of grazers are highly

Table 1
Summary of physicochemical conditions at the four studied coral reefs

| Variable | Malinidi | | | Watamu | | | Vipingo | | | Diani | | | Site test | Protection test |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | *n* | Mean | S.D. | *n* | Mean | S.D. | *n* | Mean | S.D. | *n* | | |
| Light, midday | 1364.0 | 239.9 | 24 | 1306.4 | 250.05 | 28 | 1353.6 | 205.8 | 24 | 1111.6 | 268.0 | 21 | 0.00 | NS |
| Temperature (°C) | 28.2 | 1.9 | 24 | 27.4 | 1.67 | 27 | 29.3 | 1.8 | 28 | 28.2 | 2.8 | 22 | 0.01 | NS |
| Nitrates (μg-at/l) | 2.8 | 0.2 | 5 | 0.9 | 0.0 | 5 | 1.8 | 1.0 | | 1.0 | 0.2 | 5 | 0.00 | NS |
| Phosphates (μg-at/l) | 1.4 | 0.1 | 4 | 1.0 | 0.1 | 4 | 1.0 | 0.1 | | 1.0 | 0.1 | 4 | 0.00 | NS |

One-way Anova test of differences between sites and for protection (fished vs. unfished).

Table 2

Population density (No. per 500 m$^2$) and estimated wet weights of the common herbivorous fishes in the studies sites

| | Malindi | | Watamu | | Vipingo | | Diani | |
|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Acanthuridae | | | | | | | | |
| *Ctenochaetus striatus* | 61.2 | 9.6 | 6.3 | 5.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Acanthurus nigrofuscus* | 11.0 | 8.0 | 10.3 | 4.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Acanthurus leucosternon* | 3.6 | 1.1 | 15.0 | 8.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Zebrasoma scopas* | 9.4 | 3.6 | 1.0 | 1.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Ctenochaetus strigosus* | 0.0 | 0.0 | 8.0 | 5.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Acanthurus dussumieri* | 0.0 | 0.0 | 2.5 | 1.7 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Acanthurus triostegus* | 0.0 | 0.0 | 0.0 | 0.0 | 1.2 | 1.6 | 0.6 | 0.5 |
| *Acanthurus nigricauda* | 1.2 | 2.2 | 0.5 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Naso annulatus* | 1.0 | 1.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Nebrasoma veliferum* | 0.6 | 0.9 | 0.3 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Acanthurus xanthopterus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.8 | 0.8 | 0.0 | 0.0 |
| *Acanthurus mata* | 0.0 | 0.0 | 0.3 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| Total | 88.0 | 21.0 | 44.0 | 9.6 | 2.0 | 1.6 | 0.6 | 0.5 |
| Wet Weight (kg/ha) | 372.9 | 187.4 | 229.7 | 87.0 | 10.1 | 5.9 | 2.0 | 1.1 |
| Scaridae | | | | | | | | |
| *Scarus sordidus* | 9.4 | 4.6 | 11.8 | 4.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Scarus viridifucatus* | 10.0 | 6.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Calotomus carolinus* | 0.6 | 0.9 | 8.8 | 1.9 | 0.0 | 0.0 | 0.2 | 0.4 |
| *Scarus rubroviolaceus* | 5.0 | 2.5 | 3.5 | 1.3 | 0.0 | 0.0 | 0.2 | 0.4 |
| *Scarus scaber* | 5.4 | 4.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Scarus niger* | 1.4 | 1.1 | 3.0 | 0.8 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Leptoscarus vaigiensis* | 0.2 | 0.4 | 0.5 | 1.0 | 3.6 | 2.2 | 0.0 | 0.0 |
| *Scarus frenatus* | 1.2 | 1.1 | 1.5 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Scarus gibbus* | 1.2 | 1.3 | 1.0 | 0.8 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Scarus ghobban* | 0.0 | 0.0 | 1.0 | 0.0 | 0.4 | 0.9 | 0.4 | 0.5 |
| *Scarus russelli* | 0.4 | 0.5 | 0.5 | 0.6 | 0.2 | 0.4 | 0.0 | 0.0 |
| *Hipposcarus harid* | 0.0 | 0.0 | 0.3 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Unidentified juveniles* | 0.0 | 0.0 | 0.0 | 0.0 | 38.2 | 24.9 | 10.6 | 22.0 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Total | 34.8 | 9.9 | 31.8 | 7.3 | 42.4 | 23.4 | 11.4 | 21.7 |
| Wet weight (kg/ha) | 319.6 | 87.0 | 306.5 | 116.2 | 15.6 | 3.5 | 0.7 | 1.2 |
| Pomacentridae | | | | | | | | |
| *Chyrsiptera unimaculata* | 13.00 | 6.89 | 4.50 | 1.29 | 37.40 | 12.28 | 11.20 | 4.97 |
| *Abudefduf sexfasciatus* | 9.00 | 8.60 | 27.20 | 29.40 | 5.07 | 7.28 | 5.65 | 5.15 |
| *Plectroglyphidodon lacrymatus* | 21.80 | 12.87 | 17.00 | 10.17 | 4.40 | 3.91 | 0.60 | 0.89 |
| *Pomacentrus sulfureus* | 8.00 | 4.90 | 23.75 | 23.71 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Stegastes nigricans* | 18.00 | 13.44 | 0.00 | 0.00 | 7.80 | 8.32 | 4.00 | 2.45 |
| *Dascyllus trimaculatus* | 6.60 | 9.91 | 0.00 | 0.00 | 1.60 | 2.19 | 6.40 | 3.21 |
| *Plectroglyphidodon dickii* | 6.20 | 3.96 | 2.00 | 1.15 | 0.20 | 0.45 | 0.00 | 0.00 |
| *Dascyllus reticulatus* | 1.33 | 2.31 | 6.33 | 7.57 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Abudefduf vaigiensis* | 4.80 | 4.76 | 1.00 | 0.00 | 0.20 | 0.45 | 0.20 | 0.45 |
| *Abudefduf sparoides* | 0.50 | 0.71 | 1.50 | 0.71 | 1.20 | 1.10 | 1.80 | 2.05 |
| *Pomacentrus caeruleus* | 1.40 | 1.14 | 1.67 | 1.15 | 0.00 | 0.00 | 0.20 | 0.45 |
| *Plectroglyphidodon johnstonianus* | 0.00 | 0.00 | 2.33 | 1.53 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Neoglyphidodon melas* | 0.33 | 0.58 | 0.00 | 0.00 | 1.20 | 1.79 | 0.60 | 0.89 |
| Total | 90.97 | | 87.28 | | 59.07 | | 30.65 | |
| Wet weight (kg/ha) | 17.47 | | 16.76 | | 11.34 | | 5.88 | |
| Transects (*n*) | 9 | | 6 | | 9 | | 9 | |
| Total wet weight (kg/ha) | 710.0 | 223.1 | 552.9 | 150.9 | 37.0 | 8.0 | 8.6 | 1.9 |

The Pomacentridae includes only one species, C. unimaculata, that is strictly herbivorous. All other studies are considered omnivorous (Allen, 1991). All ANOVA comparisons of wet weights between protected and unprotected reefs are highly significant ($F$ values $> 17.0$, $p < 0.0001$).

Table 3
Sea urchin abundance in the studied sties ($x$ + S.D.) based on sites within the reef

| Sea urchin species | Malindi | | Watamu | | Vipingo | | Diani | |
|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Density (No. per $m^2$) | | | | | | | | |
| *Echinometra mathaei* | 0.3 | 0.2 | 0.0 | 0.0 | 16.8 | 3.6 | 251.8 | 44.2 |
| *Diadema savignyi* | 0.0 | 0.0 | 0.1 | 0.1 | 9.2 | 1.8 | 0.0 | 0.0 |
| *Tripneustes gratilla* | 0.0 | 0.0 | 0.0 | 0.0 | 5.3 | 3.0 | 2.5 | 2.3 |
| *Diadema setosum* | 0.0 | 0.0 | 0.0 | 0.0 | 2.2 | 0.8 | 0.0 | 0.0 |
| *Echinothrix spp.* | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.1 | 0.0 | 0.0 |
| *Echinostrephus molaris* | 1.2 | 0.6 | 1.1 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Toxopneustes pileolus* | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 | 0.0 | 0.0 |
| *Stomopneustes valiolaris* | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 | 0.0 | 0.0 |
| Total | 0.9 | 0.7 | 1.1 | 0.6 | 33.7 | 3.5 | 254.3 | 42.3 |
| Wet weight (kg/ha) | | | | | | | | |
| *Echinometra mathaei* | 6.8 | 8.3 | 0.0 | 0.0 | 553.7 | 118.8 | 8309.6 | 1457.5 |
| *Diadema savignyi* | 0.2 | 0.3 | 6.9 | 9.8 | 1145.8 | 225.3 | 0.0 | 0.0 |
| *Tripneustes gratilla* | 0.0 | 0.0 | 0.0 | 0.0 | 579.3 | 327.0 | 268.0 | 248.1 |
| *Diadema setosum* | 0.0 | 0.0 | 0.0 | 0.0 | 331.1 | 119.3 | 0.0 | 0.0 |
| *Echinothrix spp.* | 0.0 | 0.0 | 0.0 | 0.0 | 90.0 | 44.5 | 0.0 | 0.0 |
| *Echinostrephus molaris* | 2.9 | 1.6 | 2.6 | 1.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Toxopneustes pileolus* | 0.0 | 0.0 | 0.0 | 0.0 | 5.6 | 9.6 | 0.0 | 0.0 |
| Total | 9.7 | 9.2 | 9.6 | 11.2 | 2709.6 | 395.7 | 8577.5 | 1259.9 |
| Diversity ($D$) | 0.34 | 0.09 | 0.07 | 0.09 | 0.64 | 0.06 | 0.02 | 0.02 |
| No. of species/site | 2.0 | 0.0 | 2.0 | 0.0 | 5.3 | 0.6 | 3.0 | 2.0 |

Comparison of the wet weights between protected and unprotected reefs is highly significant ($F = 20.3$, $p < 0.0001$).

significant (one-way ANOVA produced $F$ values $> 17.0$ for all comparisons, $p < 0.0001$). Despite moderately high variation among transects the estimates and differences have been consistent over time and with other studies (McClanahan and Obura, 1995). Herbivorous damselfishes were not a large part of the herbivore wet weight in any of the study sites. Despite the clear differences in grazer functional groups between management categories there were large differences both within management categories at the level of the species. Consequently, the major difference in grazing between management treatments is the functional groups rather than the species composition.

Substratum cover and algal composition varied significantly among the 4 sites (Table 4) with the protected reefs having a greater abundance of hard coral, coralline and calcareous algae than the unprotected reefs which had greater cover of algal turf, sand and seagrass (one-way ANOVA, $p < 0.001$). Fleshy algae was highly variable among sites and found in greater abundance in Watamu and Vipingo. The dominant brown algae in these two sites were *Sargassum* and *Turbinaria*.

### *3.3. Succession of algae on coral plates*

Succession of algae on the coral plates indicates large differences among the four sites and between fished and unfished sties (Figs. 1–4, Tables 5 and 6). The plates in the

Table 4
Percentage cover of the major substrate categories by functional groups and genera in the studies sites ($x + \text{S.D.}$) where S.D. is based on sites in each reef

| Cover categories | Malindi | | Watamu | | Vipingo | | Diani | | Site Anova | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | $F$-value | $p <$ |
| Hard coral | 40.2 | 3.6 | 38.2 | 0.5 | 31.2 | 2.4 | 15.5 | 7.5 | 19.1 | 0.000 |
| Algal turf | 14.7 | 2.5 | 22.1 | 2.4 | 31.6 | 7.6 | 44.8 | 5.5 | 25.3 | 0.000 |
| Sand | 8.8 | 7.1 | 2.5 | 1.2 | 12.6 | 4.1 | 23.0 | 3.1 | 9.7 | 0.004 |
| Seagrass | 4.2 | 4.0 | 9.0 | 2.6 | 11.3 | 2.4 | 12.6 | 2.6 | 5.7 | 0.018 |
| Coralline algae | 18.3 | 2.1 | 9.0 | 1.8 | 2.2 | 1.7 | 0.1 | 0.1 | 106.8 | 0.000 |
| Calcareous algae | 10.1 | 3.2 | 9.5 | 2.2 | 3.0 | 0.8 | 0.4 | 0.3 | 19.1 | 0.000 |
| Fleshy algae | 1.3 | 0.5 | 9.2 | 1.4 | 4.8 | 1.8 | 1.2 | 1.0 | 26.9 | 0.000 |
| Soft coral | 2.9 | 1.7 | 0.4 | 0.0 | 3.1 | 1.3 | 1.6 | 0.6 | 2.7 | NS |
| Sponge | 0.0 | 0.0 | 0.0 | 0.0 | 0.4 | 0.1 | 0.6 | 0.7 | 2.1 | NS |
| Algal Cover (cm/10 m transect) | | | | | | | | | | |
| Encrusting corallines | 225.6 | 25.9 | 108.0 | 26.9 | 3.0 | 6.8 | 7.1 | 12.5 | 148.0 | 0.000 |
| *Halimeda* | 126.4 | 43.0 | 112.3 | 24.3 | 18.6 | 15.6 | 4.1 | 3.7 | 23.0 | 0.000 |
| *Sargassum* | 0.1 | 0.2 | 48.5 | 21.3 | 21.0 | 14.9 | 1.1 | 2.3 | 11.0 | 0.001 |
| *Turbinaria* | 3.3 | 2.2 | 51.5 | 12.0 | 10.9 | 10.8 | 2.3 | 2.2 | 14.0 | 0.000 |
| *Hypnea* | 2.2 | 3.6 | 5.5 | 4.9 | 21.6 | 7.3 | 0.0 | 0.0 | 18.0 | 0.000 |
| *Dictyota* | 10.3 | 3.3 | 4.1 | 3.1 | 0.5 | 0.6 | 0.1 | 0.3 | 23.0 | 0.000 |
| *Padina* | 0.0 | 0.0 | 0.0 | 0.0 | 1.9 | 1.5 | 6.2 | 7.5 | 2.0 | NS |
| *Amphiroa* | 1.1 | 1.4 | 3.1 | 2.8 | 3.9 | 3.9 | 0.0 | 0.0 | 2.0 | NS |
| *Cystoseira* | 0.0 | 0.0 | 0.0 | 0.0 | 6.6 | 4.8 | 0.0 | 0.0 | 6.0 | 0.011 |
| *Ulva* | 0.0 | 0.0 | 0.0 | 0.0 | 1.6 | 3.0 | 0.0 | 0.0 | 1.0 | NS |
| *Codium* | 0.0 | 0.0 | 0.0 | 0.0 | 1.2 | 2.6 | 0.0 | 0.0 | 1.1 | NS |
| *Dictyosphaeria* | 0.3 | 0.7 | 0.4 | 0.0 | 0.0 | 0.2 | 0.3 | 0.6 | 0.0 | NS |
| Seagrasses | | | | | | | | | | |
| *Thalassia hemprichii* | 0.0 | 0.0 | 0.0 | 0.0 | 207.0 | 74.5 | 113.9 | 28.2 | 18.0 | 0.000 |
| *Thallasodendron ciliatum* | 54.4 | 53.2 | 103.8 | 31.5 | 3.0 | 6.6 | 12.5 | 22.6 | 6.0 | 0.010 |

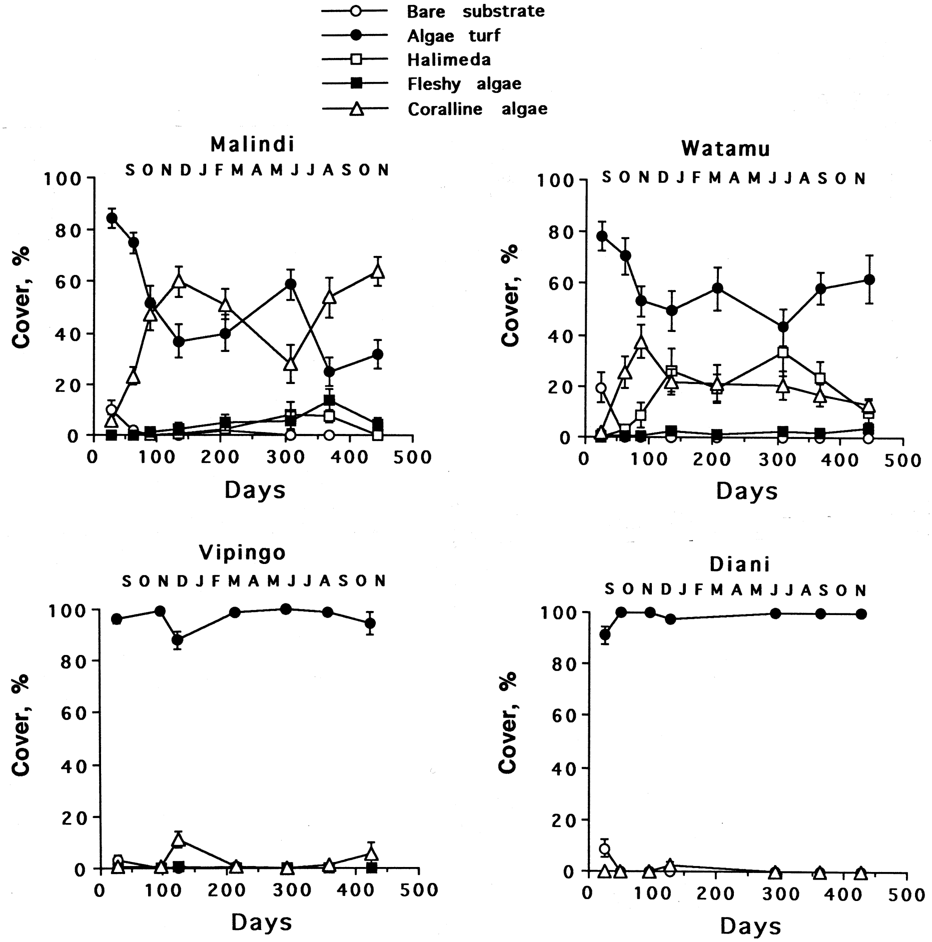

Fig. 1. Time series of the percentage cover of algal functional groups on the experimental coral plates at the four study sites over a 450 day period. Malindi and Watamu sites are marine parks dominated by herbivorous fish grazers while Vipingo and Diani are heavily fished reefs dominated by sea urchins.

unprotected reefs were unique in that they changed very little over the 450 day study period despite the strong seasonality of environmental conditions experienced by these reefs. These plates were colonized by filamentous algal turf in less than 50 days and remained stable and in this early-successional state. Algal wet weights and chlorophyll concentrations were fairly stable over the study period with algae wet weights varying around 1.1 g/25 $cm^2$, a dry decalcified weight of 0.06 g/25 $cm^2$ and chlorophyll a concentrations at 0.83 $mg/cm^2$. Casual observations on the plates in unprotected reefs were made for over 1000 days and suggest that they changed very little at the macroscopic level even over this longer period of time.

Plates in the protected reefs went through much more dramatic changes over the study period and took about 150 days for the community to stabilize. Plates established in

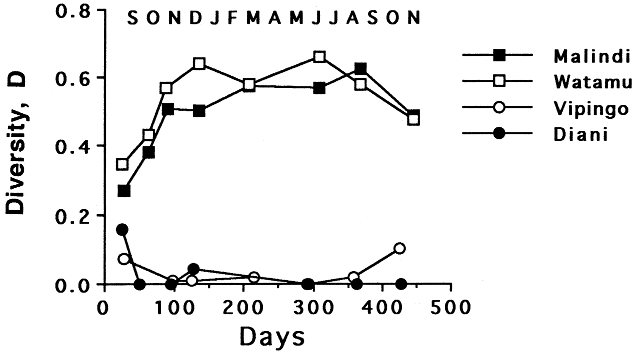

Fig. 2. Time series of the Simpson's diversity index for the algal functional groups on the experimental coral plates in the four studied reefs.

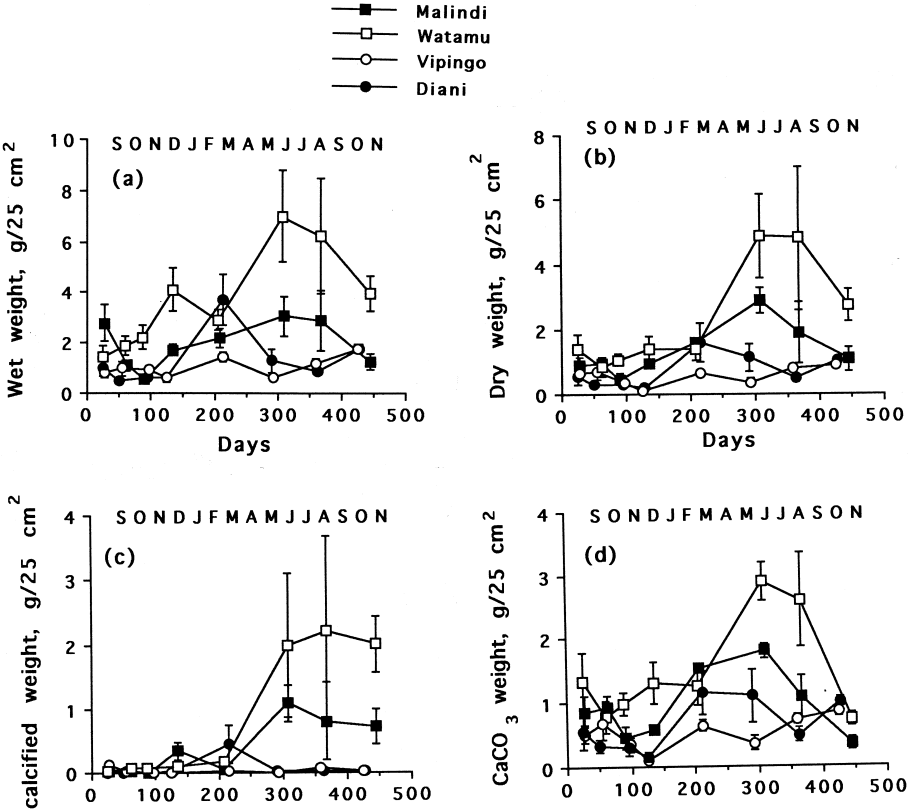

Fig. 3. Time series of the various weight measures of algae on the experimental coral plates in the four studied reefs.

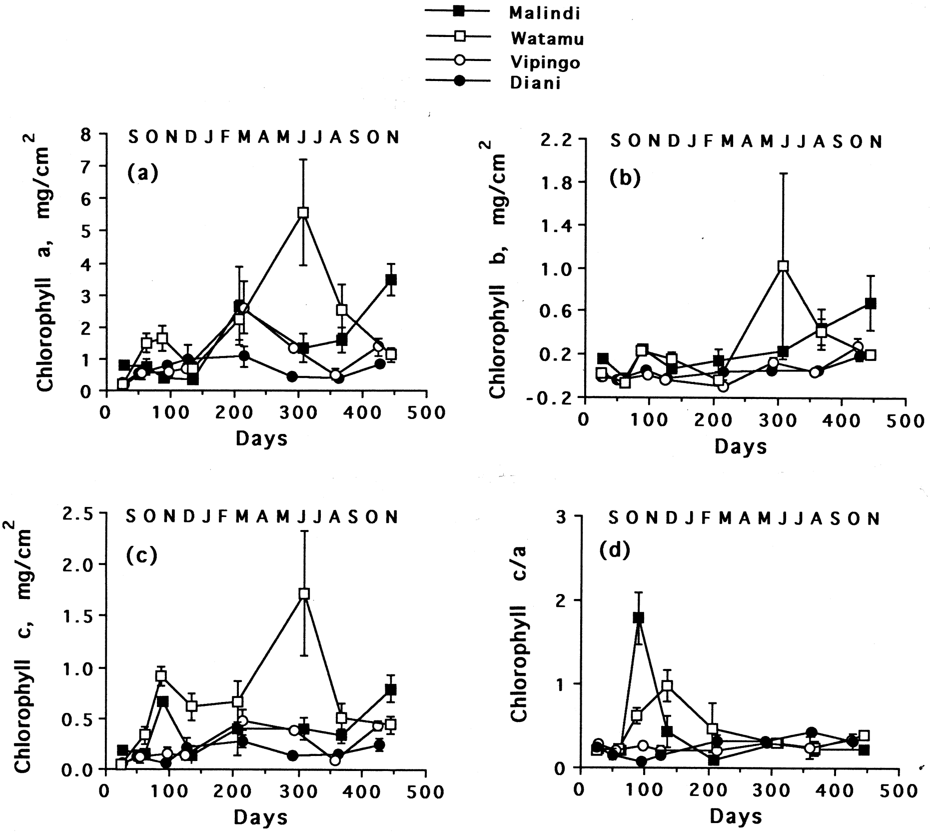

Fig. 4. Time series of chlorophyll abundance measures on the experimental plates in the four studied reefs.

Malindi and Watamu differed in that the Watamu plates developed more calcareous algae (*Halimeda*) and lower coralline algae than Malindi. In Watamu the succession of algae was from algal turf to coralline algae, followed by an increase in calcareous algae with cover estimates being fairly stable after 150 days but with a small loss of calcareous and a subsequent increase in turf algae after the April–July monsoon period. In Malindi the sequence was similar except that calcareous algae never developed greatly on most plates. The time series of algae weights suggest that the highest wet weights are associated with the southeast monsoon.

Malindi plates were most affected by the sediment-laden waters beginning in December but extending to March. Increased sediments in Malindi water were associated with a decrease in coralline algae and an increase in algal turf. The reversal of the southeast monsoon current in July clarified the water in Malindi and was associated with a reduction in algal turf and an increase in coralline algae (Fig. 1).

Comparing overall means for the study period indicates clear differences in the measured variables for reefs dominated by sea urchin or fish grazers, the time factor, and the interaction between sites and time (Table 6). The reefs dominated by fish grazers had

Table 5
Summary statistics of measurements made on the experimental coral plates in each of the 4 study sites

| Variable | Malindi | | | Watamu | | | Vipingo | | | Diani | | | Two-way ANOVA | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | *n* | Mean | S.D. | *n* | Mean | S.D. | *n* | Mean | S.D. | *n* | Sites | Time | | Interaction | | |
| Algal weight (g/25 $cm^2$) | | | | | | | | | | | | | *F* | *p* | *F* | *p* | *F* | *p* |
| Wet | 1.96 | 1.86 | 65 | 3.72 | 3.59 | 64 | 1.00 | 0.56 | 60 | 1.11 | 1.20 | 61 | 27.6 | 0.000 | 5 | 0.000 | 2.4 | 0.002 |
| Dry | 1.32 | 1.01 | 33 | 2.32 | 2.31 | 32 | 0.56 | 0.33 | 32 | 0.73 | 0.75 | 33 | 16.9 | 0.000 | 5.7 | 0.000 | 2.2 | 0.005 |
| Decalcified | 0.37 | 0.61 | 33 | 0.83 | 1.53 | 32 | 0.03 | 0.04 | 32 | 0.08 | 0.29 | 33 | 8.1 | 0.000 | 3.7 | 0.001 | 2.0 | 0.014 |
| CaCO3 | 0.95 | 0.58 | 33 | 1.49 | 1.02 | 32 | 0.53 | 0.32 | 32 | 0.65 | 0.57 | 33 | 23.8 | 0.000 | 8.7 | 0.000 | 3.3 | 0.000 |
| Chlorophyll (mg/$cm^2$) | | | | | | | | | | | | | | | | | | |
| Chl a | 1.42 | 1.42 | 32 | 1.82 | 1.78 | 31 | 1.01 | 0.96 | 30 | 0.67 | 0.47 | 32 | 5.6 | 0.002 | 10 | 0.000 | 0.0 | NS |
| Chl b | 0.24 | 0.30 | 32 | 0.22 | 0.50 | 31 | 0.04 | 0.13 | 30 | 0.04 | 0.08 | 32 | 9.3 | 0.000 | 12.2 | 0.000 | 2.3 | 0.010 |
| Chl c | 0.39 | 0.30 | 32 | 0.62 | 0.56 | 31 | 0.24 | 0.19 | 30 | 0.16 | 0.13 | 32 | 8.5 | 0.000 | 10 | 0.000 | 2.0 | 0.027 |
| Chl c/a | 0.46 | 0.63 | 32 | 0.43 | 0.35 | 31 | 0.25 | 0.11 | 30 | 0.25 | 0.16 | 32 | 4.6 | 0.005 | 3.2 | 0.011 | 2.9 | 0.002 |
| Plate Cover (%) | | | | | | | | | | | | | | | | | | |
| Bare substrate | 1.74 | 5.41 | 69 | 2.57 | 8.96 | 68 | 0.57 | 2.25 | 61 | 1.31 | 4.99 | 61 | 2.1 | NS | 22.4 | 0.000 | 2.1 | 0.010 |
| Algal turf | 50.65 | 25.59 | 69 | 60.15 | 22.09 | 68 | 96.64 | 7.29 | 61 | 98.36 | 5.14 | 61 | 175.5 | 0.000 | 8.5 | 0.000 | 7.5 | 0.000 |
| Halimeda | 2.25 | 6.73 | 69 | 15.88 | 19.83 | 68 | 0.00 | 0.00 | 61 | 0.00 | 0.00 | 61 | 30.0 | 0.000 | 4.6 | 0.001 | 2.7 | 0.001 |
| Fleshy algae | 3.99 | 8.34 | 69 | 1.76 | 3.84 | 68 | 0.08 | 0.64 | 61 | 0.00 | 0.00 | 61 | 10.8 | 0.000 | 2.8 | 0.018 | 2.4 | 0.004 |
| Coralline algae | 41.38 | 25.23 | 69 | 19.63 | 17.26 | 68 | 2.70 | 6.99 | 61 | 0.33 | 1.55 | 61 | 134.9 | 0.000 | 14.4 | 0.000 | 7.0 | 0.000 |
| Diversity (*D*) | 0.49 | 0.11 | 8 | 0.53 | 0.11 | 8 | 0.06 | 0.07 | 7 | 0.03 | 0.06 | 7 | | | | | | |

Anova based on sites is presented. ANOVA analyses based on protection were also statistically significant.

Table 6
Summary statistics of measurements made on the experimental succession plates where data is combined as protected areas dominated by herbivorous fishes (Malindi and Watamu) or unprotected areas dominated by sea urchins (Vipingo and Diani)

| | Herbivorous fish grazers | | | Sea urchin grazers | | | Grazer group | | Two-way ANOVA | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | *n* | Mean | S.D. | *n* | *F* | *p* | Time | | Interaction | |
| | | | | | | | | | *F* | *p* | *F* | *p* |
| Algal weight (g/25 $cm^2$) | | | | | | | | | | | | |
| Wet | 2.83 | 2.97 | 129 | 1.06 | 0.94 | 121 | 46.1 | 0.000 | 4.3 | 0.000 | 3.6 | 0.002 |
| Dry | 1.81 | 1.83 | 65 | 0.65 | 0.59 | 65 | 33.5 | 0.000 | 5.1 | 0.000 | 3.6 | 0.002 |
| Decalcified | 0.6 | 1.17 | 65 | 0.06 | 0.21 | 65 | 17.7 | 0.000 | 3.6 | 0.002 | 4.1 | 0.000 |
| CaCO3 | 1.21 | 0.86 | 65 | 0.59 | 0.46 | 65 | 41.7 | 0.000 | 6.8 | 0.000 | 4.6 | 0.000 |
| Chlorophyll (mg/$cm^2$) | | | | | | | | | | | | |
| Chl a | 1.61 | 1.6 | 63 | 0.83 | 0.76 | 62 | 11.9 | 0.001 | 8.3 | 0.000 | 2.2 | 0.064 |
| Chl b | 0.23 | 0.41 | 63 | 0.04 | 0.11 | 62 | 18.6 | 0.000 | 10.6 | 0.000 | 2.8 | 0.021 |
| Chl c | 0.5 | 0.46 | 63 | 0.2 | 0.16 | 62 | 18.5 | 0.000 | 8.3 | 0.000 | 0.7 | NS |
| Chl c/a | 0.45 | 0.51 | 63 | 0.25 | 0.14 | 62 | 2.9 | 0.091 | 2.7 | 0.024 | 4.5 | 0.001 |
| Plate cover (%) | | | | | | | | | | | | |
| Bare substrate | 2.15 | 7.37 | 137 | 0.94 | 3.87 | 122 | 1.9 | NS | 20.7 | 0.000 | 1.9 | NS |
| Algal turf | 55.36 | 24.3 | 137 | 97.5 | 6.34 | 122 | 396.9 | 0.000 | 6.6 | 0.000 | 10.2 | 0.000 |
| Halimeda | 9.01 | 16.22 | 137 | 0 | 0 | 122 | 34.5 | 0.000 | 3.6 | 0.004 | 3.6 | 0.004 |
| Fleshy algae | 2.88 | 6.58 | 137 | 0.04 | 0.45 | 122 | 23.4 | 0.000 | 2.6 | NS | 2.7 | NS |
| Coralline algae | 30.58 | 24.17 | 137 | 1.52 | 5.18 | 122 | 167.4 | 0.000 | 8 | 0.000 | 5.9 | 0.000 |
| Diversity (*D*) | 0.51 | 0.11 | 16 | 0.05 | 0.07 | 14 | | | | | | |

higher weights and more calcium carbonate, greater chlorophyll concentrations, greater diversity, and more coralline, calcareous and fleshy algae than sea urchin dominated reefs.

## 4. Discussion

The results of our study support the contention that sea urchin grazing is different from herbivorous fish grazing in that it maintains a benthic algal community in an arrested succession with a lower biomass, chlorophyll concentration, functional group and pigment diversity and calcium carbonate content. That different functional groups of herbivores influence the successional development of algae in different ways is clear from field studies in both the Caribbean and Pacific (Adey and Vassar, 1975; Hatcher, 1983; Hixon and Brostoff, 1983; Carpenter, 1986; Lewis, 1986; Foster, 1987; Klumpp et al., 1987; Carpenter, 1990a; McClanahan et al., 1994, 1996; Table 7) but the factors that create these patterns are less clear because they are numerous and probably interact.

The most important ways that grazers influence algal communities in the reef environment are: (1) nutrient concentrations and ratios which can change with reef herbivore functional groups (Hatcher and Larkum, 1983; Meyer et al., 1983; Wilkinson and Sammarco, 1983; Polunin, 1988; Williams and Carpenter, 1988), (2) bioerosion and associated sediment accumulation and trapping may influence algal species or functional groups able to tolerate different disturbance rates or to tolerate the anoxic conditions created by sediment trapping (Steneck, in press), (3) choosing the most susceptible algal prey can create a community of more prey-resistant species, or (4) eating or weeding of the later successional species by territorial damselfishes can promote fast-growing early successional species (Brawley and Adey, 1977; Lassuy, 1980; Sammarco, 1983), (5) energetic differences in the metabolisms and consumption rates of functional groups results in different levels of disturbance and, therefore, levels of productivity (Tilman, 1982; Klumpp and McKinnon, 1992; McClanahan, 1992, 1995a,b), (6) the intensity and frequency of disturbance differs among grazer functional groups, independent of resource requirements, and can influence factors such as productivity and nitrogen fixation (Littler et al., 1983; Steneck, 1983; Wilkinson and Sammarco, 1983; Klumpp and McKinnon, 1992; Steneck and Dethier, 1994).

Based on this and the above studies a general conceptual model of algal succession in East African coral reefs is presented (Fig. 5) which suggests that the pathway of algal succession is highly influenced by the dominant grazers, sediments and their accumulation. On recently disturbed or denuded substrates endolithic algae occurs within the first few cm of the calcium carbonate matrix (Odum and Odum, 1955; Bruggemann, 1994) and may form the earliest colonists of bare surfaces. Epilithic turf-forming algae will quickly colonize bare surfaces but the turf assemblages may differ in their species composition depending on the grazing, nutrient, light and sediment conditions of the reef (Hatcher and Larkum, 1983; Sammarco, 1983; Wilkinson and Sammarco, 1983; Bruggemann et al., 1994). The microscopic nature of turfs and the incomplete taxonomic descriptions of this assemblage has probably stunted a full understanding of the differences and factors that control this assemblage. Areas dominated by territorial

Table 7

Comparison of the probable mechanism for the control of algal assemblages due to the grazing activities of sea urchins and herbivorous fish

| Mechanisms | Territorial damselfishes | Large roaming herbivorous fishes | Sea urchins | References |
|---|---|---|---|---|
| Nutrients | Promote N fixation | Low nitrogen in faeces | High nitrogen in faeces | Williams and Carpenter (1988); Wilkinson et al. (1984) |
| Sedimentation | Low | Low | High | Birkeland (1988) |
| Prey choice | High | Intermediate | Low | Carpenter (1986); McClanahan et al. (1996) |
| Minimum resource requirements | High | High | Low | McClanahan (1992) |
| Disturbance intensity | Intermediate | High | Low | Steneck (1983); Steneck and Dethier (1994) |
| Disturbance frequency | High | Low | High | Carpenter (1984); Polunin (1988) |

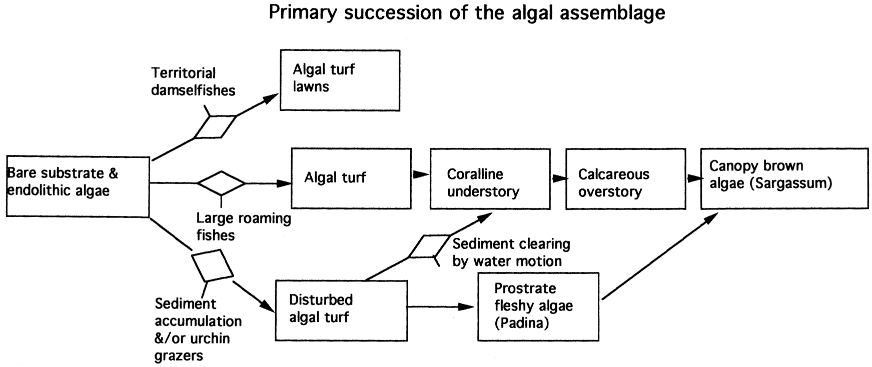

Fig. 5. Conceptual model of the successional pathways of algal functional groups under different conditions of grazer dominance.

damselfishes are arrested in succession by enhancing or concentrating nutrients such that fast-growing species have a competitive edge (Polunin, 1988) and/or by removal of the later successional species (Lassuy, 1980). Damselfishes, surgeonfishes and parrotfishes form territories (Brawley and Adey, 1977; Robertson and Gaines, 1986; Bruggemann et al., 1994) often dependent on the quality of the food at a site (Bruggemann et al., 1994) but elevated algal biomass of turfs appears most pronounced on damselfish territories (Brawley and Adey, 1977; Wellington, 1982; Sammarco, 1983). The role of territoriality among surgeonfishes and parrotfishes and its effect on algal abundance and composition requires more research but observations suggest that they do not promote turfs. The numbers of herbivorous and territorial damselfishes found in this study suggest that they are less common in East Africa than Great Barrier Reef and Caribbean reefs (Meekan et al., 1995).

Large roaming herbivorous fishes, like some surgeonfishes and most parrotfishes (Robertson et al., 1976), appear to influence algal succession by allowing succession to pass through more stages. This promotes the development of species that overgrow turf-forming species such as coralline, calcareous and fleshy algae. Some species of surgeonfish (i.e. *Ctenochaetus*) suck sediments and detritus off surfaces (Choat, 1991) which may promote succession by reducing sediment-related disturbances. It is notable that the suction-feeding *Ctenochaetus striatus* was the most abundant herbivore in Malindi coincident with the greatest cover of corallines. Bruggemann et al. (1994) report that the parrotfish *Sparisoma viride* promote corallines by cropping the more preferred and nutritious turfs. Steneck (in press) suggests that corallines can coexist with fleshy but not turf algae as areas of low herbivory can have abundant corallines below a canopy of upright fleshy algae. This suggest that the removal of sediments and turfs from the surfaces of corallines, by either water movement or grazers, may promote corallines more than the depth of the grazers bites or the intensity of herbivory. Articulated calcareous algae (*Halimeda*), which can overgrow crustose corallines, may also be promoted through the grazing activities of roaming parrotfishes but this is less clearly understood at present.

The very low abundance of crustose coralline development on the study plates in the presence of sea urchin grazing is curious as crustose corallines are expected to develop under intense herbivory (Steneck, 1986). Tropical sea urchins may graze too intensely to support corallines but corallines do develop under sea urchin grazing in areas with high water movement such as reef crests (Steneck, in press). Sea urchin grazing may also produce abundant sediments which, if accumulated by poor water movement, can be trapped by filamentous algae creating anoxic conditions detrimental to coralline algae (Steneck, in press). Consequently, the amount of water movement in sea urchin grazing areas may be important in modifying the effect of the urchin grazing and the subsequent algal succession (Fig. 5).

Large canopy-forming brown algae, such as species in the genera *Sargassum* and *Turbinaria* would appear to be the most abundant canopy-forming genera at the climax of succession. Fleshy algae, although common in sites with the lower sea urchin and fish abundance (Vipingo and Watamu), did not develop greatly on the experimental plates. This may be due to insufficient time but is more likely due to the flat shape of the plates. Flat plates may not provide the edge and associated refuge that is required for the development of these species. It was notable that articulated calcareous and some fleshy algae only formed along the edges of these plates and not on the exposed flat surfaces. Other authors have reported similar observations for recruitment of corals onto experimental plates (Sammarco, 1980; Harriott and Fisk, 1987). Observations suggest that the topographic complexity of the substratum and the availability of refuge from grazing during early stages of an organisms development will influence the development of algae. Flat surfaces provide little refuge and are, therefore, more susceptible to grazing disturbance. Consequently, plates may never develop to the same successional stage as complex surfaces. The greater abundance of fleshy algae in the unfished study sites compared to experimental plates may reflect the greater surface complexity of the reef surface than the experimental plates.

Sea urchin grazing also appears to result in a unique algal community and associated succession once sea urchin populations are reduced or removed (Carpenter, 1986; McClanahan et al., 1996). Sea urchins, like territorial damselfishes, appear to arrest successional development to turf-forming algae. Sea urchins, however, maintain algal levels below that of both territorial and roaming herbivorous fishes (McClanahan, 1992). I have previously used the concepts of resource-competition theory (Tilman, 1982, 1988; McClanahan, 1992) to argue that this pattern results from the low metabolism and nutritional requirements of sea urchins which gives sea urchins the ability to tolerate lower resource levels than fishes in the absence of predation (McClanahan, 1992, 1995b). Additionally, lack of feeding selectivity, feeding on endolithic algae and high substratum bioerosion by sea urchins (Birkeland, 1988) may contribute to their competitive superiority. This does, however, appear to conflict with the concept of escalating herbivory and the hypothesized coevolution between herbivores and coralline algae during the Cenozoic era (Steneck, 1986). As mentioned above it may be the sucking activities of fish like *Ctenochaetus* that promote corallines more than strong and deep bites.

The present escalation model of evolution suggests that sea urchins disturb algae less than herbivorous fishes (Steneck, 1986; Steneck and Dethier, 1994). This conclusion is based on observations of the differential bite depth of the herbivore functional groups into coralline thalli. Parrotfishes bite deeper into coralline algae and parrotfishes are, therefore, hypothesized to be superior resource competitors. In contrast, this study and all other experimental field studies of competition between sea urchins and non-territorial herbivorous fishes have consistently shown that sea urchins are better competitors than fishes for algal resources (Hay and Taylor, 1985; Foster, 1987; Carpenter, 1990b; Robertson, 1991; Bruggemann, 1994; McClanahan et al., 1994, 1996). I suggest instead that escalating coevolution between crustose corallines and parrotfishes may be due to a demise in the importance of sea urchins as grazers in tropical environments, not due to competition with parrotfishes, but rather due to escalating predation on sea urchins and other invertebrates since the Mesozoic (Aronson, 1990, 1992). High levels of fishing in nearshore environments in recent times appear to reduce the predators of sea urchins and other invertebrates and may be having cascading effects on grazing and primary producer populations (Aronson, 1990; McClanahan, 1990; McClanahan and Shafir, 1990; McClanahan et al., 1994, 1996). Modelling and field studies continue to accumulate evidence that indirect ecological interactions may be equally or more important in determining the structure of ecological communities than the direct effects of predation and competition (Abrams, 1992; Menge, 1995). This recognition in ecology will need to be further incorporated into the existing theory of evolution.

Alternatives to the resource-competition hypothesis need to be considered and particularly the effects of nutrients and sedimentation in controlling algal succession. Both sedimentation and nutrients can be influenced by grazers. For example, despite the fact that parrotfish have a greater bite depth into coralline algae, sea urchins are estimated to erode calcium carbonate substrates at nearly 10 times the rate of herbivorous fishes (Birkeland, 1988; but see Bruggemann, 1994). Consequently, subsequent defecation of sediments by sea urchins produces both a constant rain of sediments to the substratum and a consequent movement or saltation of sediments along reef surfaces. These sediments are incorporated into the algal turf matrix and recycled through sea urchin grazing. Measurements in Kenyan reefs suggests that loose sediments and sand are more abundant in reefs dominated by sea urchin grazers than those dominated by fish grazers (Table 4). Sedimentation from grazing and defecation could form a significant source of disturbance that maintains algae in an arrested succession. An alternative explanation is that the unfished sites favored the deposition of sediments due to the character of water movements in these sites and the high sediments and seagrass abundance and the arrested succession in these sites resulted from a greater sediment deposition rates. The relative roles of sea urchin grazing, defecation and associated sedimentation and deposition in controlling algal species composition and abundance requires further study.

This study also showed that river sediments and associated nutrients reversed the successional development in the Malindi reef from crustose corallines to increased filamentous turf coverage. Sedimentation rates in Malindi are approximately 3 times higher than in Watamu (Malindi $= 3.7$ mg/cm$^2$/day, $n = 183$ days; Watamu $= 1.2$ mg/cm$^2$/day, $n = 100$ days; data from McClanahan and Obura, 1997). In this case it is difficult to determine the various roles of sediments and nutrients in controlling algal composition but it does indicate that eutrophication does not accelerate succession towards macroalgae dominance. Rather, in the presence of abundant fish grazers, algal succession is reversed towards filamentous turf dominance. This finding is in conflict with some hypotheses that suggest that, depending on grazing intensity, eutrophication produces dominance by either crustose coralline or frondose macroalgae (Littler et al., 1991). In contrast, it supports the contention that eutrophication promotes species with a high surface-to-volume ratio such as filamentous turfs (Rosenberg and Ramus, 1984; Carpenter, 1990c). Nutrient concentrations can affect algal growth rates (Hatcher and Larkum, 1983; Lapointe, 1989; Littler et al., 1991) but this only rarely results in increased algal standing crop because other disturbances such as grazing, desiccation and waves can be much more dominant controls. If grazers are undisturbed then high nutrient loading seems to reverse rather than promote algal succession. Clearly this idea requires testing in more reef environments and under more controlled experimental conditions.

Nutrient concentrations available to algae can be affected by grazers. Sea urchin grazers can either fix nitrogen in their guts or concentrate it in their faeces (Guerinot and Patriquin, 1981; Polunin, 1988; Williams and Carpenter, 1988). Fish can concentrate nutrients into specific areas and promote the growth of algae and corals (Meyer et al., 1983; Meyer and Schultz, 1985; Polunin, 1988). Disturbed algal communities also fix nitrogen faster than undisturbed algae (Wilkinson et al., 1984). Consequently, both territorial fishes and sea urchins could promote turf dominance and lower algal biomass by increasing nutrient concentrations in their grazing sites. Researchers need to consider the possibility that high nutrients can reduce algal standing crop by promoting small fast-growing species over large canopy forming species. Many studies that find associations between eutrophication and macroalgal dominance have not sufficiently controlled for the effect of herbivore abundance and removal through fishing or other disturbances (Banner, 1974; Tomascik and Sander, 1985; Littler et al., 1991). What is clear from the above discussion and quoted studies is that it is difficult at present to distinguish the specific mechanisms for the control of algal communities by different grazing functional groups because many factors that influence algal growth and standing crop are influenced by grazers and not just the rate of removal or intensity of disturbance. More effort is required to develop experimental designs that will allow us to detect the different roles of nutrients, sediments and grazing disturbances by the different grazing species and functional groups.

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