

REPORT

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Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean

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Abstract Since the 1970s, macroalgae have become considerably more abundant on many Caribbean reefs and overfishing of grazing fishes has been implicated as a contributory factor. We explored relationships between algal cover and grazers (biomass of herbivorous fishes and abundance of the sea-urchin *Diadema antillarum*) on mid-depth reefs (12–15 m) in 19 areas at seven locations in Jamaica, Barbados, Belize, Grand Cayman and Cuba, between April 1997 and April 1998. *Diadema antillarum* density was never $>0.01 \text{ m}^{-2}$, while herbivorous fish biomass (acanthurids and scarids $\geq 12 \text{ cm}$ total length) varied from $2\text{--}5 \text{ g m}^{-2}$ in Jamaica to 17.1 g m^{-2} in Barbados, and was strongly correlated, negatively with macroalgal cover and positively with ‘cropped’ substratum (sum of ‘bare’, turf and crustose-corralline substrata) cover. However, overfishing of herbivorous fishes alone cannot explain the widespread abundance of macroalgae, as even on lightly fished reefs, macroalgal cover was mostly $>20\%$. Herbivorous fish populations on those reefs were apparently only able to maintain approximately 40–60% of reef substratum in cropped states, but due to low space-occupation by coral and other invertebrates, 70–90% of substratum was available to algae. The abundance of macroalgae on lightly fished reefs may therefore be a symptom of low coral cover in combination with the continuing absence of *Diadema antillarum*.

Key words Coral reef · Grazing · Macroalgal overgrowth · Caribbean · Herbivorous fish · *Diadema antillarum* · Phase shifts

Introduction

It is widely believed that macroalgal abundance has increased substantially on many Caribbean coral reefs in the last two decades (Ginsburg and Glynn 1994; Connell 1997). The best-documented and most extreme cases are from reefs in Jamaica (Liddel and Ohlhorst 1992; Hughes 1994, 1996), but evidence of similar increases in algal abundance, if not of quite the same magnitude, has been reported from other locations throughout the Caribbean including the US Virgin Islands, Panama, and Belize (Steneck 1994; Shulman and Robertson 1996; McClanahan and Muthiga 1998).

Released from grazing pressure, macroalgae outcompete corals by directly overgrowing corals or by pre-empting space and thus inhibiting outward growth of existing colonies and recruitment of new colonies (Lewis 1986; Hughes 1989; Tanner 1995). Thus, once a reef system becomes dominated by macroalgae beyond a certain point, there is a tendency for it to shift further towards macroalgal domination as short-lived and low-relief corals are excluded, and growth and recruitment of larger, slower-growing corals is reduced (Hughes 1996). In turn this opens up more space for algal colonisation, further reinforcing the shift towards algal domination. This scenario has been dubbed a ‘phase shift’ (Done 1992).

Whilst some researchers feel that nutrient enrichment, and consequent rapid growth of algae has been neglected as an explanation for the increase in cover (Lapointe 1997), there can be little doubt that, at many locations, reduced herbivory, following a Caribbean-wide die-off of the main invertebrate herbivore (the sea urchin *Diadema antillarum*) in 1983–1984 is a factor (Lessios 1988). In the course of that event, Caribbean *Diadema* populations suffered 95% or greater mortality, and, with a few exceptions, urchin populations have been slow to recover (Hughes et al. 1987; Carpenter 1990; Lessios 1995). Within weeks to months of the die-off, many reefs experienced rapid increases in the abundance of upright algae (Liddel and Ohlhorst 1986;

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de Ruyter van Steveninck and Breeman 1987; Levitan 1988; Morrison 1988), and where long-term data sets are available, it appears that this domination has persisted or actually increased over time (Hughes 1994, 1996).

The role of overfishing as a causal factor in the shift towards macroalgal domination has been the subject of recent debate (Hodgson 1994; Hughes 1994; Ogden and Steering Committee 1994). It has been argued that intensively fished reefs became over-reliant on grazing by urchins because of depletion of those fishes that competed with and preyed on urchins (Hay 1984; Hughes 1994). Certainly, following the loss of the majority of urchin herbivory, the most dramatic switches from coral to algal domination occurred on Jamaican reefs, which are considered to be among the most heavily fished in the region (Koslow et al. 1994), whereas reefs with more intact herbivorous fish assemblages appear to have experienced less dramatic increases, if any, in algal cover (Steneck 1994; Bruggemann 1995; Shulman and Robertson 1996). However, for the majority of affected reefs, there are insufficient long-term data on fish, urchin and algal abundance or on fishing intensity to be able to confidently assess the impact of fishing on current densities of herbivorous fishes or on any previous reliance on *Diadema* grazing.

In this paper we set out to increase understanding of the possible causes of the widespread rise in macroalgae by determining the extent of any relationships between algal cover on the one hand and densities of grazers on the other. Measurements were made across 19 reef areas in seven Caribbean locations spanning hundreds of kilometres and representing a very wide range of conditions including levels of fishing intensity. Herbivorous fishes and urchins are selective grazers, preferring to feed

on turf or encrusting and endolithic algae, rather than on upright macroalgae, which are often chemically or physically defended (Wolf 1985; Carpenter 1986; Lewis 1986; Morrison 1988; Russ and St. John 1988; Choat 1991; Bruggemann et al. 1994b; Steneck and Dethier 1994; McAfee and Morgan 1996). Within intensively grazed patches, newly settled macroalgal plants are normally consumed before they have developed sufficiently to be distinguishable by grazers, and algal assemblages are dominated by turf and crustose-coralline algae. However, in patches where grazing pressure is lower, macroalgal plants can be expected to develop and, if grazing intensity remains low, to persist (Carpenter 1986; Lewis 1986; Steneck and Dethier 1994). Our expectation therefore was that grazer biomass would be correlated negatively with macroalgal cover and positively with cover of 'cropped' substrata. (i.e. those colonised by algae but on which stands of upright macroalgae had not developed).

Methods

Study sites

Between April 1997 and 1998, we surveyed a total of 19 reef areas from seven locations in the Caribbean (Fig. 1). Each study 'area' consisted of a stretch of approximately 2 km of reef, in which four to six randomly selected reef 'sites' (i.e. approx. 125- to 150-m-long stretches of reef) were surveyed (Table 1). Where there was more than one area, as at all locations except Barbados, areas were separated from each other by a distance of 2.5–10 km (Fig. 1). All surveys were conducted on mid-depth reefs (12–15 m) as we were confident of finding comparable reef-types (gently sloping or flat sections of hard substratum) at this depth at each of our study areas.

Fig. 1 Study locations in the Caribbean: **a** Ambergris Caye, Belize (scale bar 20 km); **b** Punta Frances and Punta del Este, Isle of Youth, Cuba (scale bar 20 km); **c** Holetown, Barbados (scale bar 3 km); **d** Grand Cayman, Cayman Islands (scale bar 10 km); **e** Montego Bay, Jamaica (scale bar 2 km); **f** Negril, Jamaica (scale bar 3 km). Marine protected areas are represented by open circles, fished areas by closed circles. North is indicated by arrow in each case

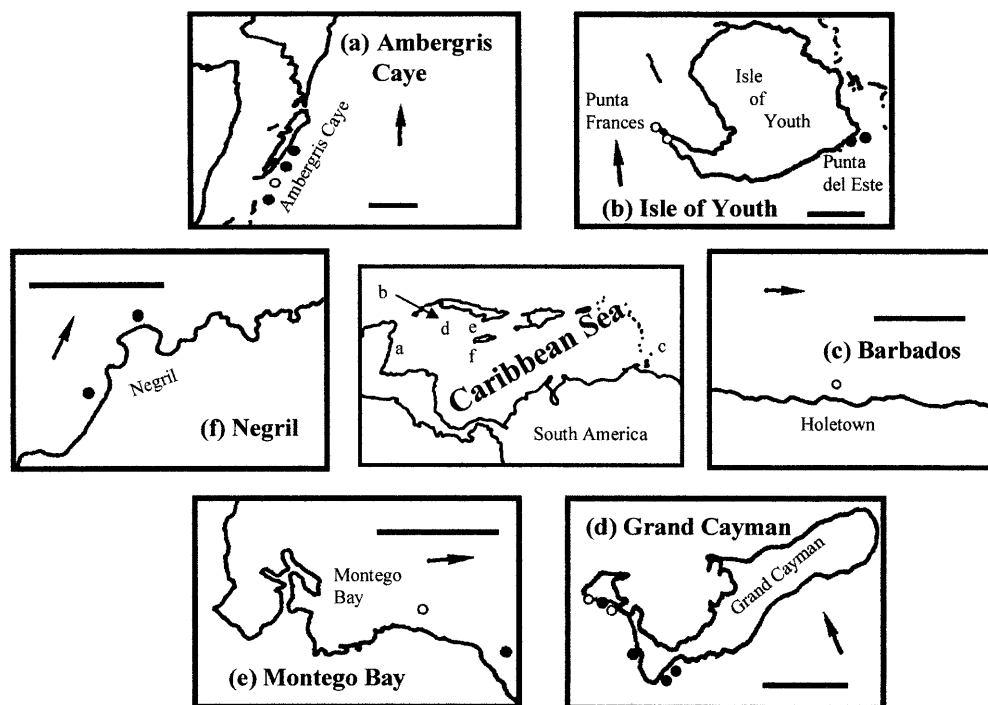


Table 1 Summary of Caribbean reef locations, areas, and sites surveyed

Location	Survey period	Survey area	Survey sites (<i>n</i>)	Co-ordinates of survey areas	Management status at time of survey ^a	Enforcement ^a
Montego Bay, Jamaica	4/97	(i)	5	77°56.0'W, 18°29.6'N	Within Montego Bay Marine Park: spearfishing banned since 1992	Negligible
		(ii)	5	77°55.4'W, 18°30.3'N	No protection	
Negril, Jamaica	5/97	(i)	5	78°21.6'W, 18°19.2'N	No protection	
		(ii)	5	78°20.1'W, 18°22.3'N	No protection	
Holletown, Barbados	6/97	(i)	5	59°38.8'W, 13°10.8'N	Within Barbados Marine Reserve (all fishing prohibited since 1981)	Uncertain
Ambergris Caye, Belize	3/98	(i)	6	87°58.6'W, 17°52.1'N	Within Hol Chan Marine Reserve (all fishing prohibited since 1987)	Effective
		(ii)	6	87°56.5'W, 17°56.1'N	No protection	
		(iii)	6	87°54.1'W, 17°59.7'N	No protection	
		(iv)	6	87°59.3'W, 17°48.4'N	No protection	
Grand Cayman	10/97	(i)	6	81°23.4'W, 19°20.3'N	'Marine Park' zone (all fishing prohibited since 1986)	Effective
		(ii)	6	81°24.1'W, 19°21.8'N	Same as Cayman (i)	Effective
		(iii)	6	81°23.7'W, 19°21.5'N	'Replenishment' zone (non-commercial linefishing permitted)	Effective
		(iv)	6	81°23.5'W, 19°18.7'N	Same as Cayman (iii)	Effective
		(v)	6	81°21.1'W, 19°15.9'N	No protection	
		(vi)	4	81°21.9'W, 19°15.8'N	No protection	
Punta Frances, Cuba	4/98	(i)	6	83°10.4'W, 21°36.4'N	Within Parques National Punta Frances (all forms of fishing prohibited for more than 20 years)	Effective
		(ii)	6	83°09.7'W, 21°35.3'N	Same as Punta Frances (i)	Effective
Punta del Este, Cuba	4/98	(i)	6	82°31.5'W, 21°32.8'N	No protection	
		(ii)	6	82°35.8'W, 21°31.2'N	No protection	

^a See 'Methods' for justifications

Where possible, one or more of the study areas at each location was within a marine protected area, as we wanted at least some of our study reefs to be in places where we could expect fishing pressure to be light. Protected-area management of many gazetted Caribbean areas is considered to be ineffective, as in Montego Bay (Maldon Miller, personal communication), but protection of some of the present areas has been well enforced, as in Punta Frances in Cuba [Punta Frances areas (i) and (ii)], where fishing licences have not been issued for 22 years (J. Angulo, personal communication), and in the Hol Chan marine reserve [Ambergris Caye, Belize, area (i)], where relatively great density of fishes within the reserve area has been repeatedly demonstrated (Polunin and Roberts 1993; Williams and Polunin, unpublished data). Among the areas in Grand Cayman that we surveyed, two were within 'marine park' zones, in which all fishing is prohibited [areas (i) and (ii)], two were in so-called replenishment zones, in which non-commercial line fishing is permitted [areas (iii) and (iv)], and two were within zones in which fishing was unrestricted [areas (v) and (vi)]. Fishing pressure is light throughout Grand Cayman, and while there is no active patrolling of the protected areas, violations of the no-fishing rules are probably rare (T. Austin, personal communication). Assessment of the management of the Holletown area, which lies within the Barbados Marine Reserve (BMR), is difficult. Abundance and biomass, especially of large trappable fishes, have been shown to be higher within shallow areas in the BMR compared to adjacent unprotected areas (Rakitin and Kramer 1996), but violations of the no fishing rule were not uncommon during the time of our surveys (personal observations).

Fishing effort on the Caribbean reefs studied has not been quantified, but studies such as that of Koslow et al. (1994) indicate

that Belize is lightly fished, while Jamaica is heavily exploited. Since grazing fishes are targeted by fishers in the intensively exploited areas which we examined (J. Angulo, personal communication; Munro 1983), we expected large variations in density of grazing fishes among the areas.

Survey methodology

Surveys of each site were conducted by two divers, working in one direction along a depth contour (between 12 and 15 m, depending on the area). The leading diver made four or five fish counts using a variation of the stationary underwater visual census method of Bohnsack and Bannerot (1986), in which all target fishes were counted within an imaginary cylinder of fixed diameter extending from the reef up to the water surface. Four replicate cylinders of 15 m diameter (Jamaica and Barbados) or five 10-m diameter cylinders (Belize, Grand Cayman, Cuba), were investigated per survey site. Replicate fish counts were separated by approximately 25 m, the distance being estimated by counting fin-kicks.

Herbivorous fishes in each cylinder were censused by an observer making two slow 360° turns while remaining in the centre of the cylinder. The aim was to make an instantaneous count in each sweep. In the first sweep, acanthurids were counted, and in the next, scarids were counted. Fish were identified to species and all lengths estimated to the nearest centimetre. Accuracy of length estimates was achieved by initially practising with pre-cut lengths of electrical cable of known length and then maintained by regularly checking estimates of length of benthic objects with a scale on the side of the recording slate. For each fish censused, biomass was

estimated, using previously published mass-length relationships for Caribbean fishes (Bohnsack and Harper 1988). We did not record fishes < 12 cm in total length because juvenile herbivorous fishes probably have minor impact on the benthos (Bruggemann et al. 1994a). Also, in our study, these fish frequently remained close to the bottom in small roving mixed-species groups, and we could not census them accurately. We think, however, that including smaller fishes would not have greatly altered the relative biomass of herbivorous fishes among study areas, as, in comprehensive surveys at one of our survey locations (Ambergris Caye), biomass of fishes smaller than 12 cm made up only 11% of total herbivorous fish biomass (Williams and Polunin, unpublished data). After completion of the fish census, the leading diver searched the area of the cylinder and recorded the number of *D. antillarum* present. All fish and *Diadema* counts were performed by the same observer.

The second diver laid out a 100-m transect line, directly following the path taken by the first diver, and photographs were taken at 30 randomly selected points along the transect line. The camera was kept at a fixed distance from the reef by use of an adjustable spacer pole attached to the camera, so that each photograph captured a similarly sized area of substratum (approximately 0.35 m²). Colour photographs were taken using a Nikonos V underwater camera with a 15-mm lens and twin flashes.

Percent cover of benthic organisms was calculated by projecting transparencies onto a white screen with a pre-determined number of 1.0-cm-diameter circles drawn on it. The category of organism at the centre of each circle was recorded. Benthic organisms were recorded in the following functional categories: 'bare' substratum (i.e. no algae or other organism discernible from photograph but presumably colonised by microalgae), sand, hard coral (scleractinians), sponge, gorgonian, other invertebrates, crustose-coralline algae, turf (mixed species assemblages of diminutive algae with canopy height < 1 cm), fleshy macroalgae (more upright and anatomically complex algae with frond extension > 1 cm), and blue-green algae. Macroalgae were identified to genera.

Statistical analysis

To enable us to look for broad relationships between herbivorous fish and benthic algal communities, we pooled biomass of herbivorous fishes into three categories – scarids, acanthurids and 'all herbivorous fish' – as experience in the Caribbean and elsewhere has indicated to us that spatial contrasts are more likely to be exhibited by aggregate than species-level data (e.g. Polunin and Roberts 1993; Jennings and Polunin 1996). We then considered two main categories of algal assemblages, namely macroalgae, and the sum of the turf, bare and crustose-coralline categories (hereafter 'cropped substrata'). Data were grouped by 'area' (representing 2-km-long sections of reef), and we used Pearson's correlation coefficient to determine whether there were relationships between the total biomass of herbivorous fish and coverage of the two principal algal categories. As we recognised the possibility of cross-correlation of scarid and acanthurid biomass with algal cover, we used partial correlations (which remove the effect of such cross-correlations) to determine the strength of associations between each fish family and the two algal categories.

One-way ANOVAs were used to test for significant differences among the 19 reef areas in biomass of herbivorous fish and percent cover of the two algal categories.

Results

Herbivorous fish biomass and urchin abundance

There was an approximate six-fold difference between the highest and lowest herbivorous-fish biomass values among the 19 reef areas, from 2.7 g m⁻² at one area in

Jamaica [Negril (ii)] to 17.1 g m⁻² in Holetown (Barbados) (ANOVA, $F = 8.3$; d.f. = 18; $p < 0.001$). Other than areas in Jamaica and Barbados, the biomass of herbivorous fish was broadly similar on most surveyed reefs, varying between 7.9 and 11.9 g m⁻² at 12 of the 14 areas (Table 2).

Scarid biomass was greater than acanthurid biomass at all study areas. Among the 19 study areas, the mean proportion of total biomass made up by scarids was 72% ($\pm 10\%$ SD), ranging from 54% at Ambergris Caye (iii) to 90% of herbivorous fish biomass at Grand Cayman (iii) (Table 2).

Diadema were very rare on studied reefs; no *Diadema* at all were recorded at 15 of the 19 areas, including all those at Punta Frances and Punta Del Este (Cuba), Ambergris Caye (Belize), and Holetown (Barbados). Where *Diadema* were present at all [Grand Cayman areas (i), (ii) and (iv), and Negril (i)], only a few individuals were observed and mean density at each of those areas was < 0.01 m⁻².

Spatial differences in benthic cover

Other than at Holetown (Barbados), mean hard-coral cover was lower than 25%, and was frequently 10% or less (Table 2). As well as having the highest coral cover, the Holetown reef also had relatively high levels of space occupation by sponges and other invertebrates; in total, around 50% of the substratum on this reef was occupied by benthic invertebrates (Table 2). In contrast, space occupation by benthic invertebrates (including corals) on reefs at all other areas was nowhere higher than 30%, ranging between 20 and 30% at Grand Cayman, but being typically < 16% at all other reef areas (Table 2). Therefore, on all but the Holetown reef, being unoccupied by benthic invertebrates, between 70 and 92% of the substratum was available for colonisation by algae (Table 2).

Among study areas, there were very large differences in the functional composition of the algal assemblages (Table 2). Macroalgae covered < 5% at Holetown, but everywhere else macroalgal cover was > 15% and in Montego Bay (Jamaica) it reached 70% (Table 2) (ANOVA among 19 areas, $F = 63.92$; d.f. = 18; $p < 0.001$). The coverage of cropped substrata also varied considerably among the 19 areas (ANOVA $F = 31.76$; d.f. = 18; $p < 0.001$), being lowest on Jamaican reefs (Negril and Montego Bay: 17–23%), but nowhere did it exceed 65%, a level of cover attained in one reef area in Belize [Ambergris Caye(iv)]. At other areas, cropped substrata covered 40–60% of the reef substratum (Table 2).

Macroalgal cover at all study locations was dominated by *Dictyota* and *Lobophora* (Table 3). It was only at the two locations with lowest herbivorous fish biomass that other taxa were at all common: *Halimeda* (13.2% cover) at Montego Bay, and *Halimeda* (12.6%), *Cladophoropsis* (8.0%), and *Sargassum* (6.5%) at Negril (Table 3).

Table 2 Mean (SE) biomass of herbivorous fish (g/m²) and percent cover of benthos in the various categories

Location	Area	Herbivorous fish			Benthic cover (%)							
		Scarids	Acanthurids	All	Coral	Other invertebrates	Macroalgae	Crustose algae	Turf algae	Bare	Other algae	Total algae
Montego Bay, Jamaica	(i)	3.7 (0.8)	1.3 (0.3)	5.1 (1.0)	9.2 (1.6)	1.9 (0.5)	70.8 (2.4)	3.5 (0.7)	13.4 (1.5)	0.5 (0.3)	0.6 (0.3)	88.9 (2.0)
	(ii)	3.7 (0.9)	0.9 (0.1)	4.6 (1.0)	6.6 (1.8)	2.2 (1.4)	70.2 (3.3)	4.4 (0.8)	15.0 (1.7)	1.1 (0.2)	0.5 (0.2)	91.2 (3.1)
Negril, Jamaica	(i)	2.4 (0.4)	1.0 (0.4)	3.3 (0.3)	5.9 (0.2)	5.1 (0.6)	64.6 (1.6)	4.4 (0.4)	16.6 (1.5)	2.0 (0.1)	1.4 (0.5)	88.9 (0.8)
	(ii)	2.1 (0.3)	0.6 (0.2)	2.7 (0.3)	9.5 (2.0)	2.7 (0.4)	67.7 (2.3)	4.0 (0.4)	14.9 (0.6)	0.9 (0.3)	0.3 (0.0)	87.8 (2.0)
Holetown, Barbados	(i)	13.3 (1.5)	3.7 (0.7)	17.1 (2.1)	36.3 (5.0)	13.0 (2.1)	3.9 (0.9)	17.7 (3.9)	28.0 (2.3)	0.0 (0.0)	1.1 (0.3)	50.7 (3.7)
Ambergris Caye, Belize	(i)	5.5 (0.6)	2.6 (0.2)	8.1 (0.5)	20.4 (1.4)	3.2 (0.8)	28.8 (2.3)	10.9 (1.3)	33.2 (2.1)	3.5 (0.5)	0.0 (0.0)	76.4 (1.5)
	(ii)	5.8 (1.4)	3.9 (0.4)	9.8 (1.6)	12.4 (2.2)	2.5 (0.6)	22.9 (1.8)	11.6 (1.6)	46.9 (2.4)	3.6 (0.7)	0.1 (0.1)	85.2 (2.8)
	(iii)	5.8 (0.9)	5 (0.4)	10.8 (1.0)	11.6 (1.2)	2.2 (0.3)	28.5 (1.7)	10.0 (1.9)	43.8 (1.6)	3.8 (0.5)	0.1 (0.1)	86.2 (1.2)
	(iv)	10.5 (1.8)	4.9 (0.8)	15.4 (2.4)	12.7 (1.0)	3.2 (0.5)	18.7 (1.8)	12.0 (1.9)	48.1 (1.2)	5.0 (0.7)	0.3 (0.1)	84.1 (1.4)
Grand Cayman	(i)	8.7 (1.3)	1.1 (0.1)	9.8 (1.3)	22.3 (1.7)	7.4 (1.2)	32.4 (1.8)	13.1 (0.5)	24.0 (1.7)	0.7 (0.2)	0.1 (0.0)	70.4 (1.4)
	(ii)	8.5 (1.0)	1.9 (0.4)	10.4 (1.0)	23.5 (2.7)	6.5 (1.0)	28.8 (1.7)	15.7 (1.1)	23.1 (2.2)	0.6 (0.1)	1.7 (0.7)	70.0 (2.8)
	(iii)	8.6 (1.3)	0.9 (0.1)	9.5 (1.2)	22.2 (2.5)	4.8 (0.7)	36.0 (3.7)	13.8 (1.3)	21.9 (1.8)	0.5 (0.2)	0.7 (0.5)	73.0 (2.4)
	(iv)	6.3 (0.8)	1.7 (0.3)	8.0 (1.0)	14.9 (2.1)	7.2 (1.3)	26.1 (2.4)	14.5 (2.0)	33.8 (3.0)	2.8 (0.2)	0.3 (0.1)	77.6 (1.9)
	(v)	9.5 (1.2)	2.3 (0.2)	11.9 (1.0)	13.4 (0.8)	8.3 (1.1)	23.0 (2.0)	23.5 (2.0)	26.0 (1.5)	1.5 (0.4)	4.2 (1.6)	78.3 (1.4)
	(vi)	9.6 (1.1)	3.4 (1.1)	12.9 (1.5)	19.5 (2.6)	6.0 (0.3)	16.6 (1.9)	14.7 (2.9)	37.4 (2.3)	2.1 (0.5)	3.9 (0.7)	74.6 (2.4)
Punta Frances, Cuba	(i)	5.5 (1.0)	3.1 (0.2)	8.6 (1.1)	12.9 (1.3)	1.4 (0.5)	48.7 (0.7)	7.4 (0.8)	28.8 (1.9)	0.7 (0.2)	0.0 (0.0)	85.6 (1.4)
	(ii)	6.0 (0.5)	3.6 (0.6)	9.6 (1.1)	13.3 (2.1)	1.7 (0.6)	49.7 (1.8)	6.7 (1.1)	27.2 (1.6)	1.4 (0.4)	0.0 (0.0)	85.0 (1.9)
Punta del Este, Cuba	(i)	7.4 (1.1)	3.4 (0.5)	10.8 (1.5)	6.6 (0.6)	4.2 (0.5)	35.7 (2.3)	12.8 (1.6)	40.1 (2.3)	0.6 (0.2)	0.1 (0.0)	89.2 (1.1)
	(ii)	4.4 (0.4)	3.3 (0.3)	7.6 (0.6)	6.8 (0.8)	2.2 (0.3)	41.8 (4.4)	10.0 (1.5)	38.5 (3.3)	0.3 (0.1)	0.4 (0.1)	91.0 (0.7)

Associations between herbivorous fish and algal cover

Both in terms of fish biomass and cover of algae, areas were grouped by location. Jamaican areas (at Montego Bay and Negril) had the lowest biomass of herbivorous fish, highest coverage of macroalgae and least coverage of the cropped substratum. The single Barbados area (Holetown) was at the other extreme, with low cover of macroalgae and high biomass of herbivorous fish, and areas in Belize (at Ambergris Caye), Cuba (at Punta del Este and Punta Frances), and Grand Cayman fell somewhere in between (Table 2, Fig. 2).

Across all areas, the biomass of all herbivorous fish was strongly correlated with algal cover, negatively with macroalgae ($r = -0.892$, $p < 0.001$; Fig. 2a), and posi-

tively with cropped substratum ($r = 0.740$, $p < 0.001$; Fig. 3a). Partial correlations indicated that biomass of both fish families was strongly negatively associated with macroalgae (for scarids $r = -0.827$, $p < 0.001$, Fig. 2b; for acanthurids $r = -0.514$, $p < 0.05$, Fig. 3b), and that acanthurid biomass was positively correlated with cover of cropped substrata ($r = 0.743$, $p < 0.001$, Fig. 3c). Scarid biomass tended to be positively associated with cover of cropped substrata, but the relationship was not significant ($r = 0.430$, $p < 0.1$, Fig. 3b).

At Holetown, where fish biomass was the highest of all studied areas, the upper threshold of cropped substratum was limited by high space-occupation by corals and sponges to just over 50% (Table 2), well below what it would have been if the trend among the other 18 areas

Table 3 Macroalgal genera with mean cover per location > 1% of benthos. *SD* Standard deviation

Location (number of areas)	% Cover	SD
Montego Bay, Jamaica (<i>n</i> = 2)		
<i>Dictyota</i>	31.7	4.6
<i>Lobophora</i>	20.9	0.7
<i>Halimeda</i>	13.2	4.9
<i>Cladophoropsis</i>	2.1	0.3
<i>Sargassum</i>	1.1	0.8
Negril, Jamaica (<i>n</i> = 2)		
<i>Dictyota</i>	24.8	0.1
<i>Halimeda</i>	12.6	3.1
<i>Lobophora</i>	9.4	2.1
<i>Cladophoropsis</i>	8.0	2.0
<i>Sargassum</i>	6.5	3.0
<i>Galaxaura</i>	1.6	1.7
Holetown, Barbados (<i>n</i> = 1)		
<i>Dictyota</i>	1.9	
<i>Lobophora</i>	1.1	
Ambergris Caye, Belize (<i>n</i> = 4)		
<i>Dictyota</i>	14.3	(1.0)
<i>Sargassum</i>	3.6	(3.2)
<i>Lobophora</i>	2.2	(3.2)
<i>Halimeda</i>	1.8	(0.4)
<i>Amphiroa</i>	1.1	(0.6)
Grand Cayman (<i>n</i> = 6)		
<i>Dictyota</i>	18.2	(5.0)
<i>Lobophora</i>	5.8	(5.2)
<i>Halimeda</i>	2.5	(0.9)
Punta Frances, Cuba (<i>n</i> = 2)		
<i>Lobophora</i>	27.3	(7.4)
<i>Dictyota</i>	19.7	(6.0)
Punta del Este (<i>n</i> = 2)		
<i>Dictyota</i>	26.9	(3.7)
<i>Lobophora</i>	5.1	(0.2)
<i>Galaxaura</i>	1.4	(1.0)
<i>Halimeda</i>	1.4	(0.4)
<i>Sargassum</i>	1.1	(1.3)

had been maintained (i.e. approx. 70%, Fig. 3a). Removing Holetown therefore enabled us to determine correlations among the 18 sites at which cover of cropped substratum was not limited by space-occupation by invertebrates. Without Holetown, those correlations were considerably stronger: for all herbivores $r = 0.827$, $p < 0.001$, for scarids $r = 0.643$, $p < 0.001$, and for acanthurids $r = 0.798$, $p < 0.001$.

Discussion

Among our 19 study areas we found a strong negative correlation between herbivorous fish biomass and macroalgal cover. Correlations cannot prove causality, but the patterns we found were consistent with the hypothesis that biomass of herbivorous fish was an important factor in the cover of macroalgae. Clearly, a linear relationship between herbivorous fish biomass and planar percent macroalgal cover is a simplistic model of macroalgal-grazer interaction in the habitat concerned and

we have therefore been careful not to overinterpret our results. However, the very strong partial correlations of macroalgal cover with acanthurids alone, and with scarids alone, indicate that both families of herbivores probably play important roles in maintaining low cover of upright macroalgae.

Diadema were extremely scarce on the studied reefs, and we can confidently assume that they were not a factor in the percent cover of different algal assemblages. Probably, though, the patterns we found would have been different if *Diadema* had been more abundant, as, prior to the Caribbean-wide mass mortality in 1983–1984, macroalgal cover was low even on heavily fished mid-depth reefs in Jamaica where sea urchins were common (Morrison 1988; Liddel and Ohlhorst 1992).

Within locations, the reef areas we surveyed were rather similar in terms of herbivore biomass and algal cover (Figs. 2 and 3, Table 2), and it was therefore only by surveying at several locations that we were able to investigate patterns from reef areas encompassing a wide range of benthic algal cover and herbivore biomass. A drawback of sampling at several locations at different time periods (Table 1) is that the overall patterns we detected might have been confounded by undetected differences among locations driven, for example, by seasonal and interannual variability. We believe that seasonality is unlikely to have been an important factor in differences among areas as most surveys were carried out in early to mid-summer (Table 1), and similarly we think it improbable that interannual variability was an important factor, as the associations between algal cover and herbivore biomass appear similar regardless of the year in which locations were surveyed (Montego Bay, Negril, Holetown, and Grand Cayman in 1997; Punta Frances, Punta del Este, and Ambergris Caye in 1998; (Figs. 2 and 3). However, as we censused only those larger fishes (≥ 12 cm) which are likely to be targeted by fishers (Russ 1991), our results may somewhat exaggerate the differences in herbivore biomass between the heavily fished Jamaican reefs and the other areas surveyed.

We have no data on availability of limiting inorganic nutrients at our study reefs, so we cannot determine the possible effect of eutrophication on macroalgal cover at any of our locations. Nutrients cannot be discounted as a factor in the differences among locations, particularly as Jamaican reefs appeared to have relatively large amounts of macroalgae even taking account of their low abundance of herbivorous fishes, and are also believed by some researchers to have been affected by elevated levels of nutrients (Goreau 1992; Lapointe 1997). Widespread eutrophication is not, though, a convincing explanation for the generally high cover of macroalgae on our study reefs, as some areas with very high cover of macroalgae were distant from any obvious source of nutrients. This would appear to be the case for Punta Frances in Cuba, for example, where the mean macroalgal cover was near 50%, while the Ambergris Caye, Belize areas, which might be considered oligotrophic

Fig. 2 Percent cover of macroalgae plotted against biomass of large herbivorous fish (≥ 12 cm): **a** acanthurids and scarids combined; **b** scarids alone; **c** acanthurids alone. Symbols represent locations: Holetown, Barbados (*solid diamonds*); Ambergris Caye, Belize (*solid triangles*); Grand Cayman (*open diamonds*); Negril, Jamaica (*solid circles*); Montego Bay, Jamaica (*open circles*); Punta Frances, Cuba (*solid squares*); and Punta del Este, Cuba (*open squares*). Error bars indicate ± 1 SE, superscript *P*'s in part **a** indicate reserve areas with effective prohibition of fishing

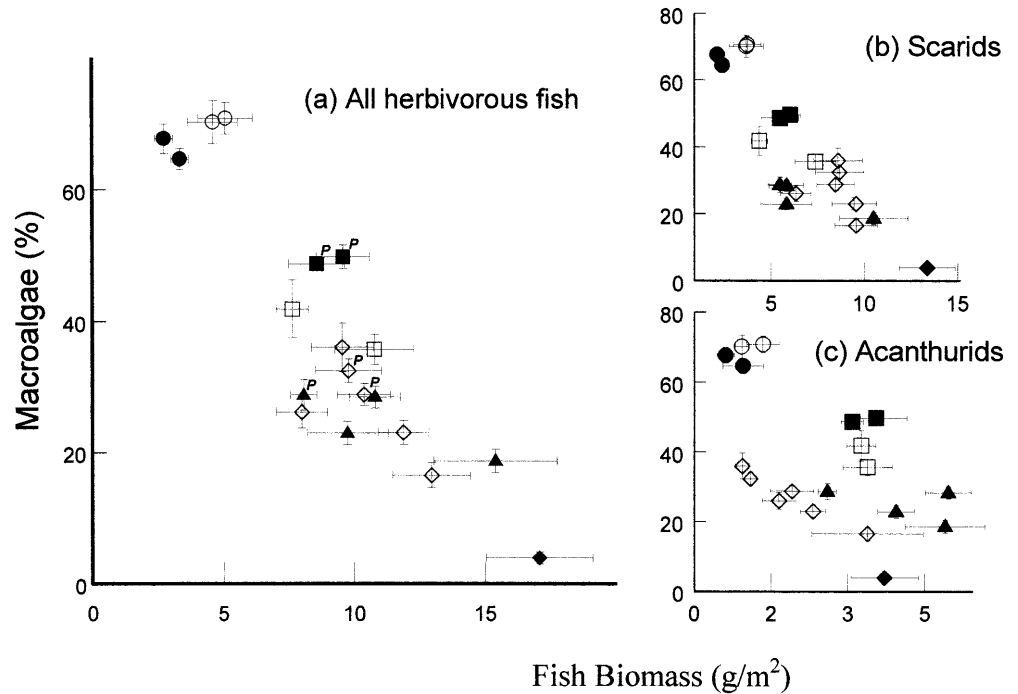
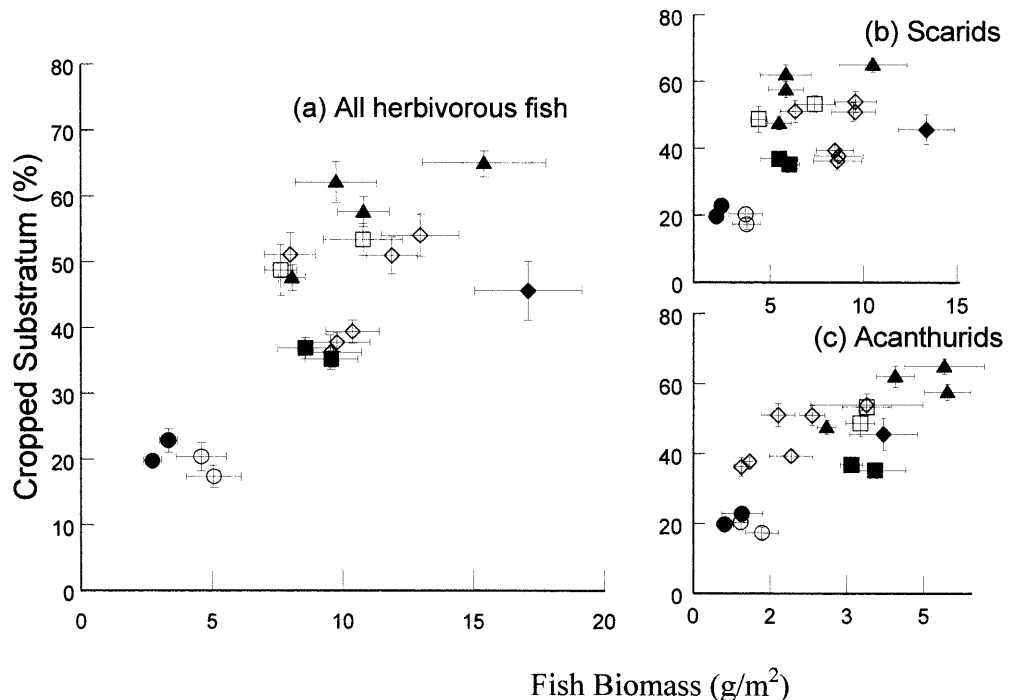


Fig. 3 Percent cover of cropped substrata plotted against biomass of large herbivorous fish (≥ 12 cm): **a** acanthurids and scarids combined; **b** scarids alone; **c** acanthurids alone. Error bars indicate ± 1 SE; symbols as for Fig. 2



(Lapointe et al. 1997), had 19–29% macroalgal cover (Table 2).

A likely consequence of herbivorous fishes feeding selectively on turf and crustose-coralline algae and tending to avoid macroalgae (Wolf 1985; Morrison 1988; Russ and St. John 1988; Choat 1991; Bruggemann et al. 1994b; McAfee and Morgan 1996) is that a mosaic of patches of different algal assemblages develops at low to moderate rates of herbivory, with grazing concen-

trated in areas dominated by more palatable algal groups. Intensive grazing within these patches will maintain them in 'cropped' states, but, in other patches, grazing pressure will be insufficient to prevent upright macroalgal plants from developing (Carpenter 1986; Lewis 1986; Steneck and Dethier 1994). By extension, and consistent with our finding of a strong correlation between herbivorous fish biomass and cover of cropped substrata, for a given assemblage of herbivores there is

probably an upper limit to the amount of benthic space that can be 'cropped down', i.e. grazed with sufficient intensity for upright macroalgae to be excluded. This may help to explain why, although fishing pressure was very light at several of our study locations (particularly Punta Frances, Cuba; Grand Cayman; and Ambergris Caye, Belize), the mean macroalgal cover was between 20 and 50% on those reefs (Table 2). We assume that, for at least some of those areas, the density of herbivorous fishes was not limited by fishing, as several of our areas were within effectively protected marine reserves (Table 1). Since most of the substratum was occupied by algal assemblages, it seems unlikely that herbivorous fish populations were food limited. Other factors such as recruitment (Doherty and Williams 1988), territoriality (Van Rooij et al. 1996), availability of hiding places (Risk 1973; Roberts and Ormond 1987), or predation (Hixon 1991) may impose an upper limit on herbivorous fish density. In our data, such an upper limit was correlated with a maximum amount of 'cropped' substratum of around 50–65% (Fig. 3). At the single Barbados study area (Holetown), approximately 50% of the substratum was occupied by corals, sponges, and other benthic invertebrates (Table 2), and so there was therefore sufficient grazing by fish alone to nearly exclude macroalgae from the limited remaining space. In contrast, on Cuban, Belize, and Grand Cayman reefs, where the total space occupied by invertebrates averaged < 25% (Table 2), the amount of grazing was insufficient to exclude macroalgae from the large amount of space available.

We cannot be certain that the low level of space-occupation by corals and other invertebrates on the surveyed Cuban, Caymanian, and Belizean reefs is a new phenomenon. However, recent reports of decline in coral cover from many locations in the Caribbean, apparently due to bleaching events and disease epidemics on an unprecedented scale (Williams and Bunkley-Williams 1990; Shulman and Robertson 1996; Aronson and Precht 1997; McClanahan and Muthiga 1998), suggest that on many reefs, coral cover is probably lower than it has been historically. It is at least plausible that part of the explanation for any general rise in macroalgal abundance on mid-depth Caribbean reefs is that some upper threshold of benthic space which herbivorous fishes are able to effectively graze down in the absence of the sea urchin *D. antillarum* has been exceeded. However, as topographically complex reefs seem to support rich and diverse fish populations (Risk 1973; Roberts and Ormond 1987), a complementary explanation might be that loss of coral cover and associated structural complexity has reduced the capacity of many reefs to support large populations of herbivorous fishes.

It is important to recognise that our finding of an apparent upper threshold equivalent to approximately 60% of benthos that can be cropped down by herbivorous fishes alone is only generally applicable to reefs at the depths we surveyed (12–15 m). Densities of both herbivorous fish and sea urchins are ordinarily much greater in shallower water (Hay 1981; Hay et al. 1983;

de Ruyter van Steveninck and Breeman 1987; Morrison 1988), and in shallow reef zones where herbivorous fish are most abundant, grazing by herbivorous fish alone can evidently be sufficient to exclude macroalgae even from reefs with low cover of sessile invertebrates (e.g. Lewis 1986; Bruggemann et al. 1994b).

Given our finding that even very lightly fished herbivorous fish populations are unable to exclude macroalgae from mid-depth reefs on which little space is occupied by other living organisms, it could be that such reefs would previously have been dependent on *Diadema* grazing. Furthermore, even if *Diadema* had generally been rare on lightly fished reefs (Hay 1984) particularly at the depths we surveyed, sea urchins could still have been locally important in locations that had lost cover of other living benthos, for example after hurricanes. In the longer term, substantial decreases in the abundance of macroalgae are only likely to occur on those reefs if either (1) there is an additional source of herbivory, such as could happen if *Diadema* populations recover to former levels, or (2) there is a significant increase in the amount of substratum occupied by other living organisms, such as corals and sponges.

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References

- Aronson RB, Precht WF (1997) Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology* 23: 326–346
- Bohnsack JA, Bannerot SP (1986) A stationary visual census technique for quantitatively assessing community structure of coral reef fishes 15. NOAA Technical Rep NMFS-41, National Oceanic and Atmospheric Administration, Miami
- Bohnsack JA, Harper DE (1988) Length–weight relationships of selected marine fishes from the southeastern United States and the Caribbean. NOAA Technical Rep NMFS-SEFC 215, National Oceanic and Atmospheric Administration, Miami, 31 pp
- Bruggemann JH (1995) Parrotfish grazing on coral reefs: a trophic novelty. PhD, Rijksuniversiteit Groningen
- Bruggemann JH, Begeman J, Bosma EM, Verburg P, Breeman AM (1994a) Foraging by the stoplight parrotfish *Sparisoma viride*. II. Intake and assimilation of food, protein and energy. *Mar Ecol Prog Ser* 106: 57–71
- Bruggemann JH, Vanoppen MJH, Breeman AM (1994b) Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different socially determined habitats. *Mar Ecol Prog Ser* 106: 41–55
- Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. *Ecol Monogr* 56: 345–363

- Carpenter RC (1990) Mass mortality of *Diadema antillarum*. I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. *Mar Biol* 104: 67–77
- Choat JH (1991) The biology of herbivorous fishes on coral reefs. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, pp 120–155
- Connell JH (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16: S101–S113
- de Ruyter van Steveninck ED, Breeman AM (1987) Deep water vegetations of *Lobophora variegata* (Phaeophyceae) in the coral reef of Curacao: population dynamics in relation to mass mortality of the sea-urchin *Diadema antillarum*. *Mar Ecol Prog Ser* 36: 81–90
- Doherty PJ, Williams DM (1988) The replenishment of coral reef fish populations. *Oceanogr Mar Biol* 26: 487–551
- Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247: 121–132
- Ginsburg RN, Glynn PW (1994) Summary of the colloquium and forum. In: *Proc Conf on the Colloquium on Global Aspects of Coral Reefs: Health, Hazards, and History*, Rosenstiel School of Marine Atmospheric Science, University of Miami, pp i–viii
- Goreau TJ (1992) Bleaching and reef community change in Jamaica 1951–1991. *Am Zool* 32: 683–695
- Hay ME (1981) Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquat Bot* 11: 97–109
- Hay ME (1984) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* 65: 446–454
- Hay ME, Colurn T, Downing D (1983) Spatial and temporal patterns of herbivory on a Caribbean fringing reef: the effects on plant distribution. *Oecologia* 58: 299–308
- Hixon MA (1991) Predation as a process structuring coral reef fish communities. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, pp 475–508
- Hodgson G (1994) Coral reef catastrophe. *Science* 266:1930–1931
- Hughes TP (1989) Community structure and diversity of coral reefs: the role of history. *Ecology* 70: 275–279
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547–1551
- Hughes TP (1996) Demographic approaches to community dynamics: a coral reef example. *Ecology* 77: 2256–2260
- Hughes TP, Reed DC, Boyle MJ (1987) Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *J Exp Mar Biol Ecol* 113: 39–59
- Jennings S, Polunin NVC (1996) Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef fish communities. *J Appl Ecol* 33: 400–412
- Koslow JA, Aiken K, Aul S, Clementson A (1994) Catch and effort analysis of the reef fisheries of Jamaica and Belize. *Fish Bull* 92: 737–747
- Lapointe BE (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnol Oceanogr* 42: 1119–1131
- Lapointe BE, Littler MM, Littler DS (1997) Macroalgal overgrowth of fringing coral reefs at Discovery Bay, Jamaica: bottom-up versus top-down control. In: *Proc 8th Int Coral Reef Symp*, Panama, Publ 1, pp 927–932
- Lessios HA (1988) Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Annu Rev Ecol Syst* 19: 371–393
- Lessios HA (1995) *Diadema antillarum* 10 years after mass mortality – still rare, despite help from a competitor. *Proc of the Royal Society of London Series B – Biological Sciences* 259: 331–337
- Levitan DR (1988) Algal–urchin biomass responses following mass mortality of *Diadema antillarum*, Philippi At Saint John, US Virgin-Islands. *J Exp Mar Biol Ecol* 119: 167–178
- Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol Monogr* 56: 183–200
- Liddel WD, Ohlhorst SL (1986) Changes in benthic community composition following the mass mortality of *Diadema antillarum*. *J Exp Mar Biol Ecol* 95: 183–200
- Liddel WD, Ohlhorst SL (1992) Ten years of disturbance and change on a Jamaican fringing reef. In: *Proc 7th Int Coral Reef Symp Publ 1*, pp 144–150
- McAfee ST, Morgan SG (1996) Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. *Mar Biol* 125: 427–437
- McClanahan TR, Muthiga NA (1998) An ecological shift in a remote coral atoll of Belize over 25 years. *Environ Conserv* 25: 122–130
- Morrison D (1988) Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. *Ecology* 69: 1367–1382
- Munro JL (1983) Caribbean coral reef fishery resources. *Stud Rev* 7. ICLARM, Manila, 276 pp
- Ogden JC, Steering Committee (1994) Coral reef catastrophe. *Science* 266: 1931
- Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Mar Ecol Prog Ser* 100: 167–176
- Rakitin A, Kramer DL (1996) Effect of a marine reserve on the distribution of coral reef fishes in Barbados. *Mar Ecol Prog Ser* 131: 97–113
- Risk MJ (1973) Fish diversity on a coral reef in the Virgin Islands. *Atoll Res Bull* 153: 1–16
- Roberts CM, Ormond RFG (1987) Habitat complexity and coral-reef fish diversity and abundance on Red-Sea fringing reefs. *Mar Ecol Prog Ser* 41: 1–8
- Russ GR (1991) Coral reef fisheries: effects and yields. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, pp 601–635
- Russ GR, St. John J (1988) Diets, growth rates and secondary production of herbivorous coral reef fishes. In: *Proc 6th Int Coral Reef Symp Publ 2*, pp 37–43
- Shulman MJ, Robertson DR (1996) Changes in the coral reefs of San Blas, Caribbean Panama: 1983 to 1990. *Coral Reefs* 15: 231–236
- Steneck RS (1994) Is herbivore loss more damaging than hurricanes? Case studies from two Caribbean reef systems (1978–1988). In: *Proc of The Colloquium on Global Aspects of Coral Reefs: Health, Hazards, and History*, Rosenstiel School of Marine Atmospheric Science, University of Miami, pp 220–226
- Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-dominated communities. *Oikos* 69: 476–498
- Tanner JE (1995) Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. *J Exp Mar Biol Ecol* 190: 151–168
- Van Rooij JM, Kok JP, Videler JJ (1996) Local variability in population structure and density of the protogynous reef herbivore *Sparisoma viride*. *Environ Biol Fishes* 47: 65–80
- Williams EHJ, Bunkley-Williams L (1990) The world-wide coral reef bleaching cycle and related sources of coral mortality. *Atoll Res Bull* 355: 1–72
- Wolf NG (1985) Food selection and resource partitioning by herbivorous fishes in mixed-species groups. In: *Proc 5th Int Coral Reef Congr Publ 4*, pp 23–28