

N.B. These are proofs.
Reproduction does not reflect
final printed quality

1st proof	2nd proof	3rd proof	final proof
-----------	-----------	-----------	-------------

Elsevier North-Holland Biomedical Press b.v. P.O. Box 1527 Amsterdam

Grafikon: 191002

Date: Page: 1 14 1st proof

IN ALL CORRESPONDENCE
CONCERNING THIS PAPER
REFER TO:

JEMBE/453

Uncorrected
Proofs

J. Exp. Mar. Biol. Ecol., 1985, Vol. 87, pp.
Elsevier

JEM 453

HERBIVORE ABUNDANCE AND GRAZING INTENSITY ON A CARIBBEAN CORAL REEF

SARA M. LEWIS¹

Department of Zoology, Duke University, Durham, N.C. 27706, U.S.A.

and

PETER C. WAINWRIGHT

Department of Anatomy, University of Chicago, Chicago, IL 60637, U.S.A.

Received 17 August 1984; revision received 12 November 1984; accepted 7 January 1985

Abstract: Herbivory is a primary factor in determining the structure of coral reef communities. Spatial variation among reef habitats in the intensity of herbivory has been documented, but underlying variation in species composition and abundance within the herbivore guild has received little attention. The distribution and relative abundances of herbivorous fishes and sea urchins across several habitats were studied on the Belizean barrier reef off the Caribbean coast of Central America. Marked variation in total herbivore density as well as major changes in the composition of the herbivore guild were found across reef habitats. Acanthurids (surgeonfishes) predominated in shallow areas (<5 m) while scarids (parrotfishes) were dominant in deeper habitats. Significant differences among habitats in an experimental assay of grazing intensity were strongly correlated with herbivore abundance. The spatial distribution of herbivorous fishes across reef habitats does not appear to be simply explained by differences in reef topography, but may depend on complex interactions among proximity to nearby shelter, predator abundance, density of territorial competitors, and local availability of food resources.

Key words: *Acanthurus*; coral reef fishes; *Diadema*; herbivory; reef topography; *Scarus*; *Sparisoma*

INTRODUCTION

Herbivores may influence profoundly the structure of coral reef communities (Stephenson & Searles, 1960; Randall, 1961; Wanders, 1977; Ogden & Lobel, 1978; Sammarco, 1982). Several distinct herbivore groups contribute to the high grazing intensity characteristic of tropical reef communities (Ogden & Lobel, 1978; Gaines & Lubchenco, 1982). On Caribbean reefs subject to minimal human disturbance, herbivorous fishes in the families Acanthuridae (surgeonfishes) and Scaridae (parrotfishes) constitute a major component of this tropical herbivore guild (Randall, 1965; Wanders, 1977; Hay, 1981; Hay *et al.*, 1983; Hay, 1984). Previous investigations of herbivory in reef communities have focussed on the role of the sea urchin grazer *Diadema antillarum* (Ogden *et al.*, 1973; Sammarco *et al.*, 1974; Carpenter, 1981; Sammarco, 1982). Few

studies have examined spatial variation in species composition and relative abundances within tropical herbivore guilds, although differences in herbivore guild composition on different reefs and among habitats on a given reef are likely to result in fundamental changes in the nature and intensity of herbivory.

In this paper, we describe variation in the distribution and relative abundances of herbivorous fishes and sea urchins for several habitats on the Belizean barrier reef. Corresponding spatial variation in grazing by herbivorous fishes is evaluated using an experimental assay of grazing intensity. We also investigate the importance of physical characteristics of reef habitats in determining the spatial distribution of herbivores.

STUDY SITES

This study was conducted at the Smithsonian Institution's field station at Carrie Bow Cay, Belize, Central America ($16^{\circ}48'N$: $88^{\circ}05'W$) during June and November 1982. This is a relatively undisturbed section of the Belizean barrier reef, subject to only minimal human fishing pressure. The topography, geology, and biological zonation of this portion of the barrier reef have been described by Rützler & Macintyre (1982). In the present investigation, a series of study sites within well-defined reef habitats were located along a transect oriented perpendicular to the reef crest (Fig. 1). These study sites are described briefly below.

THALASSIA BED

This study area was located in a shallow seagrass bed (2 m depth) with relatively sparse cover of *Thalassia testudinum* Banks ex König \approx 100 m west of Carrie Bow Cay. The study area was \approx 50 m from the nearest coral patch reef.

BACK REEF

This study site was located directly east of Carrie Bow Cay \approx 8 m seaward of the reef crest (0.5–1.5 m depth). This habitat is bordered & on the landward side by an intertidal reef flat. The substratum consists of flat, consolidated coral rubble overgrown by algal turf with scattered colonies of the coral *Porites astreoides* Lamarck.

HIGH SPUR AND GROOVE

Within the high-relief spur and groove system of the inner fore-reef, the study area was oriented along the lengths of the coral spurs (3–6 m depth). These spurs consist primarily of the corals *Agaricia tenuifolia* Dana, *Acropora palmata* (Lamarck), and *Millepora complanata* Lamarck. Sand channels which separate these coral spurs were not included in the study area.

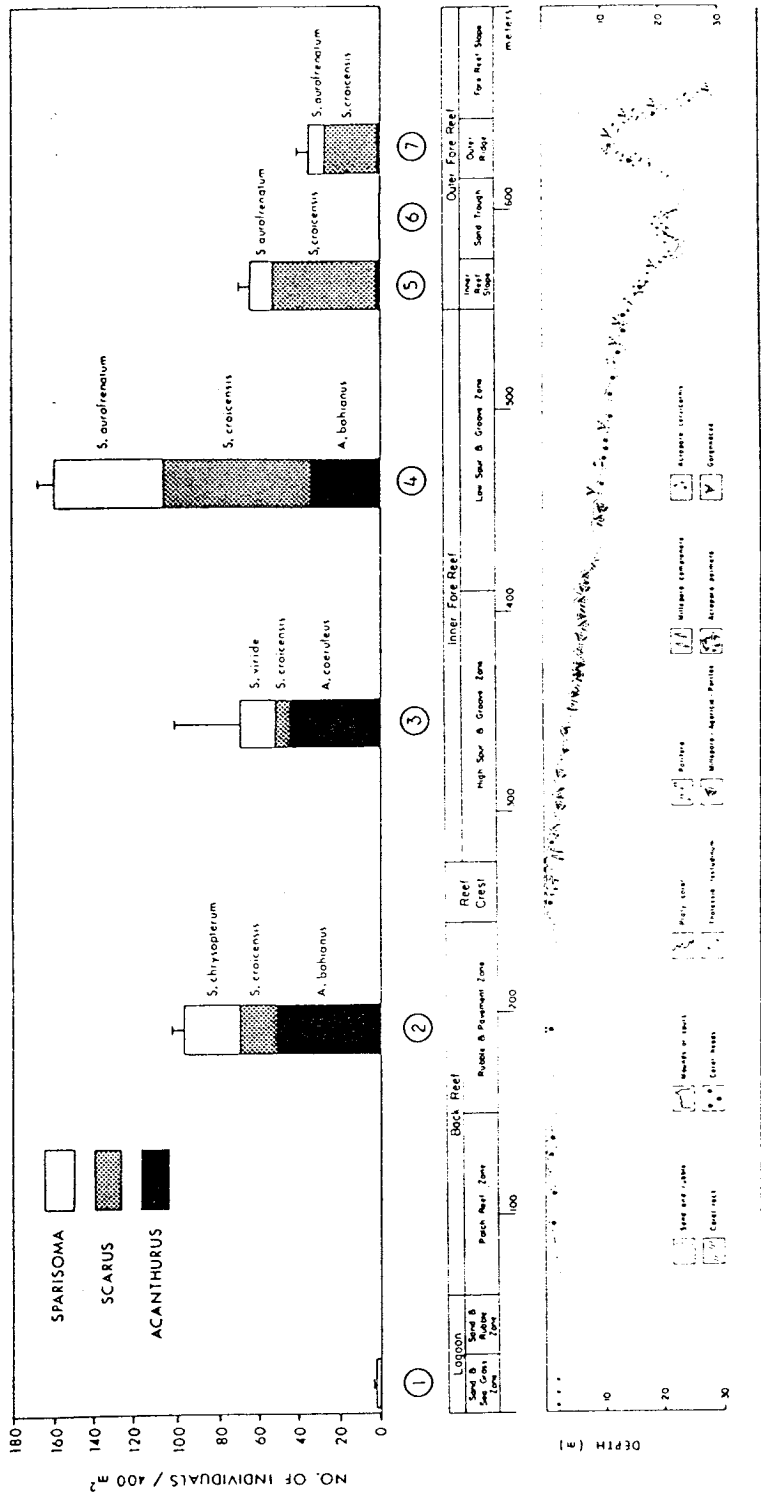


Fig. 1. Location of study sites along reef transect at Carrie Bow Cay, Belize (circled numbers refer to text). With abundances of herbivorous fishes by genus at each site (\bar{X} + SEM for total density, $n = 8$ for each site). The most abundant species within each genus are indicated. Reef transect profile courtesy of Rutzler and Macintyre (1982).

LOW SPUR AND GROOVE

This region of the inner fore-reef is characterized by low relief coral spurs with a high density and diversity of Gorgonacea, Demospongea, and scattered coral heads, primarily *Montastrea annularis* (Ellis & Solander). The study site was at 9 m depth and restricted to coral spurs.

INNER REEF SLOPE

The study area was located approximately half-way down the slope of the inner fore-reef, along a 20-m depth contour. The substratum in this habitat consists mainly of large, plate-like coral colonies of *M. annularis* and other species, with scattered Gorgonacea and Demospongea.

SAND CHANNEL

This habitat is a deep, homogeneous sandy plain located between the inner reef slope and the outer ridge. The study area was situated at 30 m depth, ≈ 35 m out from both the base of the inner fore-reef and the base of the outer fore-reef. The isolated coral patches present in some portions of the sand channel did not occur in the study area.

OUTER RIDGE

This study area was located along the top of a coral ridge which rises out of the sand channel to a height of 12–15 m below the surface. The outer forereef slope drops off steeply in the seaward direction. This habitat is dominated by dead and live *Acropora cervicornis* (Lamarck), with occasional *Montastrea annularis* heads and a variety of Gorgonacea and Demospongea.

METHODS

HERBIVORE DENSITY

Herbivorous fish populations were estimated using a modification of the visual census technique developed by Brock (1954) and reviewed by Sale (1980). Numbers of individuals encountered within 1 m on either side of a 50-m transect laid down within each habitat were counted by species. To provide estimates of abundance for rarer species, four consecutive passes were summed to give counts of individuals per 400 m². This technique is analogous to the transect census methods used to measure bird populations (Kendeigh, 1944), providing an estimate of population numbers in an area of known size. Visual censuses appear to yield reproducible estimates of population sizes within a given habitat for diurnally active, mobile fish species (Brock, 1982). The large, free-ranging herbivores of interest in this study were fishes in the families Acanthuridae (surgeonfishes), Scaridae (parrotfishes), and Kyphosidae (sea chubs).

Identifications of field-collected specimens were made following Bohlke & Chaplin (1968). Adults of most species were readily identified in the field, but small congeneric scarids were often difficult to distinguish. All unidentified *Sparisoma* < 15 cm total length were classified as juvenile *Sparisoma*. The category discussed below as *Scarus croicensis* Bloch (now *Scarus iserti* Bloch following Randall & Nelson, 1979; The earlier name is retained here for convenience) may include small individuals of other *Scarus* species; however, 30 small (4–11 cm) *Scarus* specimens collected for laboratory identification were all *S. croicensis*. For the purposes of this study, densities of initial and terminal phase scarids were pooled within species.

Eight replicate transects were conducted over several days in each habitat, four in the morning (between 0800–1100) and four in the afternoon (1300–1600). No significant differences were found between morning and afternoon counts at any study area (all $P > 0.05$, paired t -tests), and counts were combined to give an estimate of diurnal population densities. Individual counts were subjected to the square-root transformation of $\sqrt{(x + 0.5)}$ (Bartlett, 1947) to homogenize variances among reefs habitats; transformed data were used in all analyses of variance and linear regression models. All statistical analyses used the Statistical Analysis System (SAS 79.6) installed at the Triangle Universities Computation Center, Research Triangle Park, North Carolina.

Within each habitat estimates were made of daytime densities of the urchin *Diadema antillarum* Philippi, a nocturnally-active benthic grazer generally found in crevices in the reef during the day. Counts were made of individuals occurring in replicate 10-m² plots laid out along fish census transects ($n = 10$). *Diadema* counts were conducted between 0900–1500, and care was taken to search below coral ledges and crevices within each plot. *Diadema* densities were standardized to individuals per m².

GRAZING INTENSITY

Diurnal grazing rates by herbivorous fishes were measured within each habitat. Grazing intensity was estimated using modifications of the methods of Hay (1981), which provide a standard technique for assessing herbivory in reef habitats. The red alga *Acanthophora spicifera* (Vahl) Børgesen, is primarily consumed by acanthurid fishes, and rates of *Acanthophora* consumption are expected to provide reproducible estimates of grazing by this component of the herbivore guild (Lewis, in press). The seagrass *Thalassia testudinum* is primarily consumed by *Sparisoma* fishes (Lewis, in press). Rates of *Thalassia* consumption, available from the literature for five of the same reef habitats at the same location in Belize as studied here (Hay, 1981), provide complementary estimates of *Sparisoma* grazing rates.

Freshly collected specimens of *Acanthophora* ($n = 12$) spun dry (Copco Salad Spinner, Copco, Inc. N.Y.), weighed, and placed individually in weighted clothespin holders. These transplants were set out 0.5 m apart in linear arrays within each study area where they were exposed to ambient herbivores from 0730–1530. Control plants ($n = 5$) were identically prepared but were set out in cages (0.5-cm mesh hardware cloth) which

excluded all herbivorous fishes. An index of *Acanthophora* grazing intensity was calculated as the difference in mean percentage weight change between control and exposed plants at each study site. An 8-h trial was chosen to avoid complete disappearance of replicates at sites with the highest grazing rates. At each site, both the experimental and control treatments were conducted on the same day; weight losses due to fragmentation and weight gains due to growth are expected to be uniform between treatments. To avoid the possibility of entire plants having been torn loose from their holders, those replicates without any plant material remaining inside the base of the holder when collected were not included in the analysis; this occurred in < 5% of all replicates. Efforts were made to avoid placing *Acanthophora* replicates within pomacentrid territories during trials, although pomacentrids do not appear to feed directly on *Acanthophora*. Individual damselfishes (*Stegastes planifrons*, $n = 10$) were observed for 20-min periods following introduction of an *Acanthophora* transplant into their territories. While transplants were often pushed or carried out of territories, *Stegastes planifrons* was never observed to feed on plants.

Rates of *Thalassia* consumption from Hay (1981) are expressed as percentage decrease in blade length for replicate plants ($n = 21$) exposed within reef habitats near Carrie Bow Cay from 1000–1300 in March 1980.

REEF STRUCTURAL HETEROGENEITY

Topographic relief within reef zones was estimated, using a modification of methods used by Risk (1972) and Luckhurst & Luckhurst (1978), as the ratio of the areal distance between two points (X_a) to the linear distance across the substratum surface (X_s). Linear surface distance was measured by laying a fine-link brass chain conforming to all substratum contours along contiguous 2.75 m sections ($n = 4$) starting at the 10-m point on the fish census transect at each study site. Reef structural heterogeneity (SH) was calculated according to the formula

$$SH = 1 - X_a/X_s,$$

providing an index ranging from 0 (for flat substratum) to 1.

RESULTS

HERBIVOROUS FISH DENSITY

Herbivore density and relative abundances within the herbivore guild exhibited marked variation among reef habitats (Fig. 1, Table I). Herbivorous fish densities were extremely low in two habitats remote from coral-dominated areas, the sand channel and the *Thalassia* bed. Highest herbivore densities were found in the low spur and groove and back reef habitats, with significant variation across all reef habitats (Table II). Transects within habitats were conducted over several days under changing weather

TABLE I

Habitat variation in depth, structural heterogeneity (SH), herbivore density, and grazing intensity; values are given as means (SEM); ^a *Acanthophora* grazing loss calculated as the difference in mean weight loss between exposed vs. control plants; ^b *Thalassia* grazing loss from Hay (1981) as the percentage decrease in blade length of exposed plants.

	Habitat						
	<i>Thalassia</i>	Back Reef	High Spur + Groove	Low Spur + Groove	Inner Reef Slope	Sand Channel	Outer Ridge
Depth (m)	2	1	4.5	9	20	30	15
SH	0.36 (0.01)	0.15 (0.01)	0.57	0.42 (0.06)	0.54 (0.02)	0	0.49 (0.06)
<i>Diadema</i> (no. · m ⁻²)	0	0.13	4.31	0.05	0.14	0	0.69
Acanthurids (no. · 400 m ⁻²)	0.4	50.5	42.2	31.5	2.8	0	2.0
Scarids (no. · 400 m ⁻²)	0.5	45.9	26.9	128.1	61.7	0	35.2
Total fish (no. · 400 m ⁻²)	1 (0.5)	96 (7)	69 (32)	160 (9)	64 (6)	0 (0)	37 (5)
<i>Acanthophora</i> Grazing loss (%) ^a	5.3	81.7	54.6	80.7	4.9	-17.8	32.0
<i>Thalassia</i> Grazing loss (%) ^b	-	92.8	-	79.5	47.4	23.0	80.0

conditions, and low within-habitat variances suggest that the observed pattern of spatial variation in herbivore density remains relatively stable over time. Proportions of the total herbivorous fish population represented by *Acanthurus*, *Scarus*, and *Sparisoma* changed dramatically across reef zones (Fig. 1). Acanthurids predominated in two shallow reef habitats (< 5 m depth), the back reef and the high spur and groove. In contrast, *Scarus* and *Sparisoma* numerically dominated the deeper habitats. Individuals of *Kyphosus* species were not common in any habitat during this study; the highest kyphosid density (1.4 individuals per 400 m²) was found at the outer ridge, representing < 4% of total fish density at this site.

TABLE II

Analysis of variance on total herbivorous fish density ($n = 8$ for each study site, $\sqrt{x + 0.5}$ transformed data: variances homogeneous by Cochran's test, $P < 0.05$): see Fig. 2 for study site abbreviations: Scheffé multiple comparison tests ($P = 0.05$) with bars designating homogeneous subgroups.

Source of variation	d.f.	MS	F	P	r ²	
Reef habitat	6	152.7	49.8	< 0.001	0.859	
Residual	49	3.1				
High (160/400 m ²)					Low (0/400 m ²)	
LWSG	BKRF	HISG	INRS	OUTR	THAL	SAND

Nine species of herbivorous fishes were common in this study (> 1 individual per 400 m²): three acanthurid species, *Acanthurus bahianus* Castelnau, *A. chirurgus* (Bloch), *A. coeruleus* Bloch & Schneider; two *Scarus* species, *Scarus croicensis* Bloch, *S. vetula* Bloch & Schneider; four *Sparisoma* species, *S. aurofrenatum* (Cuvier & Valenciennes), *S. viride* (Bonnaterre). While species composition within this group of herbivorous fishes remained relatively constant across reef habitats, species within these three major genera showed distinct shifts in relative abundance (Fig. 1, Table III). *Acanthurus bahianus* was the dominant acanthurid at three sites, while *A. coeruleus* predominated in two other habitats. Similar shifts occurred across habitats in *Sparisoma* species dominance. *Sparisoma aurofrenatum* was the most abundant species at three deeper sites (> 5 m), while *S. chrysopteron* and *S. viride* dominated the more shallow habitats. These patterns of species replacement suggest some degree of habitat specialization within the herbivore guild. In all habitats, the genus *Scarus* was represented almost entirely by *S. croicensis*, which was the most abundant herbivore species in the three deepest habitats.

Variation among reef habitats in abundance of herbivorous fishes did not appear to be clearly related to either reef structural heterogeneity or to depth (Fig. 2); Pearson

correlation coefficients for fish density vs. structural heterogeneity and vs. depth (given in Fig. 2) were not significantly different from zero. Rank order correlation coefficients (r_s) were also not significantly different from zero for total fish density vs. either

TABLE III

Species abundances of major herbivorous fishes across reef habitats: values are given as numbers of individuals per 400 m² (means \pm SEM for $n = 8$ transects).

	Habitat				
	Back Reef	High Spur + Groove	Low Spur + Groove	Inner Reef Slope	Outer Ridge
<i>Acanthurus</i>					
<i>A. bahianus</i>	42 \pm 2	0.4 \pm 0.2	28 \pm 4	2 \pm 0.5	0.5 \pm 0.3
<i>A. chirurgus</i>	0.5 \pm 0.2	7 \pm 6	0 \pm 0	0.6 \pm 0.4	0.1 \pm 0.1
<i>A. coeruleus</i>	8 \pm 1	35 \pm 23	3 \pm 1	0.6 \pm 0.4	1 \pm 0.5
<i>Scarus</i>					
<i>S. croicensis</i>	19 \pm 4	7 \pm 3	74 \pm 4	51 \pm 5	24 \pm 4
<i>S. vetula</i>	0.5 \pm 0.3	1 \pm 0.4	0 \pm 0	0 \pm 0	2 \pm 0.7
<i>Sparisoma</i>					
<i>S. aurofrenatum</i>	1 \pm 0.4	4 \pm 1	31 \pm 5	7 \pm 1	4 \pm 1
<i>S. chrysopterygum</i>	14 \pm 3	1 \pm 0.3	1 \pm 0.5	0 \pm 0	0.3 \pm 0.1
<i>S. rubripinne</i>	3 \pm 1	1 \pm 0.4	0 \pm 0	0 \pm 0	0 \pm 0
<i>S. viride</i>	3 \pm 1	11 \pm 2	7 \pm 2	2 \pm 1	3 \pm 0.4
<i>Sparisoma</i> juveniles	5 \pm 1	0 \pm 0	14 \pm 2	1 \pm 1	0 \pm 0

structural heterogeneity ($r_s = 0.32$, $P = 0.48$) or vs. depth ($r_s = -0.46$, $P = 0.29$). A linear regression model incorporating both factors explained only 15% of the total variance in fish abundance (F for the regression = 0.363, $P = 0.72$).

DIADEMA DENSITY

Diadema antillarum also varied in abundance across reef habitats (Table I). *Diadema* densities were strongly correlated with changes in structural heterogeneity across habitat ($r_s = 0.83$, $P = 0.02$). The highest mean *Diadema* density (4.3 individuals per m²) was found in the high spur and groove habitat, where crevices within the foliate corals provided refuges for juveniles. All remaining study sites had diurnal *Diadema* densities of <1 individual per m². Observations at night indicated increased movement of *Diadema* within habitats, but little migration between habitats. When standardized densities (individuals per m²) of herbivorous fishes and *Diadema* were compared, four habitats showed greater herbivorous fish densities (*Thalassia* bed, back reef, low spur and groove, and inner reef slope). By October 1983, the mass mortality of *Diadema* that occurred throughout the Caribbean (Lessios *et al.*, 1984) had reduced *Diadema* densities

to 0.01 individuals per m² in the high spur and groove and had entirely eliminated *Diadema* in all other study sites.

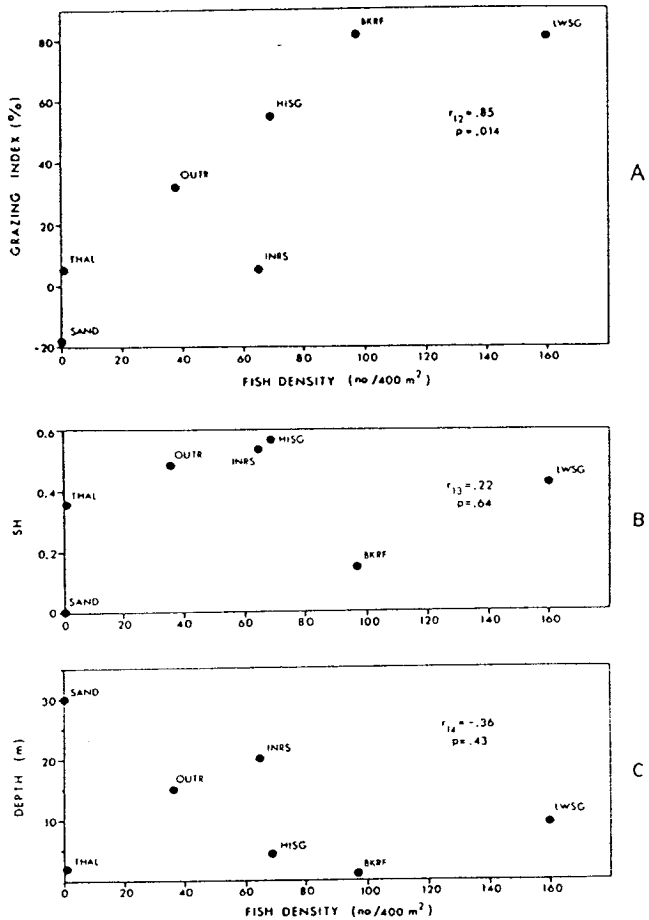


Fig. 2. Scattergrams of A, *Acanthophora* grazing index vs. total herbivorous fish density, B, reef structural heterogeneity vs. herbivorous fish density and C, depth vs. herbivorous fish density: each point represents mean values for both variates in each habitat; Pearson correlation coefficients and associated probability levels shown; Hotelling-Williams test shows $r_{12} > r_{13}$ ($z = 1.71$, $P = 0.04$) and $r_{12} > r_{14}$ ($z = 2.83$, $P = 0.002$); THAL, *Thalassia* bed; BKRF, back reef; HISG, high spur and groove; LWSG, low spur and groove; INRS, inner reef slope; SAND, sand channel; OUTF, outer ridge.

GRAZING INTENSITY AND HERBIVOROUS FISH DENSITY

Differences among habitats in *Acanthophora* grazing intensity were highly significant ($\chi^2 = 57.7$, $P < 0.001$, Kruskal-Wallis). Grazing rates on exposed *Acanthophora* plants ranged from 99% weight loss in the low spur and groove to 1% weight gain in the *Thalassia* beds (Fig. 3). Three habitats showed significantly greater weight loss in plants

exposed to grazers compared to plants protected from grazers ($P < 0.05$, Mann-Whitney U -tests). Among these habitats, the proportion of exposed replicates which were completely consumed increased from the high spur and groove (50%), To the back reef (69%), to the low spur and groove site (92%) (Fig. 3), indicating increasing grazing rates. In the sand channel, greater weight loss of control vs. exposed plants resulted in a negative grazing index.

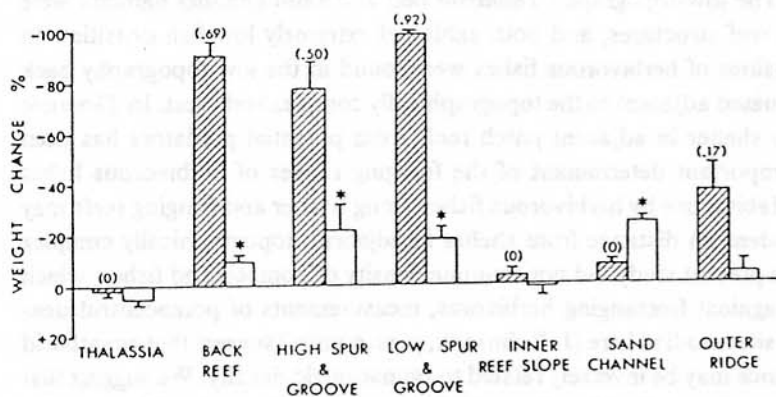


Fig. 3. Variation among habitats in grazing rates on transplanted *Acanthophora* plants: for each habitat mean percentage weight change (+ SEM) of plants exposed to herbivorous fishes (shaded bars) and protected by cages from herbivores (unshaded bars) are shown; asterisks indicate significant differences between the two treatments for a given habitat ($P < 0.05$, Mann-Whitney U -tests); the proportion of exposed replicates which were completely consumed is shown in parentheses above histograms.

Acanthophora is primarily consumed by the acanthurid component of the herbivorous fish guild (Lewis, in press). Grazing rates measured by *Acanthophora* consumption were directly related to total herbivorous fish density (Fig. 2A), and highly correlated with acanthurid density ($r_s = 0.86$, $P = 0.01$). While *Thalassia* is consumed primarily by *Sparisoma* fishes, (Lewis, in press), previous measurements of *Thalassia* consumption across five reef habitats were not correlated with *Sparisoma* abundance measured in this study ($r_s = 0.5$, $P = 0.39$). This lack of significant correlation may perhaps be due to comparison of data from different years and different seasons.

DISCUSSION

This study demonstrates marked spatial variation in abundance within the herbivore guild across the Belizean barrier reef. Significant between-habitat variation in relative abundance was found for two major groups of herbivorous fishes, with acanthurid fishes predominant in shallow habitats and scarid fishes dominant in deeper habitats. Similar results from previous studies in the Red Sea (Bouchon-Navaro & Harmelin-Vivien, 1981), Caribbean (Randall, 1963; Barlow, 1985), and Indo-Pacific (Bradbury &

Goeden, 1974; Jones & Chase, 1975) suggest that this pattern of depth distribution of acanthurids and scarids may be characteristic of many reef systems.

It has been suggested that physical habitat characteristics, particularly topographic complexity, may determine local distributions of reef fish populations (Hiatt & Strasburg, 1960; Randall, 1963; Goldman & Talbot, 1976; Luckhurst & Luckhurst, 1978). However, the distribution of herbivorous fishes across reef habitats in the present study does not appear to be simply explained by differences in reef topography. Diurnal densities of herbivorous fishes were not correlated with either habitat structural heterogeneity or depth. The low-topography *Thalassia* bed and sand channel habitats were both remote from reef structures, and both exhibited extremely low fish densities. In contrast, high densities of herbivorous fishes were found in the low-topography back reef, which was situated adjacent to the topographically complex reef crest. In *Thalassia* beds, proximity to shelter in adjacent patch reefs from potential predators has been shown to be an important determinant of the foraging ranges of herbivorous fishes (Randall, 1965). Habitat use by herbivorous fishes along barrier and fringing reefs may be similarly dependent on distance from shelter in adjacent, topographically complex habitats. While the present study did not estimate density of pomacentrid fishes, which defend territories against freeranging herbivores, measurements of pomacentrid densities at four of the sites studied here (J. Bohnsack, pers. comm.) suggest that acanthurid and scarid abundance may be inversely related to pomacentrid density. We suggest that spatial distributions of acanthurid and scarid fishes may be determined by complex interactions of several factors, including proximity to shelter, predator abundance, density of territorial competitors, and local availability of food resources.

Reef topographic complexity plays a more direct role in determining the spatial distribution of *Diadema*, which is dependent on the availability of shelter against diurnally active predators (Randall *et al.*, 1964).

The relative importance of two major herbivore groups, urchins and fishes, in contributing to overall grazing rates has been shown to vary widely among reefs in the Caribbean (Ogden *et al.*, 1973; Wanders, 1977; Hay, 1981; Sammarco, 1982; Hay, 1984). It has been suggested (Randall, 1963; Ogden, *et al.*, 1973; Hay, 1984) that these differences are related to geographical variations in levels of human fishing activity; increased levels of trap-fishing and spear-fishing may not only directly reduce populations of herbivorous fishes, but may also mediate urchin abundance by reducing populations of urchin predators. Few studies have provided quantitative estimates of abundance for herbivorous fishes and urchins. The present study location along a remote section of the Belizean barrier reef provided an opportunity to examine a reef community which has been subject to minimal human disturbance. Herbivorous fishes outnumbered the urchin grazer *Diadema* in four of seven reef habitats considered in the present study. In two reef habitats where *Diadema* was more abundant, observed *Diadema* densities (0.7–4.3 individuals per m²) were generally lower than *Diadema* densities previously reported from Caribbean reefs which have been fished more intensively (5–71 individuals per m²; Ogden *et al.*, 1973; Sammarco, 1982; Hay, 1984).

While relative abundance may not directly predict relative contribution to overall grazing rates, the present study indicates that herbivorous fishes comprise a major portion of the herbivore guild on undisturbed reefs. The relative importance of herbivorous fishes on reefs throughout the Caribbean has certainly increased since the recent mass-mortality of *Diadema* throughout the Caribbean (Lessios *et al.*, 1984).

Fundamental differences in foraging behavior, feeding rates, and feeding preferences among herbivore groups (Earle, 1982; Ogden, 1976; S. M. Lewis, in prep.) suggest that variation within the herbivore guild may profoundly influence both the nature and intensity of herbivory in different reef habitats. The spatial variations in herbivore abundance, species composition, and grazing intensity described in this study are likely to play an important role in determining benthic species distributions within coral reef communities.

ACKNOWLEDGEMENTS

This research was supported by a Smithsonian Institution Bacon Predoctoral Fellowship and by a grant from the Lerner-Gray Fund for Marine Research of the American Museum of Natural History to S. M. L. We thank J. Bohnsack, M. Hay, M. and D. Littler, & A. Motten, and P. Reinthal for their critical reading of the manuscript. This is Contribution No. 157 of the Smithsonian Institution's IMSWE Reef and Mangrove Study, which is partially supported by the Exxon Corporation. We are also grateful for logistic support provided by K. Rützler (Program Director).

REFERENCES

- BARLOW, G. W., 1975. On the sociobiology of four Puerto Rican parrotfishes (Scaridae). *Mar. Biol.*, Vol. 33, pp. 281-293.
- BARTLETT, M. S., 1947. The use of transformations. *Biometrics*, Vol. 3, pp. 39-53.
- BÖHLKE, J. E. & C. C. G. CHAPLIN, 1968. *Fishes of the Bahamas and adjacent tropical waters*. Livingston Publishing Company, Wynnewood, PA 771 pp.
- BOUCHON-NAVARO, Y., & M. HARMELIN-VIVIEN, 1981. Quantitative distribution of herbivorous reef fishes in the Gulf of Aqaba, Red Sea. *Mar. Biol.*, Vol. 63, pp. 79-86.
- BRADBURY, R. H. & G. GOEDEN, 1974. The partitioning of the reef slope environment by resident fishes. In, *Proceedings of the Second International Symposium on Coral Reefs*, Great Barrier Reef Committee, Brisbane, pp. 167-178.
- BROCK, R. E., 1982. A critique of the visual census method for assessing coral reef fish populations. *Bull. Mar. Sci.*, Vol. 32, pp. 269-276.
- BROCK, V. E., 1954. A preliminary report on a method of estimating reef fish populations. *J. Wildl. Mgmt.*, Vol. 18, pp. 297-308.
- CARPENTER, R., 1981. Grazing by *Diadema antillarum* Philippi and its effect on the benthic algal community. *J. Mar. Res.*, Vol. 39, pp. 749-765.
- EARLE, S. A., 1972. The influence of herbivores on the marine plants of Great Lameshur Bay, with an annotated list of plants. In, *Results of the Tektite Program: ecology of coral reef fishes*, edited by B. B. Collette & S. A. Earle, *Nat. Hist. Mus. Los Angeles County Sci. Bull.*, Vol. 14, pp. 17-44.
- GAINES, S. D. & J. LUBCHENCO, 1982. A unified approach to marine plant-herbivore interactions II. *Biogeography. Annu. Rev. Ecol. Syst.*, Vol. 13, pp. 111-138.
- GOLDMAN, B. & F. H. TALBOT, 1976. Aspects of the ecology of coral reef fishes. In, *Biology and geology of coral reefs, Vol. III*, edited by O. A. Jones & R. Endean, Academic Press, N. Y., pp. 125-153.

- HAY, M.E., 1981. Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distributions. *Aquat. Bot.*, Vol. 11, pp. 97-109.
- HAY, M.E., 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology*, Vol. 65, pp. 446-454.
- HAY, M.E., T. COLBURN & D. DOWNING, 1983. Spatial and temporal patterns of herbivory on a Caribbean fringing reef: the effects on plant distributions. *Oecologia*; (Berlin), Vol. 58, pp. 299-308.
- HIATT, R.W. & D.W. STRASBURG, 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.*, Vol. 30, pp. 65-127.
- JONES, R.S. & J.A. CHASE, 1975. Community structure and distribution of fishes in an enclosed lagoon in Guam. *Micronesica*, Vol. 11, pp. 127-148.
- KENDEIGH, S.C., 1944. Measurement of bird populations. *Ecol. Monogr.*, Vol. 14, pp. 69-105.
- LESSIOS, H.A., D.R. ROBERTSON & J.D. CUBIT, 1984. Spread of *Diadema* mass mortality through the Caribbean. *Science*, Vol. 226, pp. 335-337.
- LEWIS, S.M., in press. Herbivory on coral reefs: algal susceptibility to herbivorous fishes. *Oecologia* (Berlin).
- LUCKHURST, B.E. & K. LUCKHURST, 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Mar. Biol.*, Vol. 49, pp. 317-323.
- OGDEN, J.C., 1976. Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. *Aquat. Bot.*, Vol. 2, pp. 103-116.
- OGDEN, J.C. & P. LOBEL, 1978. The role of herbivorous fishes and urchins in coral reef communities. *Environ. Biol. Fish.*, Vol. 3, pp. 49-63.
- OGDEN, J.C., R. BROWN & N. SALESKY, 1973. Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. *Science*, Vol. 182, pp. 715-717.
- RANDALL, J.E., 1961. Overgrazing of algae by herbivorous marine fishes. *Ecology*, Vol. 42, pp. 812.
- RANDALL, J.E., 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Carib. J. Sci.*, Vol. 3, pp. 31-47.
- RANDALL, J.E., 1965. Grazing effect on seagrasses by herbivorous marine fishes. *Ecology*, Vol. 46, pp. 255-260.
- RANDALL, J.E., W. SCHROEDER, & W.A. STARCK, 1964. Notes on the biology of the echinoid *Diadema antillarum*. *Carib. J. Sci.*, Vol. 4, pp. 421-433.
- RANDALL, J.E. & G. NELSON, 1979. *Scarus japonensis*, *S. quoyi* and *S. iserti*- valid names for parrotfishes presently known as *S. capistratoides*, *S. blochii*, and *S. croicensis*. *Copeia*, Vol. 1979(2), pp. 206-212.
- RISK, M.J., 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll. Res. Bull.*, Vol. 153, pp. 1-6.
- RÜTZLER, K. & I. MACINTYRE, 1982. The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize. In: *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize*. In: *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize*, edited by K. Rutzler & I. Macintyre, *Smithsonian Contributions to the Marine Sciences*, Vol. 12, pp. 9-46.
- SALE, P.F., 1980. The ecology of fishes on coral reefs. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 8, pp. 367-421.
- SAMMARCO, P.W., 1982. Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. *J. Exp. Mar. Biol. Ecol.*, Vol. 65, pp. 83-105.
- SAMMARCO, P.W., J. LEVINTON & J.C. OGDEN, 1974. Grazing and control of coral reef community structure by *Diadema antillarum*: a preliminary study. *J. Mar. Res.*, Vol. 32, pp. 47-53.
- STEPHENSON, W. & R.B. SEARLES, 1960. Experimental studies on the ecology of intertidal environments at Heron Island I. Exclusion of fish from beach rock. *Austr. J. Mar. Freshwater Res.*, Vol. 2, pp. 241-267.
- WANDERS, J.B.W., 1977. The role of benthic algae in the shallow reef of Curacao III. The significance of grazing. *Aquat. Bot.*, Vol. 3, pp. 357-390.