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REPORT

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Herbivorous fish assemblages and herbivory pressure on Laamu Atoll, Republic of Maldives

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Abstract While herbivory is recognized as a fundamental process structuring coral reef communities, herbivore assemblages and processes are poorly described for reefs in the Indian Ocean region. We quantified herbivorous fish assemblage structure (abundance and diversity) in Laamu Atoll, Republic of Maldives, in four reef habitat types: faro reef flats, faro reef slopes, inner and outer atoll reef slopes (20 sites in total). Herbivorous fish assemblages, representing a total of 30 species, grouped strongly by habitat type, with the highest absolute abundance observed on faro reef flats and lowest abundance on inside atoll rim reef slopes. Removal of *Thalassia* seagrass blades by ambient herbivore assemblages was used in a bioassay to assess relative herbivory pressure among four habitat types (eight sites). Also, at one site a choice herbivory assay was performed to assess herbivore preference among four benthic plants across three depth zones. Relative herbivory, as indicated by *Thalassia* assays, was highest on inside atoll rim reef slopes and lowest on outside atoll rim reef slopes. *Thalassia* consumption did not correspond to overall herbivorous fish abundance, but corresponded more closely with parrotfish abundance. In the choice assays, herbivores showed strong preferences among plant types and consumption of most plant types was higher at mid-depth than in the shallow reef flat or deep reef knoll zones.

Keywords Herbivory · Herbivorous fishes · Assemblage structure · Maldives

Introduction

Coral reefs are perhaps unique ecosystems in terms of their high rates of primary production coupled with extremely high rates of transfer of this primary production to primary consumers (Hatcher 1990). Hay (1991) argues that this coupling of high production with high consumption in tropical coral reefs makes plant/herbivore interactions among the most important structuring factors for these communities. A major manifestation of herbivore control of benthic communities is the role that coral reef herbivory plays in mediating competition between fast-growing benthic algae and relatively slow-growing corals (Miller 1998), allowing corals to flourish by keeping macroalgal standing crop limited to virtually nil.

A rich literature concerning herbivory on Caribbean coral reefs has documented strong influence by herbivores on benthic community structure via small-scale experimental studies (Carpenter 1986; Lewis 1986; Morrison 1988) and via the region-wide reduction in herbivory after the 1983 epizoic die-off of a dominant herbivore, *Diadema antillarum* (reviewed by Lessios 1988). There is some debate regarding possible anthropogenic (i.e. overfishing) influence on the dominance of urchins in herbivory processes in many Caribbean sites studied in the 1970s and early 1980s (Hay 1984; Knowlton 1992; Jackson 1997). However, there is little doubt that fishes are the dominant herbivores on Caribbean reefs since the *Diadema* die-off, as urchin recovery has been minimal (but see Aronson and Precht 2000). Overall, fishes on tropical coral reefs have high diversity, high abundance, and high per capita consumption rates

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Electronic supplementary material to this paper (Appendix 1) can be obtained by using the Springer LINK server located at http://dx.doi.org.1007/s003380100166.

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relative to both temperate fishes (Gaines and Lubchenco 1982) and invertebrate herbivores (Andrew 1989).

The influence of herbivory in structuring Indo-Pacific reefs has received relatively less attention and most published studies are restricted to Australia's Great Barrier Reef (GBR) region. Comparisons of herbivory and herbivorous fish communities in the GBR document that nearshore reefs relative to offshore reefs show reduced influence of herbivorous fishes on benthic algal communities (Scott and Russ 1987), reduced abundance of herbivorous fishes (Russ 1984a), and reduced diversity of overall fish fauna (Williams and Hatcher 1983). Klumpp and Pulfrich (1989) confirm that fishes, as opposed to invertebrates, are the dominant herbivores on the Great Barrier Reef. Nutrient enrichment experiments at One Tree Reef on Australia's Great Barrier Reef did not exhibit expected increases in algal standing stock due to herbivory (Hatcher and Larkum 1983). More recently, McCook (1996) has demonstrated that the long-observed cross-shelf gradient in macroalgal standing stock, often presumed to result from water-quality gradients, is in fact largely attributable to increased herbivory on the offshore reefs.

For the Indian Ocean region, reports on herbivore assemblage structure are limited (Chabanet et al. 1995; Jennings et al. 1996; Letourneur 1996a, 1996b). Extensive work on the behavior and feeding patterns within the family Acanthuridae was completed by Robertson et al. (1979), Robertson and Polunin (1981), and Robertson and Gaines (1986). Hay (1984) used herbivory bioassays in the Seychelles to document relatively higher herbivory pressure on shallow reef slopes in comparison to adjacent reef flat and sand-plain habitats. Lastly, extensive studies on herbivory and herbivore assemblages in overfished and marine reserve areas in Kenya have shown that intense fishing has strong direct and indirect impacts on herbivore assemblage structure, herbivory intensity, and resulting benthic community structure (McClanahan and Shafir 1990 ; McClanahan 1994 ; McClanahan et al. 1994).

The Republic of Maldives is a string of coral reef atolls off the southwest coast of India. Despite an economy that is essentially completely dependent on marine resources including fisheries, the reef fish stocks are among the least exploited as the artisanal fisheries have traditionally focused on pelagic species, especially tuna. Thus, Maldives reef fish communities are relatively undisturbed and present a valuable opportunity to examine herbivorous fish communities and herbivory processes in a reef system with relatively little trophic disruption.

In this study, we sought to quantify herbivorous fish assemblage structure across habitat types and relate herbivore populations to rates of herbivory, estimated by a bioassay technique, across habitat types on reefs in Laamu Atoll, Republic of Maldives.

Methods

Study area

Laamu Atoll (2.0°N, 73.5°E) lies in the southern third of the atoll chain comprising the Republic of Maldives (Fig. 1). The Laamu Atoll lagoon reaches a depth of 73 m. The atoll rim has fringing reefs on the lagoon side and the outer, oceanic side. Fringing reefs on both sides have similar zonation with a shallow sandy lagoon, reef flat, reef crest, and reef slope. The outside slope drops precipitously to about 30–50 m, slopes gently for about 0.5 km, and then drops off to abyssal depths (Anderson et al. 1992). The inside reef slopes gently to about 20 m depth and grades into a sandy bottom. In the central portion of the lagoon, pillar reefs called faros reach from the sandy lagoon floor to within a few meters of the surface. Zonation in faros was similar to the fringing reefs except they do not have a sandy lagoon. Study sites were chosen for both their representativeness of these habitats as well as proximity to the Oceanographic Society's laboratory (near site I2, Fig. 1). All surveys were conducted June–July 1997, which falls just after the shift to the SW monsoon. The portion of the atoll where our study sites were located receives high wave energy during this season.

Herbivorous fish assemblages

Twenty sites were surveyed for herbivorous fish density and assemblage structure (families Acanthuridae, Scaridae, and Siganidae) among four habitat types: faro reef flats, faro reef slopes, and reef slopes both inside and outside the atoll rim (Fig. 1). At each site, eight 100-m^2 transects (20×5 m, width by visual estimation) were searched for all fish of the aforementioned families greater

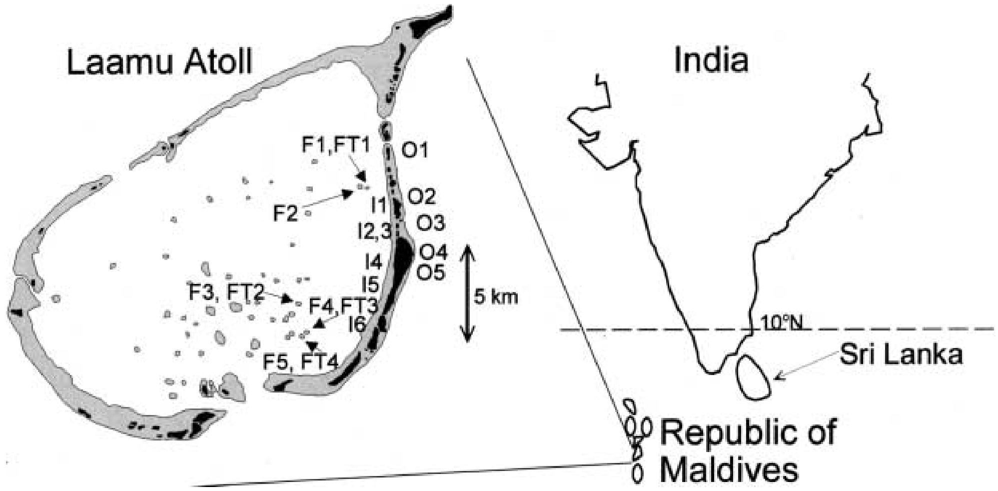

Fig. 1 Map of sites surveyed for herbivorous fish assemblage and *Thalassia* assays (additional sites I7 and I8). *Alpha-numeric code* indicates habitat type and corresponds to site codes in other tables and figures. *FT* Faro reef top; *F* faro reef slope; *I* reef slope inside atoll rim; *O* reef slope outside atoll rim

than 5 cm total length. Fish were enumerated by species. Observers were trained to estimate transect width by placing construction flags at a distance estimated to be 2.5 m from each side of the length of a transect line. The actual distance was then measured and biases made known to observers. This process was repeated until observers could accurately estimate transect width. Parrotfish (Scaridae) in the Maldives are dichromatic, so initial phase and terminal phases were also enumerated in order to determine if the separate phases show different distribution patterns.

A nested ANOVA was used to assess differences in mean species density among habitat types and among sites nested in habitat types (Zar 1984). Tukey tests were used to make pairwise comparisons for significant factors. Data were log (x + 1) transformed due to heterogeneous variances. Total and family herbivore density were similarly tested. Multivariate analyses were performed using MVSP software (Kovach Computing Services, Pentraeth, Isle of Anglesey, Wales, UK). The percent similarity coefficient was used to examine the similarity of species density among the four habitat types. Cluster analysis was performed using the group average linkage method. Relationships between depth of survey and species abundance were examined with a Pearson correlation coefficient, and significance was judged using Bonferroni adjusted probabilities (Zar 1984). Depth relationships were also investigated by creating histograms of the seven most abundant species, including both parrotfish phases, by depth in 3-m categories.

Herbivory processes

Relative grazing intensity was compared among the same four habitat types (faro reef flat, faro reef slope, and reef slopes inside and outside the atoll rim) using a bioassay technique. Assays were performed at two sites in each habitat type (eight sites in total). Thirty-centimeter pieces of polypropylene rope were prepared by placing three clean, 5-cm lengths of *Thalassia* seagrass blades securely between the twisted twines. At each site ten such ropes were placed on the reef and left available for grazing for 91 (11) min (SD). After retrieval, *Thalassia* blades were scored as follows: 1 = not eaten, 2 = < 50% consumed, 3 = 51–90% consumed, and 4 = completely consumed. These scores were treated as ranks and the mean ranks for each rope (mean of three blades per rope) were used as replicates to test for significant differences among sites by non-parametric Kruskal-Wallis ANOVA followed by Dunn's tests (pairwise post-hoc comparisons) to examine the similarity of sites of the same habitat type.

At one inside atoll rim site (I2 on Fig. 1), the grazing preferences of herbivores were examined by presenting four common macrophytes for consumption: *Eucheuma cottonii*, *Thalassia* sp., *Padina* sp., and *Lobophora* sp. *Eucheuma cottonii* is an exotic species which is being cultivated in an experimental mariculture facility in nearby lagoons, while the latter three species are all naturally abundant in nearby habitats. The site was divided into three depth zones: shallow reef flat (1–3 m), reef slope (10 m), and knoll (15–20 m). The knoll habitat is a deeper coral mound consisting of plate and massive corals. In this assay, each rope contained one frond of each of the four macrophyte types, and 30 ropes were presented in each of the three habitats. The ropes were collected after approximately 3 h and each plant piece scored in the same manner as the *Thalassia* bioassay. Scores were used as ranks in non-parametric Kruskal-Wallis ANOVAs with Dunn's post-hoc comparisons to test for differences in consumption between reef zones for each plant type.

Results

Herbivorous fish assemblages

Total herbivorous fish density was highest in the faro reef flat habitat type and lowest on the inside atoll rim habitat type (Table 1, Fig. 2). Acanthurids were most

Table 1 Summary of mean density of herbivorous fish as (number of fish)·100 m^{-2} (±1 SE) in Laamu Atoll, Republic of Maldives. Site codes are as described in Fig. 1 and indicate habitat type of the site: *O* Reef slope outside atoll rim; *I* reef slope inside atoll rim; *F* faro reef slope; *FT* reef flat on faro tops

Site	O1	O2	O3	O4	O5	I1	I2	I3	I4	I5	I6	F1	F2	F3	F4	F5	FT1	FT2	FT3	FT4
Depth (m)	8.9 (0.9)	8.1 (1.1)	9.7 (0.8)	7.1 (0.9)	11.4 (1.2)	7.0 (0.8)	9.2 (0.0)	16.5 (1.1)	8.5 (0.8)	8.1 (1.1)	5.4 (0.3)	6.8 (0.3)	5.4 (0.8)	6.0 (0.5)	7.0 (0.9)	7.7 (0.6)	1.4 (0.0)	0.9 (0.0)	1.2 (0.0)	1.2 (0.0)
Acanthuridae (12 species)	16.9 (1.4)	22.4 (3.6)	22.5 (2.2)	20.0 (3.8)	14.5 (2.7)	12.2 (1.6)	6.2 (1.6)	6.4 (1.0)	6.4 (1.2)	8.6 (1.7)	14.7 (3.3)	15.4 (2.3)	16.9 (5.1)	15.9 (1.9)	10.8 (1.3)	14.1 (2.1)	28.9 (3.5)	18.7 (1.7)	21.5 (2.7)	22.6 (3.5)
Scaridae (14 species)	5.4 (1.7)	2.6 (0.4)	3.0 (1.6)	1.5 (0.6)	0.8 (0.3)	9.4 (3.9)	2.5 (0.4)	3.4 (1.3)	7.3 (1.9)	10.0 (3.1)	15.3 (4.0)	6.6 (2.0)	9.0 (2.0)	19.6 (2.8)	9.9 (3.0)	11.0 (3.8)	3.9 (1.9)	3.0 (0.7)	2.9 (0.6)	7.6 (2.5)
Siganidae (4 species)	–	0.3 (0.3)	0.1 (0.1)	0.1 (0.1)	0.3 (0.3)	–	–	–	0.2 (0.2)	–	2.9 (0.9)	0.3 (0.3)	1.0 (0.5)	0.4 (0.3)	0.6 (0.3)	0.3 (0.3)	0.3 (0.3)	0.9 (0.6)	0.4 (0.3)	0.8 (0.4)
Total herbivores	22.3 (1.9)	25.3 (4.0)	25.6 (2.9)	21.6 (3.3)	15.5 (2.7)	21.6 (4.9)	8.8 (1.6)	10.1 (2.1)	13.9 (3.1)	18.6 (4.8)	32.9 (6.8)	22.3 (3.7)	26.9 (6.4)	35.9 (4.4)	21.2 (3.4)	25.4 (5.5)	33.0 (3.6)	22.6 (2.2)	24.8 (3.0)	31.0 (4.0)

abundant among faro reef flat and outside atoll rim reef slope sites, while scarids showed the opposite pattern. Thirty herbivorous fish species were observed during this study, with surgeonfish (Acanthuridae) being represented by 12 species, parrotfishes (Scaridae) by 14 species, and rabbitfish (Siganidae) by 4 species (Appendix 1, see electronic supplementary material). Eleven species showed significant density differences among habitat types (Table 2). Faro reef flats were characterized by higher than average abundances of *Acanthurus lineatus*, *A. luecosternon*, and *A. nigrofuscus*. Initial phase (IP) *Cetoscarus bicolor*, *Naso literatus*, and IP *Scarus sordidus* were most abundant on faro reef slopes. The reef slope inside the atoll rim was characterized by high abundance of IP *Hipposcarus harid*. The surgeonfish *A. luecosternon*, *Ctenochaetus strigosus*, and *Zebrosoma desjardini* were most abundant on reef slopes outside the atoll rim. Clustering revealed distinct grouping by habitat type (Fig. 3). Outside atoll rim reef sites were 74.5% similar, faros 61.1%, and inside atoll rim reef sites 51.0%. Three of the four faro reef flat sites were 77.6% similar, with the fourth site grouping with outside atoll rim reef sites.

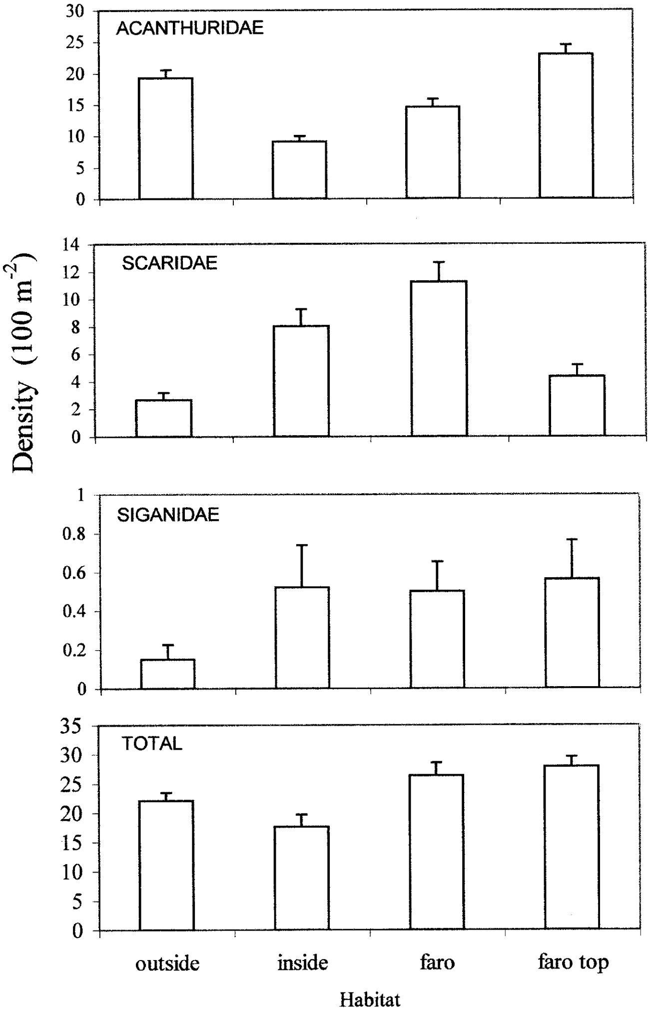

Fig. 2 Herbivorous fish density, for three herbivore families and total, sampled in visual transects among four reef habitat types ($n = 4$–5 sites within each habitat type)

Nine of the 45 correlations between depth and species [including both initial (IP) and terminal phase (TP) parrotfish] were significant and all were negative. How-

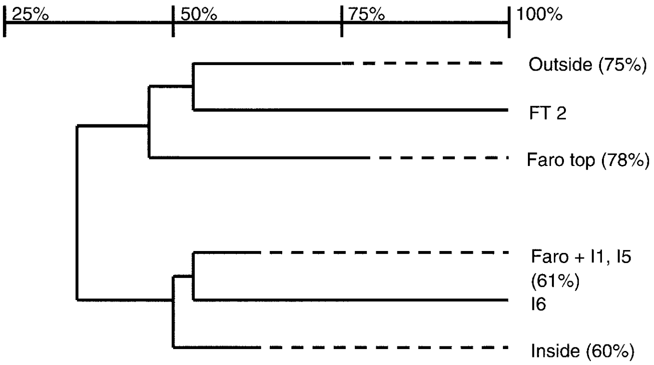

Fig. 3 Cluster diagram showing relationship of herbivore assemblage and habitat types. *Site codes* correspond to Fig. 1 and Table 1. Habitat types that clustered together are represented as a group and individual sites that did not cluster with their habitat type as their site code. For example, all outside atoll rim reef slopes clustered together and were 75% similar as measured by the percent similarity index

Table 2 Significant results of nested ANOVA with habitats and sites nested within habitats as fixed factors (*ns* non-significant; * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$). Significant differences show the results of pairwise comparison testing for effect of the main factor habitat type. Habitat types examined are the reef flat on top of faros (*farotop*), reef slope in faros (*faro*), inside atoll rim (*inside*), and outside atoll rim (*outside*). *IP* Initial phase; *TP* terminal phase

Species	Habitat	Site	Significant differences
Acanthurus lineatus	***	ns	Farotop > faro = outside = inside
A. luecosternon	***	*	Outside = farotop > faro > inside
A. nigracauda	*	***	Inside > outside
A. nigrofuscus	**	***	Farotop > faro = outside = inside
Ctenochaetus striatus	***	***	Farotop > faro > inside > outside
C. strigosus	***	***	Outside > farotop = inside = faro
Naso literatus	***	ns	Faro > inside = outside = farotop
Total Acanthuridae	***	***	Farotop = outside > faro > inside
Cetoscarus bicolor (IP)	***	**	Faro > farotop = outside = inside
Hipposcarus harid (IP)	***	**	Inside > faro = outside = farotop
Scarus frenatus (TP)	*	ns	Faro > farotop, farotop > outside
Scarus ghobban (IP)	*	ns	Inside > farotop
Total Scaridae	***	***	Faro > farotop = outside, faro = inside, inside = farotop, inside > outside
Grand total	***	***	Farotop = faro = outside > inside

ever, after adjusting for the high number of correlations calculated, only *Acanthurus lineatus* ($r = -0.37$, $p < 0.01$), *A. luecosternon* ($r = -0.32$, $p < 0.05$), and *Ctenochaetus striatus* ($r = -0.49$, $p < 0.001$) remained significant. Figure 4 shows that *A. lineatus* was rarely observed in water greater than 3 m deep, while *A. luecosternon* density decreased gradually with increasing depth. The two most abundant *Ctenochaetus* species, *striatus* and *strigosus*, appear to have opposite distributions related to depth. *Ctenochaetus striatus* was most abundant in shallow water, < 3 m depth, with a secondary rise in abundance after 12 m depth. The opposite pattern was observed for *C. strigosus*; the species showed increasing abundance to 12 m depth, then a decrease thereafter. The remaining five species all showed peak densities at 6 m. Thereafter, *Scarus niger* and TP *S. sordidus* decreased in density until secondary peaks at 15 or 18 m depth. IP *S. sordidus* showed no consistent pattern with depth, while *Zebrasoma scopas* appeared to be equally abundant at depths greater than 3 m.

Herbivory processes

There was significant variation in the rates of herbivory among sites and habitat types in standardized *Thalassia* assays (Fig. 5A). Relative grazing rates were highest at the inside atoll rim reef slopes and lowest in areas subjected to heavy waves and surge (outside the atoll rim and faro reef flats). The two inside sites were statistically similar to each other (Dunn's test $p > 0.05$) as were the two outside sites. However, the two faros sampled were

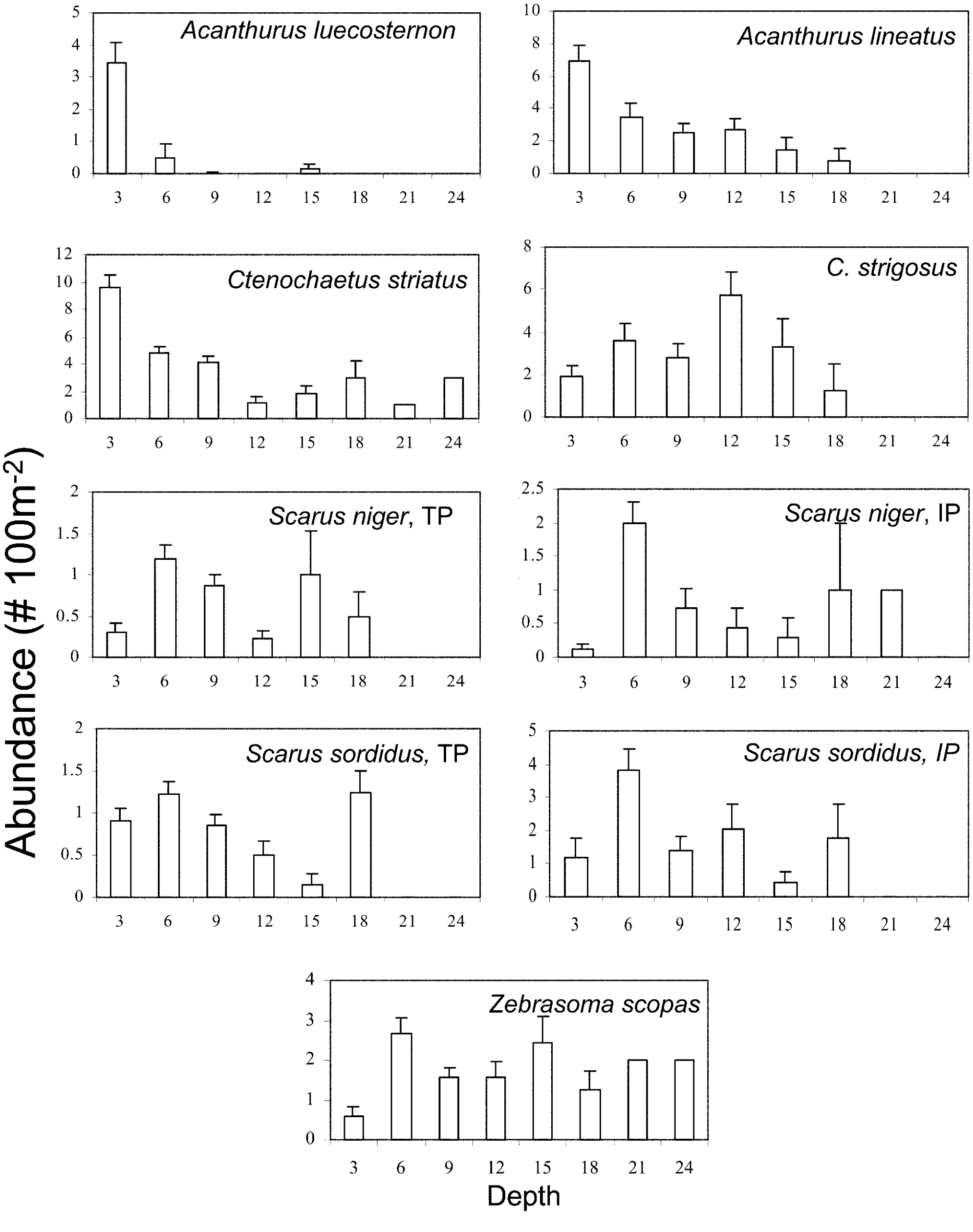

Fig. 4 Mean abundance (number of fish per transect) + 1 SE of the seven most abundant herbivorous fish species in 3-m-depth strata. Data are pooled for all habitat types and sites ($n = 160$ transects). Initial phase (*IP*) and terminal phase (*TP*) fish are presented separately for the two scarid species where they are readily discernible

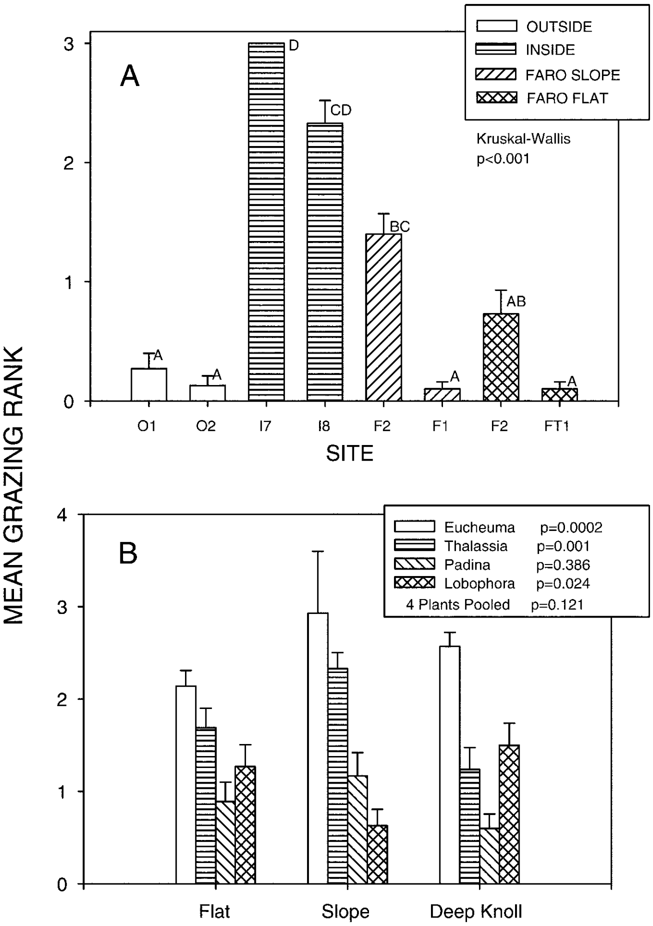

Fig. 5 Relative herbivory pressure at Laamu Atoll. *Bars* represent mean grazing rank score (+1 SE, see text). **A** Comparison among two sites of each of the four habitat types as measured by the *Thalassia* assay ($n=10$ ropes per site, three blades per rope). Standard error for site 3 was zero since all replicates had grazing rank $=3$. *Bars with the same letter* do not differ significantly ($p>0.05$) according to Dunn's pairwise post hoc comparisons. **B** Comparison of herbivore preference among four plant types in three depth zones at site I2. *P* Values from Kruskal-Wallis non-parametric ANOVA; $n=29$–30 for each plant type

substantially different from each other and obscured any similarity of relative herbivory by habitat types (faro slope versus faro flat).

The choice assay comparing herbivore preference among plant types in three depth zones (site I2) indicated significant selectivity of grazers (Fig. 5B), with the exotic *Eucheuma cottonii* experiencing the highest rates of consumption, *Thalassia* intermediate, and *Lobophora* and *Padina* experiencing similarly low consumption. Three of the four plant types displayed significant variation in susceptibility to herbivores among depth zones (Fig. 5B, Kruskal-Wallis non-parametric ANOVAs). Three species suffered highest consumption in the mid-depth slope habitat, the exception being *Lobophora* sp., which had the lowest proportion of blades consumed in the slope habitat compared to the other two habitats. Overall herbivory rates among the three depths at this site (four plant types pooled) did not differ significantly ($p=0.121$). The herbivorous fish assemblage at the reef slope and knoll sites (sites I2 and I3, Table 1) appears quite similar.

Discussion

Herbivorous fish assemblages

This article reports for the first time on the structure of herbivorous fish assemblages among coral reef habitat types in the Republic of Maldives. We show that certain species of fish were most abundant on a particular coral reef type. In this study, three types of coral reef slopes were examined as well as one type of reef flat. Herbivorous fish assemblages were more similar among sites within a particular coral reef type than among types; our study sites clustered into four groups which corresponded to the four coral reef types studied. Faro and inside atoll rim reef slopes were most similar to each other with respect to herbivorous fish composition and quite dissimilar to outside atoll rim reef slopes and faro reef flats. Clustering of sites among habitat types appeared to be mainly due to the differential distribution of acanthurids and scarids, the former being more abundant among faro reef flat and outside atoll rim reef slope sites and the latter more abundant among faro and inside atoll rim reef slopes. There are a number of possible explanations for this result. These include differences in algal preferences among families or species (Choat 1990), species interactions including territoriality (Robertson and Gaines 1986) and schooling patterns (Choat and Bellwood 1985), and differential habitat use (Jennings et al. 1996). The present study did not collect information on the abundance of preferred food items at study sites. However, the potential role of major differences among habitats such as depth and environmental gradients can be examined for their utility in explaining observed fish abundance patterns.

Depth distributions indicate that depth significantly influenced the abundance of the nine most abundant species. Several species were most abundant in depths less than 3 m, while others clearly showed peaks of abundance at 6 m. However, depth alone does not explain the similarity in assemblage structure among outer atoll rim reef slopes and faro reef flats as opposed to faro and inside atoll rim reef slopes. For example, *Acanthurus luecosternon* was significantly more abundant on outer atoll rim reef slopes and faro reef flats than faro and inner atoll rim reef slopes (Appendix 1; see electronic supplementary material). Yet, the mean depth of sites (±1 SE) outside the atoll rim was 9.0 (0.7) and in faro reef flats 1.2 (0.1). Also, there was no significant difference in the average depth of sites in the three reef slope habitat types (Tukey HSD multiple comparison test, $p>0.05$). Similarly, *Ctenochaetus strigosus* were more abundant on outer rather than inner atoll rim reef slopes (Appendix 1; see electronic supplementary material).

Yet there is essentially no difference in the average depth of these sites (9.0 versus 9.1 m depth).

While it is not possible to examine the abundance of species relative to the distribution of their preferred prey items, we can examine some of the general characteristics of these habitats which might influence the observed distribution patterns. Clearly, faro reef flats and outer atoll rim reef slopes share very few characteristics. However, one important feature they both share is that they are subjected to intense wave action, whereas the other two reef slope types are generally more protected. Faro reef tops are shallow, averaging only 1.2 m depth. During our sampling season (the SW monsoon) these sites are subjected to heavy waves. Similarly, outer atoll rim reef slopes bear the brunt of oceanic waves travelling across the Indian Ocean. At times, surge can be felt down to 20 m (R. Sluka, personal observation). This result is similar to data presented by Williams (1982) who showed that changes in the abundance and species composition of herbivorous fish assemblages on the Great Barrier Reef around Raine Island were related to the incident wave energy. Both inner atoll rim and faro reef slopes were similar in the structure and exposure to wave energy. These reef slopes appeared to be structurally more complex than outer atoll rim reef slopes, as evidenced by the height of corals relative to the slope and the amount of massive coral growth (R. Sluka, personal observation). Outer atoll rim reef slopes tended to be steep slopes with mostly plate coral growth forms and a greater abundance of the calcareous algae *Halimeda* spp.

In the current study, *Acanthurus lineatus* was mostly restricted to faro reef flats. This result is similar to Russ's (1984b) study on zonation patterns in the Great Barrier Reef. He studied five coral reef zones from the back reef to reef slope. In his study, *Acanthurus lineatus* was only found on the reef crest. This species was not found on the reef flats in his study. However, reef flats in Russ's study differed from the faro reef flats in this study in their wave exposure. Russ (1984a) describes his reef flat study sites as situated 75–150 m behind the windward reef crest. This would indicate that the waves broke on the crest and were substantially reduced by the time they reached the reef flat study area. In contrast, faro reef flat sites in the Maldives were situated within the circular faro reefs and were 20–50 m in diameter. During the SW monsoon (May–October), these faro reef flats experience considerable wave energy. Any wave action will produce surge on the reef flats, especially at low tide when the depth at these sites is reduced below 1 m. A similar pattern was found for *Acanthurus nigrofuscus* and *Ctenochaetus striatus*. In both this study and Russ's (1984b), these species were more abundant in coral reef zones subjected to greater wave exposure. Russ (1984b) also noted, similar to this study, that *Acanthurus nigrofuscus* was more abundant in the shallower zones. This study and that of Russ (1984b) also found that *Scarus niger* was more abundant in deeper than shallower zones.

The territorial microherbivores *Ctenochaetus striatus* and *C. strigosus* are known to mutually exclude each other from their respective territories, yet have broad overlap in habitat use (Robertson and Gaines 1986). However, in the Maldives, there appears to be a greater segregation by habitat and depth. *C. striatus* was least abundant on outer atoll rim reef slopes, while *C. strigosus* was most abundant in this habitat type. Figure 4 shows that these species were most abundant at different depths. The former species was most abundant in shallow depths (< 3 m) with a secondary peak at 18 m. *C. strigosus*, however, had a unimodal distribution almost opposite that of *C. striatus*; abundance peaked at 12 m depth. The reasons behind this greater segregation in the Maldives versus Aldabra, the Seychelles, are unknown, but one cause might be that these species competed more strongly at the Maldivian study sites.

There were very few differences in habitat use among initial and terminal phases of a particular parrotfish species. Of the 14 parrotfish species, only four exhibited differential habitat use. There did not appear to be any pattern among phases or species.

Herbivory processes

Significant variation in relative herbivory pressure among reef zones as measured by the *Thalassia* bioassay and the choice assay is consistent with the results of Hay (1984) at two sites in the Seychelles. His study found highest herbivory pressure in reef slope habitats as compared with reef flats and deep sand plains, a pattern similar to that on Caribbean reefs. The current study also showed highest consumption of three out of four plant types in reef slope zones, compared with adjacent depth zones (Fig. 5B).

Among habitat types, low *Thalassia* consumption pressure was observed at the outside atoll reef slope habitat type and at one of the two faro sites (both faro slope and faro flat habitat types). High wave energy may explain the low consumption rate in the outside reef slope habitat type. The substantial difference in herbivory pressure between the two faro sites sampled may result from divergent ecological history. Many faros in Laamu Atoll, especially those closest to the atoll villages, were previously mined for building material (Sluka and Miller 1998). The specific history of the two faros sampled is not documented, however.

Interestingly, the highest relative consumption in the *Thalassia* assay was at the inside atoll rim habitat type, where total herbivorous fish density was lower than the other sampled habitats. One factor that may result in discrepancies between herbivore density and consumption rate has to do with the sizes of the individual fish. Harmelin-Vivien (1984) reports similar densities of scarids and acanthurids in lagoonal and outer atoll reefs at Tikehau Atoll in French Polynesia. However, because large adults were more prevalent on the outer reefs, and juveniles more abundant in lagoonal habitats, the areal biomass of herbivorous fishes was greater on the outer slope than the lagoonal reefs. Acanthurids are also reported as the predominant herbivorous fishes on the outer reef slopes.

Lastly, it is known that *Thalassia* assays primarily indicate consumption by Scaridae (McClanahan et al. 1994). In fact, density of Scaridae across habitat types shows a more congruent pattern with consumption in the *Thalassia* assay than does total herbivorous fish density (Figs. 2 and 5A). Acanthurid density was higher than scarid density in each habitat type sampled in the current Laamu Atoll study, contrasting with herbivorous fish assemblages reported in the Caribbean where scarids often dominate acanthurids in both density and diversity (Schmitt 1997 ; Schmitt et al. 2001). Hence, *Thalassia* assays may be a less useful indicator of overall herbivory processes in the Indian Ocean than in the Caribbean.

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