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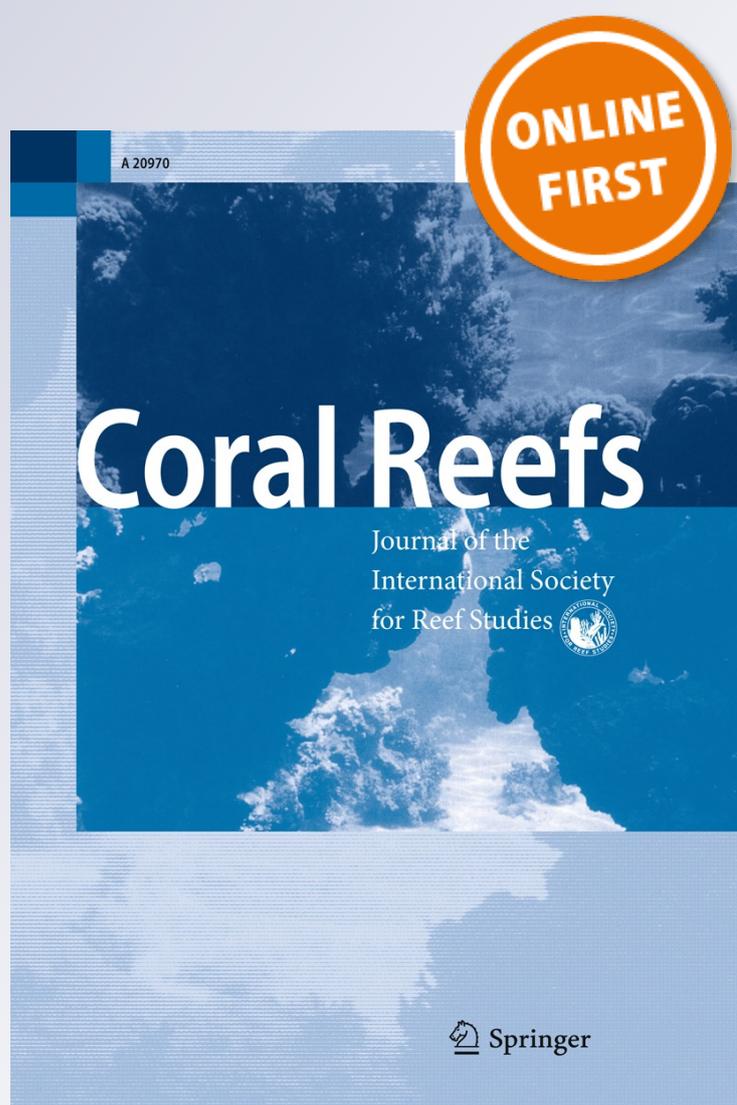
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Seasonally changing habitat use patterns among roving herbivorous fishes in the southern Red Sea: the role of temperature and algal community structure

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Abstract Coral reefs are characterized by intense herbivory. Spatial patterns in herbivory—particularly along the depth gradient—influence the distribution and abundance of algae. Depth gradients in herbivorous reef fishes are generally assumed to be temporally stable, but this assumption has rarely been questioned. Here, we use underwater visual census and herbivore exclusion experiments to study the community composition and temporal patterns in habitat use by roving herbivorous fishes in an environment characterized by profound seasonal changes in algal biomass and distribution and extreme summer temperatures. Among the 18 species of roving herbivores recorded, parrotfishes were dominant in species richness and biomass, while regional endemic species represented 77 % of the total biomass. During most of the year, roving herbivores aggregate in the shallow reef zones and their biomass declines with depth. The herbivore community on the reef flat is distinct from that in deeper zones. The former is characterized by *Siganus rivulatus*, *Acanthurus gahhm* and *Hipposcarus harid*, while the deeper reef zones are

characterized by *S. ferrugineus*, *Chlorurus sordidus* and *Ctenochaetus striatus*. In summer, the distinct community structures among reef zones are lost as reef flat herbivores tend to exploit deeper reef zones and some reef crest species venture on to the reef flat. This summer change in herbivore distribution is also reflected in reduced turf biomass and increased yield to herbivores in the deeper reef zones. Habitat use is related to the feeding mode such that browsers dominate the reef flat and scrapers the reef crest, while the seasonal changes correspond to changes in availability of targeted algal resources. These seasonal changes appear to be driven by the extreme temperatures in summer, reaching 36 °C on the shallow reef flat.

Keywords Grazing · Habitat use · Seasonality · Macroalgae · Endemic · Browsers

Introduction

Herbivory is an important force structuring benthic communities of coral reefs (Steneck 1988). Herbivores mediate the competition between corals and algae by causing favorable conditions for coral recruitment and growth (e.g., Mumby et al. 2007), prevent excessive growth of macroalgae (e.g., Hughes et al. 2007) and may facilitate reversal of benthic communities into a coral dominated state (e.g., Bellwood et al. 2006). Maintenance of high herbivore diversity is considered to augment the resilience of coral reefs to disturbance (Bellwood et al. 2004; Burkepile and Hay 2008). This is in part due to the diversity in feeding mechanisms of reef herbivores (Choat 1991) with varying impact on the benthos (Hixon and Brostoff 1996; Burkepile and Hay 2010). Moreover, some key ecosystem functions such as macroalgal consumption or bioerosion may be

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covered by only one or few species (Bellwood et al. 2003; Hoey and Bellwood 2009).

Difference in habitat use between reef herbivores may cause marked variation in grazing pressure among coral reef habitats. Species-specific preferences for certain reef zones appear to be common on coral reefs, and the patterns are influenced by numerous factors including food choice, interference competition, predation and hydrodynamics (Robertson and Gaines 1986; Fox and Bellwood 2007). Whatever the drivers, the vertical zonation of herbivores is known to influence the distribution of benthic algae on coral reefs (Hay 1981; Fox and Bellwood 2007).

Seasonal changes in vertical distribution and community structure of fishes are ubiquitous in temperate rocky shores and reefs (Ebeling and Hixon 1991; Zander et al. 1999). Temporal stability of habitat use patterns in tropical reef fishes is often assumed (Russ 1984b; Letourneur 1996), but has rarely been tested. Seasonal changes in habitat use and community structure of tropical reef fishes may be prevalent on coral reefs which experience significant seasonality. Indeed, many coral reefs are influenced by monsoons or upwelling which cause variations in environmental conditions that drive dramatic changes in composition and abundance of benthic algae (Diaz-Pulido and Garzon-Ferreira 2002; Ateweberhan et al. 2006a). The effect of these seasonal variations on fish populations and in particular on the habitat use of herbivorous fishes has not been studied.

The highly seasonal environment of the southern Red Sea (Sheppard et al. 1992) is suitable to investigate the effects of changing conditions on coral reef ecological processes. In this region, shallow reef zones are characterized in the cool season (November–April) by high cover and biomass of canopy-forming and foliose macroalgae, whereas the hot season (May–October) algal turfs dominate (Ateweberhan et al. 2006a). Ateweberhan et al. (2006a) reported increases in turf algae biomass in summer on the shallow reef flats but concomitant decreases in the deeper reef zones. These authors hypothesized that grazing activity partly shifts from shallow to deeper zones during the hottest months. They attributed this to the movement of reef flat herbivores to the deeper reef zones, possibly driven by high temperatures and/or increased predation risk due to reduced habitat complexity in summer. In this study, we use visual census and herbivore exclusion experiments to describe the community structure and patterns of habitat use by roving herbivorous fishes and to test whether these vary seasonally.

Materials and methods

Study site and environmental setting

The study was conducted between July 2006 and May 2008 on the fringing reef of Sheikh Said Island near Massawa,

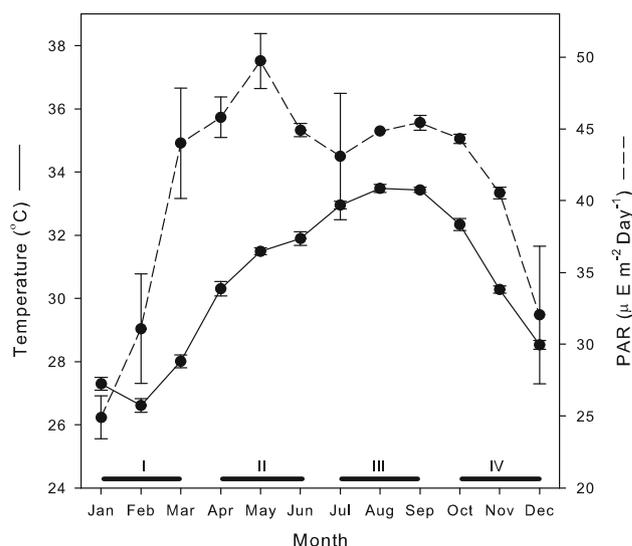


Fig. 1 Sheikh Said Island southern Red Sea, Eritrea: mean monthly water temperature and surface irradiance. Fish counting periods are indicated in *roman numerals*

Eritrea (15°35'N; 39°29'E) (see map in the Electronic Supplementary Material, ESM Fig. S1). This 1- to 10-m-deep reef has a gently sloping profile and a 30- to 45-m-wide coral growth zone. Four reef zones were identified based on the topography and the composition of benthic communities: the reef flat (0–1 m), the reef crest (0–2 m), the shallow fore reef (2–6 m) and the deep fore reef (6–10 m). For detailed description of the substrate and biotic communities of the zones see Ateweberhan et al. (2006a) and Afeworki et al. (2011).

Field measurement of sea surface temperature and surface irradiance at the study site (see ESM for details) indicates significant seasonal changes in both parameters (Fig. 1). The mean monthly water temperature (at 2 m depth) ranges from 27.7 °C in January to 33.4 °C in September (Ateweberhan et al. 2006a) with summer temperatures regularly exceeding 36 °C on the reef flat (Ateweberhan et al. 2005). Tides are semidiurnal with a mean amplitude of 0.7 m.

Turf biomass and yield to herbivores

Turf algae biomass and yield to herbivores were assessed on the reef crest, the shallow fore reef and the deep fore reef zones every 2–3 months from September 2007 to April 2008. Horizontal surfaces of the dominant dead coral substrates were selected, that is, dead *Porites* colonies on the reef crest and shallow fore reef and dead *Echinopora* colonies on the deep fore reef (Afeworki et al. 2011). At least four such large dead coral substrates covered by turf algae (100 % cover) were selected haphazardly for each month \times zone combination. Small (10 \times 10 \times 3 cm) cages of galvanized mesh wire (mesh size 1 cm) were used

to exclude a small part of each dead coral (<20 % of the total surface) from grazing by roving herbivorous fishes, while substrates outside cages remained accessible to such herbivores. Sea urchins are rare on the study site, and their grazing impact is assumed to be minimal. At the end of 3–6 days, pieces of substrate from inside and outside the cages were chiselled off, placed in separate plastic bags and kept chilled during transport to the lab. Turfs were carefully removed using a scalpel, taking care not to include substrate bound endolithic or crustose coralline algae. A piece of aluminum foil of known areal density was modelled over the substrate and carefully trimmed to match the irregular edges of the substrate sample. The surface area was then estimated by dividing the mass of the piece by the mass per unit area of the aluminum foil. To determine the ash-free dry mass (AFDM), samples were dried at 60 °C and ashed at 550 °C in a muffle furnace for 8.5 h.

Previous studies have demonstrated that the effects of caging on the biomass and species composition of turf algae, on irradiance and on water flow are negligible (e.g., Hixon and Brostoff 1985; Smith et al. 2001; Vermeij et al. 2010). Therefore, and given the short duration of the experiments, cage controls were not used in the present study.

Density and biomass of roving herbivorous fishes

Species-level visual censuses of the roving herbivores from the families Acanthuridae (surgeonfishes), Kyphosidae (rudderfishes), Labridae (parrotfishes) and Siganidae (rabbitfishes) were conducted along belt transects by snorkelling on the reef flat and reef crest and by using SCUBA in the shallow fore reef and deep fore reef zones. In each zone, six replicate 30 × 5 m transects were haphazardly laid out and their positions permanently marked using metal stakes hammered into the substrate. Individual fishes were identified and placed in 5 cm size categories. Estimation of fish size was practiced outside the study area using PVC pipes of various lengths and by spearing fish whose size was estimated underwater beforehand. Mean error and precision in length estimation were 0.51 and 2.5 cm, respectively. Seasonal effects were investigated by conducting censuses during each of four periods: January to March (I), April to June (II), July to September (III) and October to December (IV) (Fig. 1). All censuses were conducted by the same observer (Y.A.) between 10,00 and 16,00 h at high tide, to minimize variation associated with tidal movements of fishes (ESM Table S6, Figs. S4 and S5). Fish densities were converted into biomass using length–weight relationships (ESM Table S1) taking the midpoint of each size class.

Based on feeding preferences, roving herbivores are classified into scrapers (small excavators), macroalgal

browsers and grazers (Green and Bellwood 2009). Specifically, *Kyphosus vaigiensis*, *Siganus luridus* and *S. rivulatus* are identified as macroalgal browsers, *Acanthurus gahhm*, *A. sohal*, *Ctenochaetus striatus* and *Siganus stellatus* as grazers and *Hipposcarus harid*, *S. collana*, *S. ferrugineus* and *Chlorurus sordidus* as scrapers.

Data analysis

Variation in biomass and yield of turf algae biomass were examined among zones and seasons using ANOVA and untransformed data. Variation in total density/biomass of all roving herbivores and that of the individual species was tested by a repeated-measures ANOVA (RMA) taking zone as a between subject factor and period as repeated measure. For all the parametric tests, normality of data was tested with the Kolmogorov–Smirnov goodness-of-fit test and equality of variances using the Levene's test. Fish density data were log transformed, and biomass data were square root transformed to fulfill the assumptions of parametric tests. Assumption of sphericity was tested by Mauchly's sphericity test, and the Greenhouse-Geisser correction was applied when that assumption was violated. Multiple comparisons between zones were tested using Tukey's honestly significant test.

Differences in community structure of roving herbivores among zones were tested using permutation-based analyses of similarity (ANOSIM) on Bray-Curtis similarities between square root transformed biomass values. Among-zone variation in the composition of species and functional groups was further investigated by principal components analysis (PCA) of the square root transformed biomass data. The effect of the repeated measure, period and its interaction with zone was assessed using second-stage community analysis (Clarke et al. 2006).

Results

Turf biomass and yield

Biomass of turf algae and yield to herbivores varied among reef zones and with time of year and showed significant zone × month interaction (Fig. 2, ESM Table S2). On the reef crest, turf biomass remained the same except for a slight decrease in September. On the shallow fore reef, biomass of turfs declined gradually from the cool to the hot season, with the lowest biomass in September. On the deep fore reef, turf biomass remained high throughout the year except during September when there was a sharp drop. Overall, yield was highest on the reef crest and lowest on the deep fore reef, but this varied among periods. While yield on the reef crest remained high in all months, it increased from lowest values

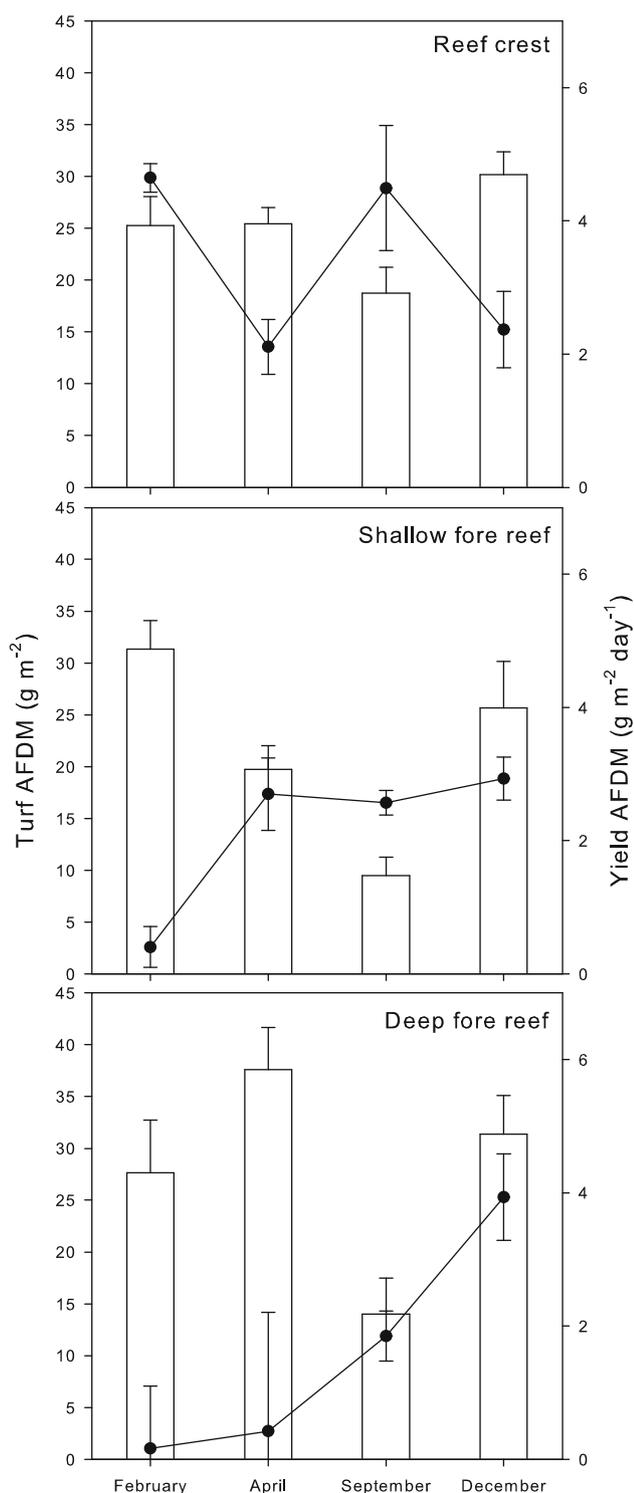


Fig. 2 Spatial and temporal patterns in turf algae biomass and yield to herbivores at Sheikh Said Island, southern Red Sea, Eritrea. Bars are mean \pm SE of turf biomass, Dots are mean \pm SE of yield to roving herbivores

in February to higher yields during the warmer parts of the year in the two deeper zones. Overall, yields were highest in September and December.

Spatial and temporal variation of total abundance of roving herbivores

A total of 18 species of roving herbivores were encountered in the course of the study, comprising 9 parrotfishes, 3 rabbitfishes, 5 surgeonfishes and one rudderfish (ESM Table S3). Six of these were rare and are not considered further (ESM Table S3). Among the 12 common species, five are endemic to the Red Sea and the Arabian Sea: *A. gahhm*, *A. sohal*, *S. ferrugineus*, *S. collana* and *S. rivulatus*. Together, these regional endemics represent 77 % of total roving herbivore biomass (Fig. 3). Averaged over all zones, the two dominant roving herbivores on this fringing reef are *S. ferrugineus* and *S. rivulatus*, representing, respectively, 34 and 23 % of the total biomass (Fig. 3, ESM Table S3). Among the four families investigated, parrotfishes were the dominant group both in terms of species richness and biomass representing 51 % of the total reef wide roving herbivore biomass (ESM Table S3).

Roving herbivores had a non-uniform distribution across the four reef zones, and their distribution among zones varied with period (significant period \times zone interaction) (Fig. 4, ESM Table S4.). Total herbivore density ranged from a maximum of $15,267 \pm 3,416$ ind. ha⁻¹ on the reef flat to a minimum of 433 ± 261 ind. ha⁻¹ on the deep fore reef. The corresponding values for biomass were $1,479 \pm 728$ kg ha⁻¹ on the reef flat and 77 ± 62 kg ha⁻¹ on the deep fore reef. Overall, total density and biomass were highest in the two shallowest zones, intermediate on the shallow fore reef and lowest on the deep fore reef. Although the density of roving herbivores was lower on the reef crest than on the reef flat, the biomass was similar in both zones due to the fact that the reef crest supported larger bodied fishes than the reef flat.

For each period, a post hoc test for zone was conducted to interpret the period*zone interaction term. Distribution of roving herbivores among zones remained the same throughout the year except during the hot July to September period when the shallow fore reef supported similar herbivore density and biomass as the two shallowest zones (Fig. 4). In all periods, the deep fore reef supported the lowest number of herbivores except during the cool January to March period when total density equals that on the shallow fore reef. In summary, roving herbivores aggregate in the two shallowest zones (reef flat and reef crest) except during the hottest months when the shallow fore reef supports similar abundance as the two shallower zones.

Roving herbivorous fish communities and their seasonal changes

Numerically, browsers were the dominant group, accounting for 56 % of the total count, followed by

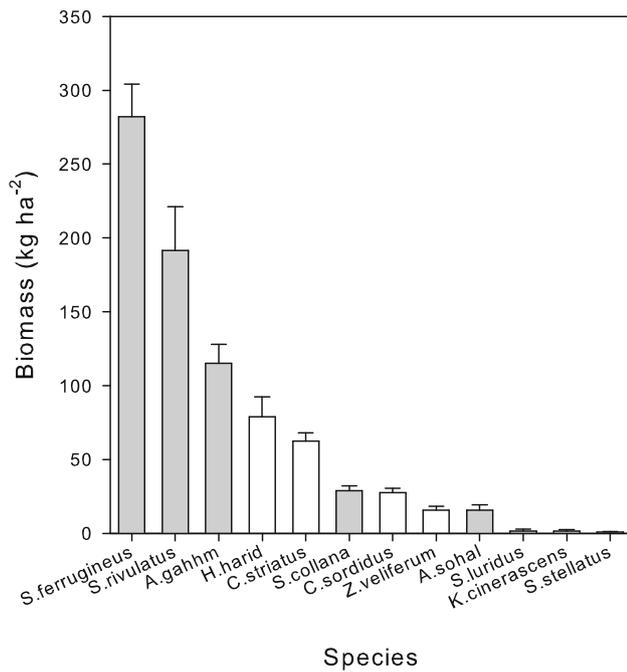


Fig. 3 Regional endemics dominating roving herbivore biomass at the fringing reef of Sheikh Said Island, Eritrea. Bars represent mean biomass (\pm SE) averaged over four reef zones and four periods. Gray bars regionally endemic species; open bars widespread species

scrapers (30 %) and grazers (14 %). In terms of biomass, scrapers were dominant, representing 51 % of total biomass, twice as much as browsers (24 %) and grazers (25 %).

RMA tests of all the investigated species showed that their abundance varied significantly among zones (Fig. 5) (ESM Table S5). This was reflected in the community composition of roving herbivores which differed significantly between zones (ANOSIM: Global $R = 0.615$, $P = 0.001$). Also, PCA showed clear among-zone differences in the composition of species and functional groups (Fig. 6). The first two axes explained 85.2 % and 93.5 % of the variation for the analysis based on species and functional groups, respectively. Along the first principal axis, the reef flat was distinct from the other reef zones being characterized by *S. rivulatus*, *H. harid*, *A. gahhm* and *S. collana* (Fig. 6a). Along the second principal axis, the high biomass of scrapers (mainly *S. ferrugineus*) and to a lesser extent that of grazers (mainly *C. striatus*) differentiated the reef crest from the reef flat and deeper zones (Fig. 6a). The reef flat was positively associated with browsing due to the high biomass of *S. rivulatus* (Fig. 6b) and the reef crest with scrapers and grazers.

Seasonal change in habitat use is reflected in the MDS plots which indicate that the herbivore community of the reef flat remains distinct for much of the year except during the hottest months from July to September when the

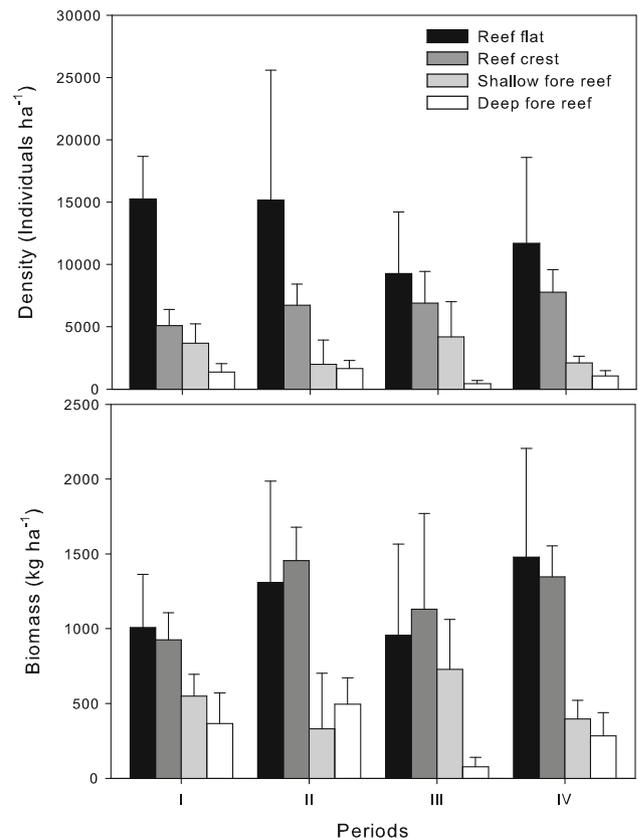


Fig. 4 Total roving herbivore density and biomass in four reef zones during four periods at Sheikh Said Island, southern Red Sea, Eritrea. I: January–March; II: April–June; III: July–September; IV: October–December. Bars indicate means and their 95 % confidence interval

community structure of the reef flat becomes similar to that of the reef crest and shallow fore reef (Fig. 7). Cluster analysis based on the second-stage similarity matrix (derived from the similarity matrices of the four periods) confirms the above results: species distribution among the four reef zones during July to September is most dissimilar from species distributions during the other times of year (Fig. 7). Six species were responsible for this seasonal change in habitat use as indicated by the significant zone \times period interaction in the RMA (Fig. 6, ESM Table S5). These were *A. gahhm*, *C. striatus*, *C. sordidus*, *S. collana*, and *S. ferrugineus*.

Discussion

Regional comparisons of herbivore community structures

The roving herbivore community of the fringing reef of Sheikh Said Island is strikingly different from those in the northern Red Sea. There, browsing rabbitfishes represent

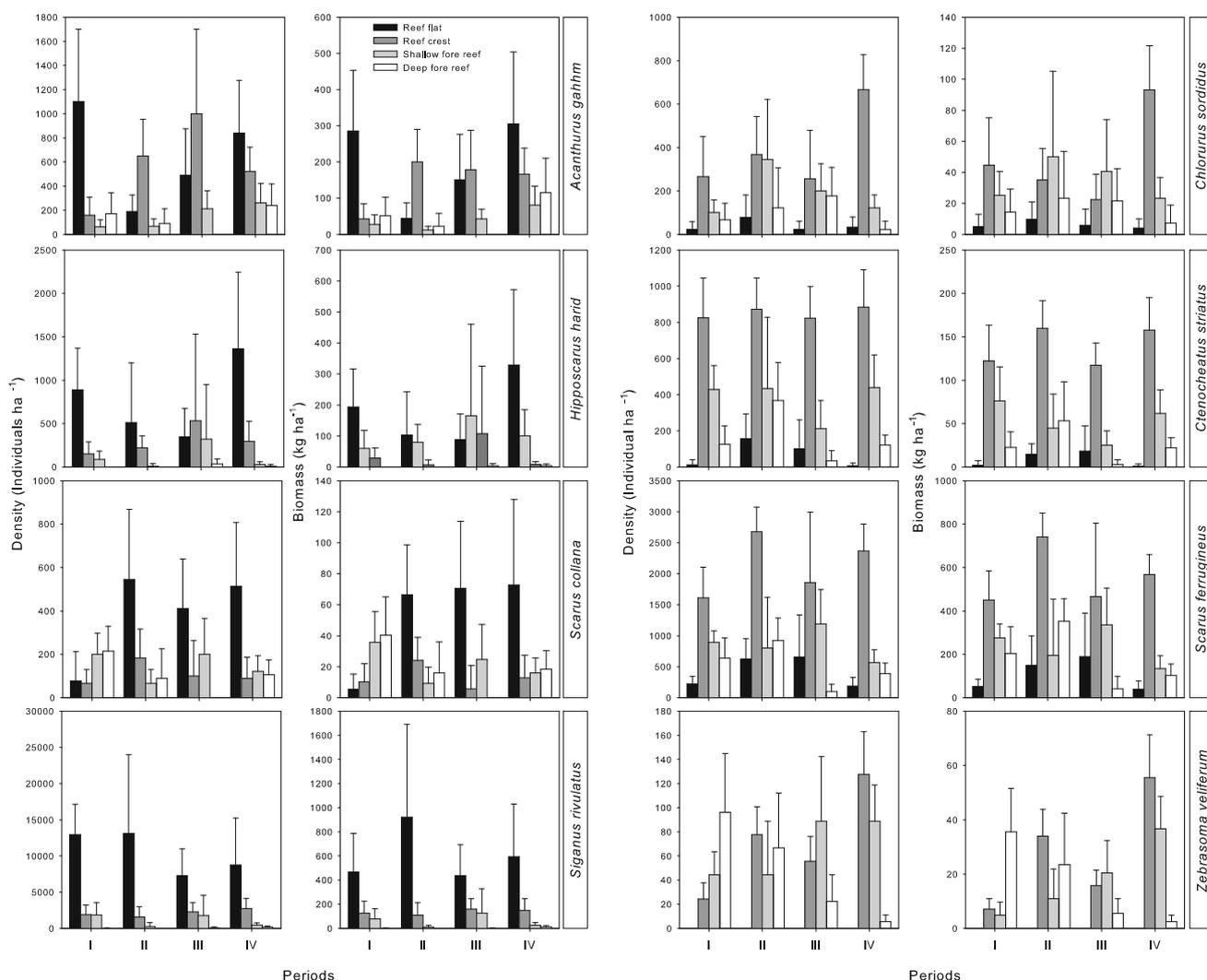


Fig. 5 Roving herbivorous fishes of Sheikh Said Island, southern Red Sea, Eritrea. Seasonal patterns in the distribution of biomass and abundance among four reef zones. *Left-hand panels* show roving herbivores that are dominant on the reef flat; *right-hand panels*

represent those that have highest abundance on the reef crest. I: January–March; II: April–June; III: July–September; IV: October–December. *Bars* represent mean values and 95 % confidence interval

<2 % of all roving herbivores, excavating parrotfishes are well represented both in terms of diversity and abundance and reef flats are dominated by grazing/detritivorous surgeonfishes such as *Acanthurus nigrofuscus* and *A. sohal* (Bouchon-Navaro and Harmelin-Vivien 1981; Alwany et al. 2009; Brokovich et al. 2010). In contrast, our study site in the southern Red Sea supports large populations of the browsing *S. rivulatus*, scraping parrotfishes *S. ferrugineus*, *S. collana* and *H. harid* dominate herbivore biomass, and there is a high abundance of the grazing surgeonfishes *A. gahhm* and *C. striatus*. Large excavating parrotfishes are absent. This may be typical of the southern Red Sea, as similar patterns of community composition were observed on the fringing reefs in the Gulf of Zula, located 80 km to the south of the present study site (Y.A. pers obs).

Siganus rivulatus feeds primarily on erect macroalgae (Lundberg and Lipkin 1979) and is known to cause seasonal reduction in macroalgal biomass (Ateweberhan et al. 2006a; Sala et al. 2011). The high abundance of this species appears to be associated with the availability of extensive macroalgal beds in the southern Red Sea (Sheppard et al. 1992; Turak et al. 2007). These macroalgal beds experience massive seasonal shedding that enriches the detrital pool (Ateweberhan et al. 2005, 2006a, b). Since a substantial proportion of the food that scrapers and grazers ingest is detritus (Choat et al. 2002, 2004), the large biomasses of these functional groups recorded here may be associated with the increased availability of detritus. These findings suggest different trophic structures on coral reefs in the southern and northern Red Sea, particularly regarding the importance of browsing and detritivory.

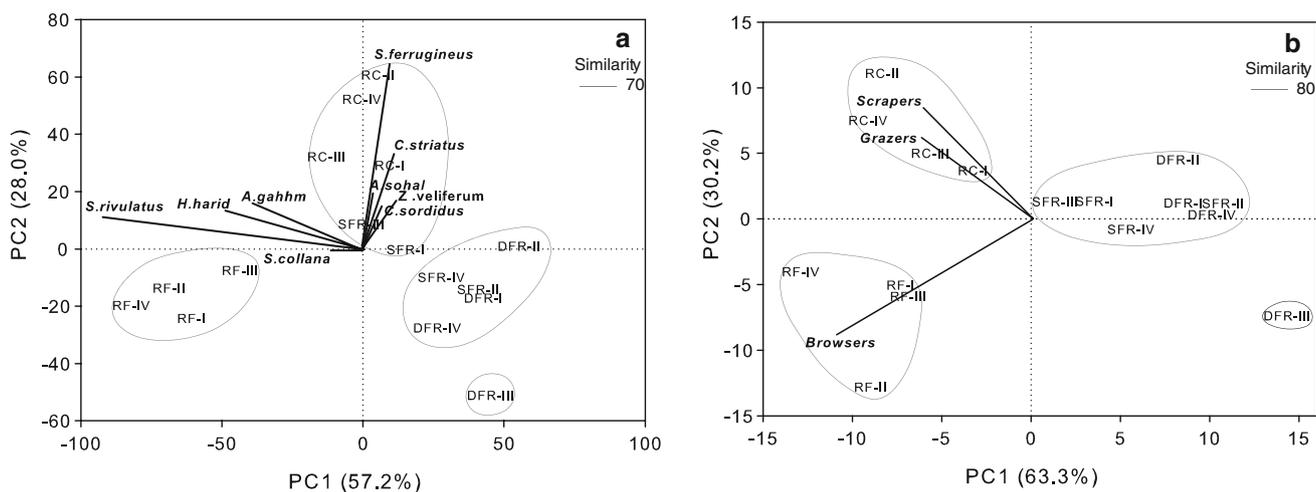


Fig. 6 Roving herbivorous fishes of Sheikh Said Island, southern Red Sea, Eritrea. Principal components analysis showing the variation in the composition among four reef zones at the level of species (a) and of feeding functional groups (b). Vectors show the correlation of

species and/or functional group with the principal axes. *RF* reef flat, *RC* reef crest, *SFR* shallow fore reef, *DFR* deep fore reef. I: January–March; II: April–June; III: July–September; IV: October–December

The gradients in environmental conditions and herbivore communities along the south–north axis of the Red Sea are comparable to the inshore–offshore gradients of the GBR. The inshore reefs of the GBR, due to high turbidity, high nutrient levels and large macroalgal stands, are comparable to the southern Red Sea reefs, while the northern Red Sea reefs, having deeper waters, more developed and diverse coral taxa and low cover of macroalgae resemble those of the outer shelf reefs of the GBR (Roberts et al. 1992; Sheppard et al. 1992; Wismer et al. 2009; De'ath and Fabricius 2010). Reefs with abundant macroalgae support larger populations of browsers, grazers and scrapers (Williams and Hatcher 1983; Russ 1984a; Cheal et al. 2012) while excavating taxa are more diverse and abundant on the coral rich sites (Alwany et al. 2009; Hoey and Bellwood 2008). These resemblances suggest that herbivore communities may vary in a predictable manner depending on the environmental conditions and associated state of the benthic communities. For example, it is plausible that the relative abundance of excavators and scrapers may be influenced by the diversity and cover of scleractinian corals since excavators feed more on live corals than scraping taxa (Bellwood and Choat 1990; Francini et al. 2008; Alwany et al. 2009). Likewise browsers and detritivores will be expected to be abundant in the macroalgae dominated areas (Ferreira et al. 2004; Hoey et al. 2011) where high amounts of detrital matter are generated. The importance of variation in these food sources and their nutritional quality for shaping the community structure of roving herbivores has not been investigated (Clements et al. 2009). Clearly, more detailed studies are needed to understand the role of diet and availability of resources in shaping these communities.

Depth-related changes in herbivore abundance and composition

The decline in herbivore biomass and grazing intensity with depth is common to all coral reefs and appears to be associated with lower temperature, reduced algal productivity and increased predation risk in deeper waters (Hay et al. 1983; Russ 2003; Fox and Bellwood 2007; Brokovich et al. 2010). Lack of shelter and presence of large predators in deeper waters could deter herbivores from foraging at deeper reef zones (Parrish and Boland 2004; Leichter et al. 2008). However, at our study site, topographic complexity of the deep fore reef zone is similar to that of the shallower zones and higher than that on the reef flat (ESM Fig. S2), yet this zone supports the lowest biomass of roving herbivores. It is therefore unlikely that lack of shelter causes the depth gradient in herbivore abundance.

In contrast, both temperature and primary production are correlated with depth and both are known to influence grazing intensity (Cebrian and Lartigue 2004; Smith 2008). For the depth range covered in this study (0–10 m), a steep decline in algal productivity owing to the diminishing light levels can be expected (see Vine 1974; Hay 1981; Klumpp and Mckinnon 1992), while the associated drop in temperature will be small with a negligible effect on consumption rates (e.g., Brokovich et al. 2010). Hence, reduced algal productivity is likely the main driver of declining herbivore biomass with depth. The observation that the taxa that incorporate most living plant matter in their diet show the greatest decline in abundance with depth (Choat et al. 2004) underpins the role of primary productivity.

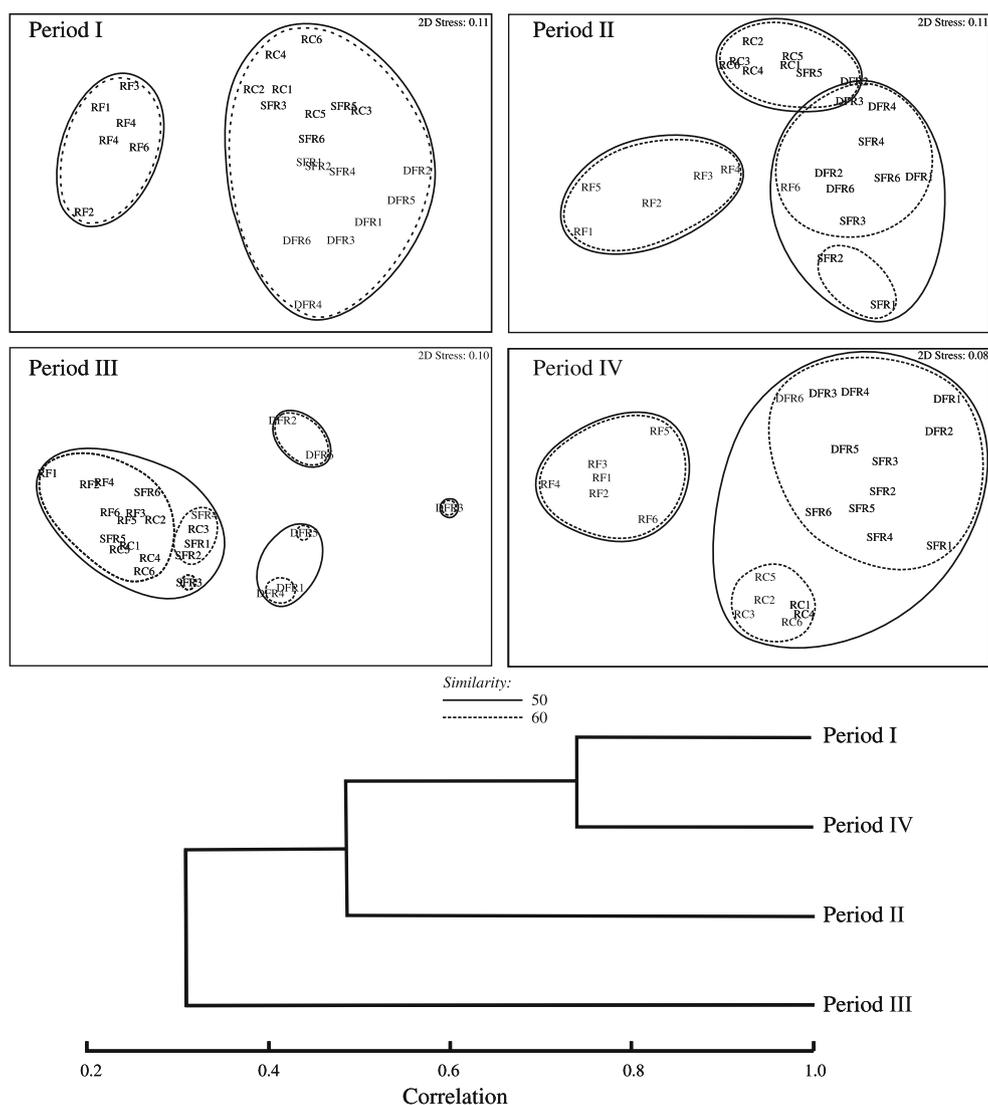


Fig. 7 Seasonal changes in the structure of the roving herbivore community among four reef zones at Sheikh Said Island, southern Red Sea, Eritrea. MDS plots based on first-stage similarity matrices are shown for each season. The cluster analysis is based on second-

stage similarity matrix. *RF* reef flat, *RC* reef crest, *SFR* shallow fore reef, *DFR* deep fore reef. Numbers indicate replicate transects at each zone. I: January–March; II: April–June; III: July–September; IV: October–December

Species interaction is unlikely to have contributed to community differences as all investigated taxa are non-territorial roving herbivores forming multispecies groups (with the exception of relatively uncommon *A. sohal*). It is also unlikely that differences in hydrodynamics between the reef flat and the reef crest drive community differences as the study site is located in a sheltered bay, and the area in general is known for its calm conditions.

The reef flat and reef crest zones do differ in the composition of benthic algae and in topographic complexity. The reef flat has the lowest topographic complexity and is dominated by erect foliose and canopy-forming macroalgae during the cool season (Ateweberhan et al. 2006a). The reef crest is largely dominated by crustose corallines, turf

algae and living corals (Ateweberhan et al. 2006a; Afeworki et al. 2011). A combination of feeding preferences and anti-predator adaptations appears to determine how these species use the reef zones.

Seasonal changes in habitat use patterns

We report significant seasonal changes in community structure of roving herbivorous fishes among depth zones. Our results differ from other findings where spatial patterns persist over time, implying stability in habitat use among reef fishes (Russ 1984b; Letourneur 1996; Brokovich et al. 2006). The discrepancy may be due to the highly seasonal nature of the southern Red Sea. Shallow reef flats in this

region experience extreme summer temperatures that effect dramatic changes in benthic community, alternating between a canopied state in the cool season to a turf-dominated flat expanse in summer (Ateweberhan et al. 2006a). In summer, scrapers and grazers can potentially benefit from the increased availability of this resource on the reef flat. Indeed, typical reef crest herbivores, that is, the detritivorous *C. striatus*, and the scrapers *C. sordidus* and *S. ferrugineus* slightly increased their abundance on the reef flat in summer. Interestingly, the scraper *S. collana* mainly forages on the reef flat for most of the year except during the cool season when its peak abundance shifted to deeper reef zones. This species apparently avoids the reef flat during the period of peak canopy development by macroalgae, possibly due to lack of food resources or due to the deterrent effect of dense macroalgal stands (Hoey and Bellwood 2011). Thus, the patterns of seasonal change in habitat use by these species appear to be correlated to their feeding modes.

It is notable that the reef crest species such as *S. ferrugineus* and *C. striatus* fail to respond to the seasonal increase in turf biomass on the reef flat. Previous studies have suggested that such patterns may be related to the lack of shelter and increased risk of predation on the reef flat (e.g., Randall 1965; Nemeth and Appeldoorn 2009; Verges et al. 2011). Interestingly, the roving herbivores that dominated the reef flat are schooling species with drab coloration, two characteristics that have been hypothesized to reduce predation risk (Montgomery et al. 1989; Borsa et al. 2007). Abundant resources on the one hand and predation risk on the other hand may represent a strong selective pressure for cryptic coloration and the tendency for schooling in species that frequent the topographically less complex portions of the reef. Indeed, this is considered the major cause in the radiation of two distinct life styles in the family Siganidae: the drab, fusiform reef flat frequenting species such as *S. rivulatus* and the more reef associated deep bodied and colorful ones such as *S. stellatus* (Borsa et al. 2007).

During summer, water temperatures on the reef flat of our study site regularly exceed 36 °C (Ateweberhan et al. 2005), values which are considered to be critical for resident coral reef fishes in other locations (Mora and Ospina 2001; Eme and Bennett 2009). It is possible that the observed seasonal change in habitat use patterns in roving herbivores may be related to these extreme temperatures and to species- or size-related differences in temperature tolerance. In summer, we recorded lowered turf biomass and increased yield to grazers in deeper zones. Previously, records have shown an opposite trend on the reef flat with higher accumulation of biomass of turfs and increased survivorship of primary laterals of macroalgae (Ateweberhan et al. 2005, 2006a). These observations suggest a transfer in grazing pressure from shallow to deeper reef

zones in summer that may partly be due to the extreme temperatures at the shallow reef zone. However, our census data only showed a negligible seasonal shift of roving herbivore biomass to the shallow fore reef in summer. The discrepancy between grazer impact and census suggests that a more frequent (monthly) and direct assessment of herbivore impact (such as by video) is needed. Moreover, assessment of temperature tolerance by roving herbivores is required to clarify the role of temperature. In any case, reduced herbivore impact on the reef flat during summer has the potential to provide reef flat macroalgae a refuge from grazing during part of the year, leading to recruitment success and/or lowered grazing-induced loss of primary laterals.

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