Biomass and Abundance of Herbivorous Fishes on Coral Reefs off Andavadoaka, Western Madagascar

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Abstract—The biomass and abundance of four herbivorous fish families were surveyed in the region of Andavadoaka, south-west Madagascar, investigating the effects of fishing intensity, reef geomorphology and benthic cover. Distance from the village was used as a proxy for fishing effort, with sites closest to the village assumed to have the highest fishing intensity. Both overall herbivore biomass and abundance increased with distance from shore (p=0.002, p<0.001), as well as with increased hard coral cover (p<0.001, p<0.001). Acanthurid biomass (p<0.001) and abundance (p<0.001) increased significantly with distance from the village, as did the abundance of Pomacentridae (p=0.001). Conversely, siganids decreased in biomass with increased distance from the village (p=0.019). Associations between herbivorous fish families and benthos were manifested in a significant (p<0.001) increase in acanthurid and pomacentrid biomass with increased hard coral cover. Sites with increased turf algae displayed lower scarid biomass (p=0.002) and abundance (p=0.032), while siganid abundance increased (p=0.002) as turf algae increased. Reef type has previously been suggested to be an important factor influencing fish biomass, however the results of this study suggest that this has little effect on herbivore biomass in the region. Benthic cover and fishing intensity appear to influence the biomass of herbivorous fish communities more on the reefs of Andavadoaka, highlighting the importance of Marine Protected Areas to protect both corals and fish.

INTRODUCTION

Coral reefs worldwide are declining in health, due largely to overharvesting (Jackson *et al.* 2001; Pandolfi *et al.* 2003), pollution (McCulloch *et al.* 2003), climate change (Wilkinson 2002; Hughes *et al.* 2003) and disease (Harvell *et al.* 1999, 2002). A phase shift from coral to fleshy algal dominance is most commonly observed (McClanahan *et al.* 2001; Graham *et al.* 2006), with early warning signs including a loss of macrofauna (Hughes 1994) and a decline in fish stocks (Bellwood *et al.* 2004). Herbivorous fishes are partly responsible for the maintenance of healthy coral reefs by influencing the structure of benthic communities (Hatcher 1981; Carpenter 1990).

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If grazing by reef fishes is reduced due to over-fishing, macroalgae can outcompete corals by colonising space and thereby inhibiting coral growth and recruitment (Hughes 1989; Tanner 1995; Knowlton 2001). Macroalgae also affect coral health indirectly by stimulating pathogenic microbes associated with corals, resulting in increased coral mortality (Kuntz *et al.* 2005). Herbivorous fishes play such a significant role in maintaining low macroalgal cover on reefs (Nystrom and Folke 2001; Bellwood *et al.* 2004) that they are considered a keystone guild in Indo-Pacific reef systems (Choat 1991). Grazing fishes are herbivores that prefer turf-forming, encrusting and endolithic algae over large upright macroalgae, which often have chemical defences (Bellwood and Choat 1990; Choat 1991; McAfee and Morgan 1996). Intensive grazing limits the establishment of macroalgae since newly settled algae are consumed before they can be distinguished from other algae and thus their establishment is prevented (Carpenter 1986; Lewis 1986).

Of the main grazing fish groups in Indo-Pacific coral reef systems, the families Acanthuridae (surgeonfish), Siganidae (rabbitfish) and Scaridae (parrotfish) are predominantly grazers, while the Pomacentridae (damselfish) include many grazing taxa. Acanthurids and scarids reduce algal growth (Bellwood *et al.* 2004, Mumby *et al.* 2006), and the latter also clear substratum for coral recruits by their excavating feeding activity (Bellwood *et al.* 2004). Grazing damselfish keep algae cropped and promote high algal diversity (Hixon and Brostoff 1996). Fished coral reefs have a higher abundance of fleshy algae, probably caused by a lower abundance of herbivorous fishes (McClanahan *et al.* 1996).

Whilst there have been numerous studies of herbivorous fish biomass and benthic cover on coral reefs, few have been conducted in Madagascar. Benthic communities and physical structure of the Grand Récif de Tulear were investigated in the 1960s and early 1970s (Mauge 1967; Pichon 1971; Harmelin-Vivien 1977, 1979). This barrier reef forms part of a larger coral reef system that stretches for over 450 km in the south-west of Madagascar. Few marine ecological studies have been undertaken in the intervening decades and little attention was given to Madagascar's south western reef system until the recent initiation of several marine conservation programmes in the region (Gillibrand *et al.* 2007; Nadon *et al.* 2007). Recent investigations in the region of Andavadoaka, some 200 km north of Toliara in south-west Madagascar, have revealed reef fish species richness and trophic pyramids that resemble other less impacted reefs in the western Indian Ocean region (Gillibrand *et al.* 2007). These findings suggest that reduced fishing pressure retains greater fish assemblage diversity, indicating that fishing pressure plays an important role in regulating species diversity and abundance on these reefs (Harris *et al.* 2010, Gillibrand *et al.* 2007, Nadon *et al.* 2007).

Nadon *et al.* (2007) also found that offshore patch reefs, subjected to lower fishing effort than nearshore fringing reefs, supported a higher abundance of fish and greater hard coral cover than other geomorphological reef types in the Andavadoaka region. In fact, the fish populations on these patch reefs were more abundant than those found in both protected and unprotected areas of Kenya and Tanzania, while the more impacted fringing and barrier reefs of Andavadoaka supported similar abundances to those found on comparable reefs in Kenya and Tanzania (McClanahan *et al.* 1999; Nadon *et al.* 2007). While fish abundance and diversity have been investigated in south-west Madagascar, few studies to date have focused on exploitation and habitat health on fish biomass. Newman *et al.* (2006) showed that increased fish biomass suppressed algal abundance; it is thus hypothesised that reefs with low fishing pressure have a higher herbivorous fish biomass and hard coral cover.

Marine protected areas (MPAs) have been developed worldwide in an effort to protect coral reef communities from anthropogenic pressures. Indeed, MPAs can be highly effective in protecting fish stocks, with a rapid rise in species richness post closure (Russ and Alcala 2004; McClananhan *et al.* 2007). Kenyan MPAs have recorded rapid increases in scarids

following closure of reefs to fishing, followed by a slower rise in acanthurids, and a shift in the benthic community towards an increasing dominance of calcifying algae with duration of closure (McClananhan *et al.* 2007). However, attainment of ecological states similar to those of unfished reefs takes considerable time, particularly on heavily impacted reefs where fishing continues adjacent to a protected area (Russ and Alcala 2004; Abesamis and Russ 2005; McClananhan *et al.* 2007). Since the protection of herbivorous fish appears vital to the health of coral reefs (Choat 1991; Polunin and Klumpp 1992), we investigated herbivorous fish biomass in the Andavadoaka region of south-west Madagascar relative to benthic cover, reef geomorphology and fishing pressure (measured as distance from the village). This provided ecological information on herbivorous fish communities relevant to the proposed protection and management of coral reefs in the area.

MATERIALS AND METHODS

Study Site

Andavadoaka village is situated on the south-west coast of Madagascar facing the Mozambique Channel (Fig. 1). The reefs of Andavadoaka comprise offshore barrier reef fragments, nearshore coastal fringing reefs and lagoonal patch reefs. A broken line of sand islands and cays form the boundary of an approximately 8 km wide lagoon, 10-30 m deep. The islands are characterised by a fringing barrier reef on their seaward side protecting the lagoon, within which are located a number of patch reefs at depths of 5-25 m. Coastal fringing reefs run adjacent to the coast on the shoreward side of the lagoon.

Andavadoaka and 23 surrounding villages collectively manage the Velondriake Locally-Managed Marine Area (LMMA), incorporating a network of protected coral reefs, seagrass beds and mangroves. Velondriake's aim is to protect the region's fisheries and ecosystems from increasing fishing pressure, driven by increases in the coastal population and a shift from subsistence to market-driven fisheries
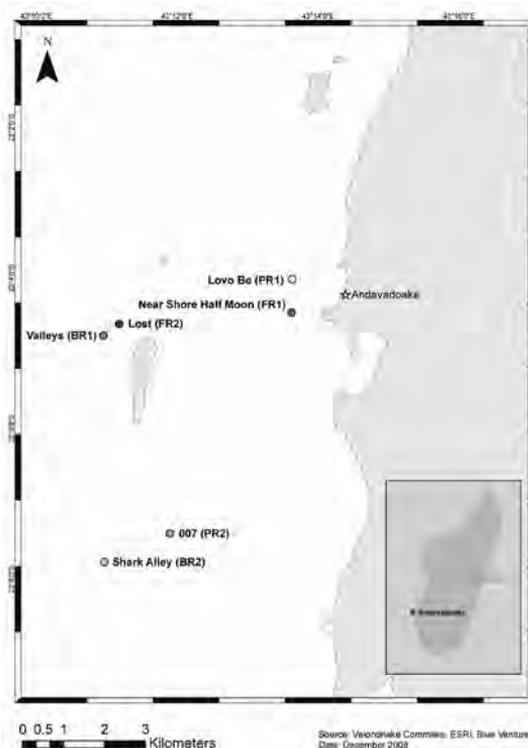
Figure 1. Map of study location with survey sites and the village of Andavadoaka. PR1 and PR2= patch reefs, FR1 and FR2 = nearshore fringing reefs, BR1 and BR2 = offshore (barrier) fringing reefs.

Assessing herbivorous fish biomass

The biomass of Acanthuridae, Pomacentridae, Siganidae and Scarinae was surveyed using SCUBA along ten replicate transects at six sites (Table 1). The six reef sites comprised three geomorphological reef types: patch reefs (PR1 & 2), nearshore fringing reefs (FR1 & 2), and offshore (barrier) fringing reefs (BR1 & 2) (Table 2, Fig. 1). Each transect was 20 m x 5 m and fish were counted up to 5 m above the reef. Transect length was limited to 20 m due to the small size of 'sausage-shaped' patch reefs in the area. Transects were placed randomly on the reefs at a depth of between 8 and 12 m. Fish were identified to family level, counted and their fork length was estimated (± 10 mm) visually. Surveyors were trained in length estimation using the fiddle-sticks technique (English *et al.* 1997). All species were identified in each target family with the exception of the family Acanthuridae; here only species classified as browsers, grazers or grazers/

detritivores were included in the study (Table 1) (Choat 1991, Choat and Clements 1998, Choat *et al.* 2002, Myer 1991, Robertson *et al.* 1979). While grazers/detritivores consume only a small amount of algae, many are abundant schooling species and, as such, consume significant amounts of turf algae (Choat 1991, Choat and Clements 1998, Choat *et al.* 2002, Myer 1991, Robertson *et al.* 1979, Sommer *et al.* 1996). Pomacentrids classified as mainly algal feeders were included in the survey (Table 1) (Frédérich *et al.* 2009). A three minute acclimatisation period was adhered to before commencing the survey to reduce disturbance from placement of the transect line. Counts were undertaken by swimming at a slow, constant speed along the transect line, recording all target fish observed.

Assessing benthic cover

Benthic cover was surveyed using linear Point Intercept Transects (PITs) conducted by SCUBA (English *et al.* 1997). A 10 m taught transect was laid out at a depth of 8 to 15

Table 1. Fish species observed and included in the study on Andavadoaka reefs, with their trophic category.

Family	Species	Trophic group	Source
Acanthuridae	*Acanthurus dussumieri*	Grazers/detritivores	Myer 1991
	Acanthurus leucosternon	Grazers/detritivores	Robertson *et al.* 1979
	Acanthurus nigricauda	Grazers/detritivores	Choat et al. 2002
	Acanthurus nigrofuscus	Grazers/detritivores	Myer 1991
	Naso brevirostris	Browsers	Choat & Clements 1998, Choat *et al.* 2002
	Naso lituratus	Browsers	Choat & Clements 1998
	Naso unicornis	Browsers	Choat 1991, Choat & Clements 1998, Choat *et al.* 2002
	Zebrasoma desjardinii	Grazers/detritivores	Choat 1991
	Zebrasoma scopas	Grazers/detritivores	Choat 1991, Choat *et al.* 2002, Robertson *et al.* 1979)
Pomacentridae	*Amphiprion akallopisos*	Grazers/detritivores	Frédérich *et al.* 2009
	Plectroglyphidodon lacrymatus	Grazers	Choat 1991, Frédérich *et al.* 2009
	Pomacenturs baenschi	Grazers/detritivores	Frédérich *et al.* 2009
Siganidae	*Siganus argenteus*	Grazers/detritivores	Choat 1991, Choat *et al.* 2002
	Siganus sutor	Grazers/detritivores	Choat 1991, Choat *et al.* 2003
Scaridae	*Cetoscarus bicolor*	Scrapers/small excavators	Bellwood and Choat 1990
	Scarus ghobban	Scrapers/small excavators	Bellwood and Choat 1990
	Scarus niger	Scrapers/small excavators	Bellwood and Choat 1990
	Scarus rubroriolaceus	Scrapers/small excavators	Bellwood and Choat 1990
	Scarus sordidus	Scrapers/small excavators	Sommer *et al.* 1996

Table 2. Reefs surveyed at Andavadoaka with information on reef type and number of point intercept transects per site.

Site name	Reef type	Site abbreviation	Number of benthic PITs
Nearshore Half Moon	Nearshore fringing reefs	FR1	9
Lost		FR2	6
Love Be	Patch reefs	PR1	3
007		PR2	10
Valleys	Offshore (barrier) fringing reefs	BR1	9
Shark Alley		BR2	10

m, continuous with the substratum. The benthic community or substratum underlying each 20 cm marker was recorded, yielding 50 points per 10 m transect. The number of replicate transects varied between 3 and 10 per site (Table 2). Mean cover of hard coral (HC), macroalgae (MA) and turf algae (TA) (thin algal filaments <1 cm long) were calculated per site (Fig. 2).

Analytical methods

Fish biomass values were calculated from length estimates using published length-weight conversions for each family (Table 3) (Kochzius 1997, Letoumeur 1998, Letoumeur *et al.* 1998, Murty 2002). These values were multiplied by the number of fish of each size, providing an estimate of total biomass (g.m^{-2}) per family for each transect. Mean biomass (± standard error) was calculated for each site in g.100 m^{-2} for each family.
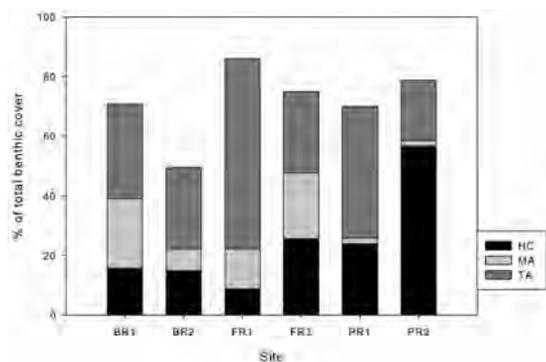
Figure 2. Hard coral, macroalgae and turf algae as a percentage of total benthic cover per site on the Andavadoaka reefs. FR1=Nearshore Half Moon, FR2=Lost, PR1=Lovo Be, PR2=007, BR1=Valleys, BR2=Shark Alley.

One-way ANOVA was performed per site for biomass of each family and total biomass (all families). ANOVA was also conducted on numerical density data (numbers of fish per m^2). Significant ANOVA results (p <0.05) were subjected to post-hoc analysis (Tukey Honestly Significant Difference with a family-wise error of 5%) to identify differences in mean biomass and mean abundance between sites. Kruskall-Wallis (KW) tests were used where the assumptions underpinning ANOVA analysis were not met, this being done when the residuals were highly skewed. Post-hoc analysis was not performed when differences were not significant.

Step-wise backward regression was used to assess the impact of the following variables on the biomass and abundance of each of the four fish families, and on their total biomass and total abundance: HC, MA, TA, the distance from Andavadoaka village in kilometres (DIST) and reef type. The regression model considers Reef Type 1(fringing reef) as baseline, with the coefficient of Reef Type 2 (patch reef) indicating the difference between reef types 1 and 2. Similarly the coefficient of Reef Type 3 (barrier reef) indicates the difference between reef types 3 and 1. The samples size for the regression models was 60. Minitab™ v.15 was used to perform all statistical analyses.

Fish community data were examined for patterns associated with site characteristics using two techniques. The

Table 3. Constants used to estimate biomass (M) from length (LT) for major families of grazing fish on Andavadoaka reefs according to the formula $M=aLT^b$.

Family	Species	a	b	Source
Acanthuridae	*Acanthurus fuscus*	0.0089	3.278	Letourneur, 1998
Pomacentridae	*Pomacentrus coelestis*	0.037	2.63	Kochzius, 1997
Scaridae	*Scarus ghobban*	0.0233	2.919	Murty, 2002
Siganidae	*Siganus fuscescens*	0.0162	3.01	Letourner *et al.*, 1998

six sites were assigned distance categories of Near (1.19 & 1.25 km), Medium (5.39 & 5.83 km) and Far (7 & 8.61 km) from dependent human communities and tested within a similarity matrix of sites based on Bray Curtis similarity measures of square root-transformed abundance and biomass data derived from one-way Analysis of Similarity using Primer v6 (Primer-E Ltd). Spearman's rank correlations were also determined between the above matrices and a matrix of normalized Euclidean distance similarity measures of the sites derived from distance from human community (km) data, hard coral cover (%), macroalgal cover (%) and turf algal cover (%) using the BIO-ENV procedure in Primer v6 .

RESULTS

Total herbivore biomass differed significantly between sites (ANOVA, $F_{site}(5,54) = 8.84$, p <0.001 and KW, $H_{site}(5) = 27.536$, p <0.001). PR2 was the most different, having a significantly higher herbivorous fish biomass than all the other sites (Fig. 3a, Table 4). PR2 also had a higher pomacentrid and acanthurid biomass (apart from BR2 in the latter case) than all the other sites.

The regression model revealed that the herbivorous fish biomass increased with increasing distance from the nearest village (p = 0.002) and with increasing percentage hard coral cover (p <0.001). Turf algae and macroalgal cover did not contribute significantly to observed patterns of variance in total biomass between sites.

The biomass of Acanthuridae (ANOVA, F(5,54) = 7.793, p <0.001) was significantly correlated with location, with PR2 exhibiting a higher acanthurid biomass than all survey sites apart from BR2 where no difference was observed (Fig. 3b). The biomass of each family was tested against the pre-determined factors, the significant factors being displayed in Table 5. Acanthurid biomass increased with increasing distance from shore (p = 0.001) and with percentage of hard coral cover (p < 0.001). Pomacentrid (ANOVA, $F_{site}(5,54) = 4.933$, p < 0.001 and KW, $H_{site}(5) = 13.723$, p = 0.017) biomass also manifested significant differences between sites, with PR2 having a significantly higher biomass than all other sites (Fig. 3c). The regression model revealed that pomacentrid biomass increased with increased percentage of hard coral cover (p < 0.001).

There were no differences in siganid and scarid biomass between sites (ANOVA, $F_{site}(5,54) = 1.294$, p = 0.280 and KW, $H_{site}(5) = 8.887$, p = 0.114, Fig. 3d; and ANOVA, $F_{site}(5,54) = 2.231$, p = 0.056, Fig. 3e respectively). However, the siganid biomass decreased with distance from the shore (p=0.019) and the scarid biomass (p = 0.002) decreased as the percentage cover of turf increased. One replicate at FR1 had a much higher biomass and abundance of siganids than any other site or replicate, and one replicate at BR1 had a much higher scarid biomass and abundance than any other site or replicate. When these abnormal values were included in the data-set they influenced the results, giving rise to inaccurate conclusions; these outliers were thus excluded from the analyses.

Total fish abundance varied between sites (ANOVA, $F_{site}(5,54) = 34.23$, p < 0.001). While there were differences between several sites (Table 4), PR2 displayed higher abundance than all other sites (Tukey HSD, all p values < 0.001 Fig. 3f). In contrast FR1 had a significantly lower herbivorous fish abundance than all sites apart from PR1. Acanthurid
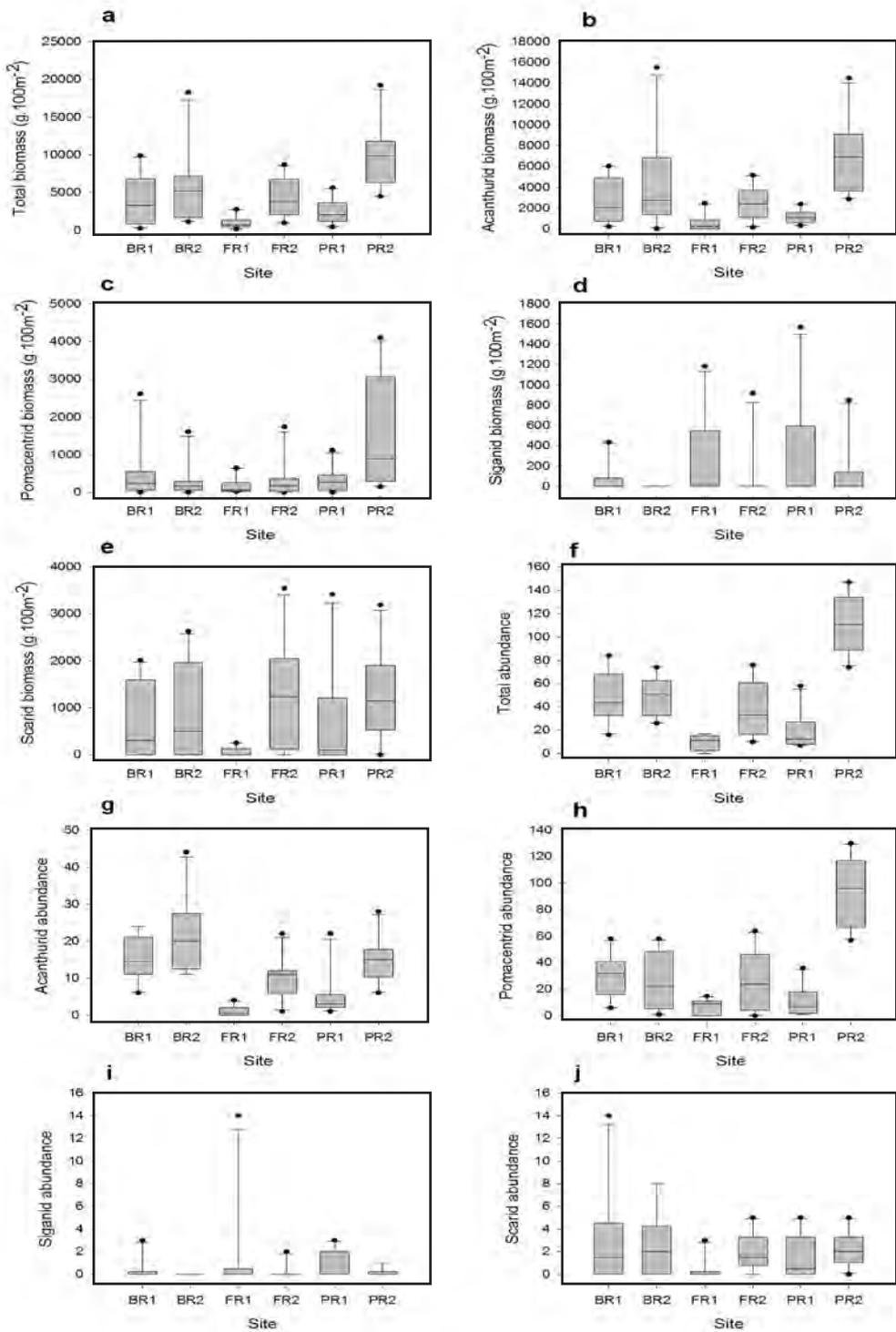
Figure 3. Box plots of biomass (a-e) (g.100 m^{-2}) and abundance (f-j) (individuals.100 m^{-2}) for each fish family on the Andavadoaka reefs. The data are ordered and split into quartiles, the middle line being the median. • = outliers. Note that the scale of the Y axes are different.

Table 4. Pairs of sites with significant mean differences in fish family biomass (g.100m^{-2}) or abundance, using the Tukey Honestly Significantly Difference Post-Hoc Test with a family-wise error rate of 5%.

Total Biomass

Sites	Mean difference	Range	P-value
PR2-FR1	8972.39	(4621.21, 13323.57)	<0.0001
BR2-FR1	4622.81	(271.64, 8973.99)	0.0311
PR2-FR2	5852.83	(1501.65, 10204.00)	0.0028
PR2-PR1	7441.43	(3090.25, 11792.60)	<0.0001
BR1-PR2	-6148.5	(-10499.67,-1797.32)	0.0015
BR2-PR2	-4349.58	(-8700.75, 1.60)	0.0501

Acanthurid biomass

Sites	Mean difference	Range	P-value
PR2-FR1	6447.2	(2916.10, 9978.29)	<0.0001
BR2-FR1	3935.33	(404.23, 7466.43)	0.0206
PR2-FR2	4515.87	(984.77, 8046.97)	0.0051
PR2-PR1	5794.82	(2263.72, 9325.92)	0.0002
BR1-PR2	-4396.23	(-7927.33, -865.13)	0.0068

Pomacentrid biomass

Sites	Mean difference	Range	P-value
PR2-FR1	1432.26	(427.23, 2437.25)	0.0013
PR2-FR2	1278.5	(273.49, 2283.51)	0.0054
PR2-PR1	1289.67	(284.66, 2294.68)	0.0049
BR1-PR2	-1110.81	(-2115.82, -105.80)	0.0222
BR2-PR2	-1309.62	(-2314.64, -304.61)	0.0041

Siganid Biomass

NA – equal mean counts

Scarid Biomass

Sites	Mean difference	Range	P-value
FR2-FR1	1196.21	(-27.21, 2419.64)	0.0588
PR2-FR1	1206.36	(-17.07, 2429.79)	0.0554

Total abundance

Sites	Mean difference	Range	P-value
FR2-FR1	28.5	(3.317, 53.683)	0.0179
PR2-FR1	100	(74.817, 125.183)	<0.0001
BR1-FR1	38.8	(13.617, 63.983)	0.0004
BR2-FR1	39.9	(14.717, 65.083)	0.0003
PR2-FR2	71.5	(46.317, 96.683)	<0.0001
PR2-PR1	91.3	(66.117, 116.483)	<0.0001
BR1-PR1	30.1	(4.917, 55.283)	0.0105
BR2-PR1	31.2	(6.017, 56.383)	0.0072
BR1-PR2	-61.2	(-86.383, -36.017)	<0.0001
BR2-PR2	-60.1	(-85.283, -34.917)	<0.0001

Acanthurid abundance

Sites	Mean difference	Range	P-value
FR2-FR1	8.8	(0.202, 17.398)	0.042
PR2-FR1	14	(5.402, 22.598)	0.0002
BR1-FR1	14.1	(5.502, 22.698)	0.0002
BR2-FR1	20.4	(11.802, 28.998)	<0.0001
BR2-FR2	11.6	(3.002, 20.198)	0.0027
PR2-PR1	9.9	(1.302, 18.498)	0.0152
BR1-PR1	10	(1.402, 18.598)	0.0138
BR2-PR1	16.3	(7.702, 24.898)	<0.0001

Pomacentrid abundance

Sites	Mean difference	Range	P-value
PR2-FR1	85.7	(61.217, 110.183)	<0.0001
PR2-FR2	66.1	(41.617, 90.583)	<0.0001
PR2-PR1	81.3	(56.817, 105.783)	<0.0001
BR1-PR2	-62.4	(-86.883, -37.917)	<0.0001
BR2-PR2	-66.9	(-91.383, -42.417)	<0.0001

Siganid abundance

NA – equal mean counts

Scarid abundance

NA – equal mean counts

abundance was significantly lower at FR1 compared to all other sites, apart from PR1. Although the pomacentrid abundance was higher at PR2 than any other site, there were no distinct patterns between sites in the other fish families. Total fish abundance was found to increase with distance from shore ($p<0.001$) and percentage of hard coral cover ($p<0.001$).

The mean abundance of Siganidae and Scaridae did not differ significantly between sites (ANOVA, $F_{site}(5,53)$ = 1.383, p = 0.245; KW, $H_{site}(5)$ = 6.566, p = 0.255, Fig. 3i; and $F_{site}(5,53)$ = 1.549, p = 0.191, Fig. 3j respectively). However, siganid abundance increased as the percentage cover of algal turf increased (p = 0.002), while scarid abundance decreased with increasing algal turf (p = 0.032). No other factor contributed to the observed patterns in either siganid or scarid abundance.

A single factor ANOSIM based on distance zone (Near, Medium and Far) revealed a significant effect (Global R = 0.182, p = 0.001), with pairwise tests showing significant differences between Near and Medium (R = 0.135, p = 0.003), Near and Far (R = 0.352, p = 0.001) and Medium and Far reefs (R = 0.065, p = 0.039) for square root-transformed fish biomass.

Trajectory plots for the four families revealed that the more distant sites were characterized by a greater biomass of scarids and acanthurids, with siganids and pomacentrids being more evenly distributed (Fig. 4).

Multivariate investigations of community data (correlations between resemblance matrices based on Bray-Curtis similarities in square root-transformed biomass and abundance values and a resemblance matrix based on Euclidean distances of normalized values) for the site variables: distance from Andavadoaka village, hard coral cover, macroalgae and turf algae were generally weak. Turf algal cover (r_s, 0.416) yielded the highest correlation coefficient and the interaction between turf algal cover x distance from human communities followed a close second (r_s, 0.414). While, the sensitivity of these analyses is somewhat compromised by the environmental data being derived from single assessments of each reef rather than each fish transect, as the relationships investigated were, in the main, of qualitative differences between reefs rather than ecological associations between the fish families and their habitat, we feel the tests were adequate for our purposes.
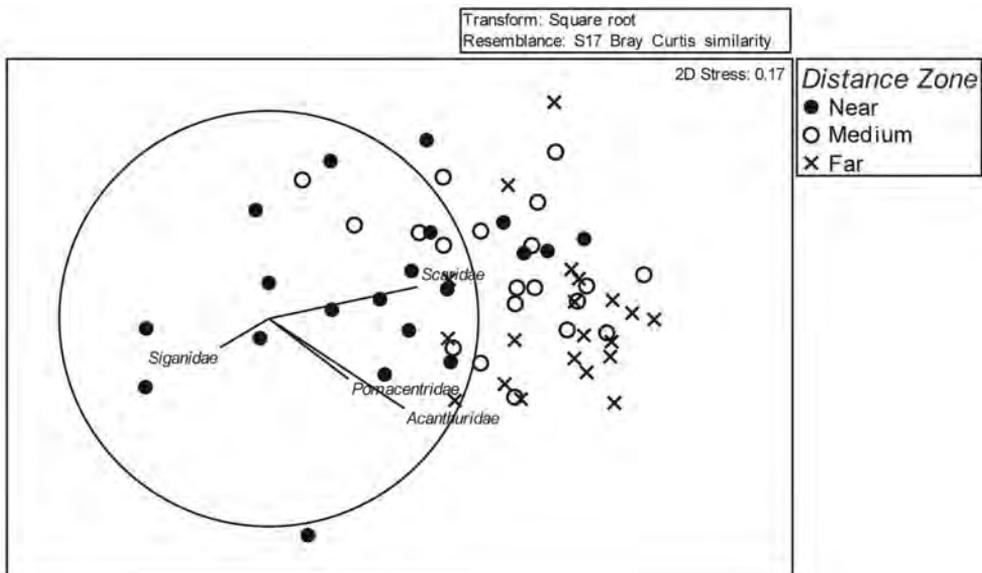
Figure 4. MDS plot of square root-transformed biomass values using Bray Curtis similarity for four fish families on coral reefs near (1.19 & 1.25 km), medium (5.39 & 5.83 km) and far (7 & 8.61 km) from Andavadoaka, with a vector plot for each family.

Table 5. Significant factors for each herbivorous fish family in terms of biomass (g.100m^{-2}) and abundance. Intercept, baseline biomass or abundance when the other explanatory variables have been taken into account; Distance is that from the shore in kilometres; Hard is the % hard coral cover; Turf is the % turf cover; 'Reef Type 2' takes the value one if the site is a Patch reef, and zero otherwise; 'Reef Type 3' takes the value one if the site is a Barrier reef, and zero otherwise; Reef type 1 (fringing reef) is the reference reef.

Type	Species	Explanatory variable	Mean	SD	P-value
Biomass	Total	Distance	420.75	130.07	0.002
		Hard	110.9	25.32	<0.0001
	Acanthuridae	Distance	264.3	78.72	0.0014
		Hard	64.16	15.35	0.0001
	Pomacentridae	Hard	24.322	3.374	<0.0001
	Siganidae	Intercept	321.71	83.33	0.0003
		Distance	-35.94	14.84	0.0186
	Scaridae	Intercept	1739.7	313.001	<0.0001
		Turf	-26.01	8.123	0.0022
Abundance	Total	Intercept	-20.53	5.9522	0.0011
		Hard	2.568	0.2362	<0.0001
		Reef Type 2	-19.02	8.1916	0.0239
		Reef Type 3	29.966	6.1424	<0.0001
	Acanthuridae	Distance	2.3294	0.1496	<0.0001
	Pomacentridae	Intercept	-78.79	24.1012	0.0019
		Hard	3.1371	0.4406	<0.0001
		Turf	0.8974	0.3704	0.0187
		Reef Type 2	-24.98	8.6416	0.0055
		Reef Type 3	31.666	8.8714	0.0008
	Siganidae	Turf	0.0082	0.002556	0.0021
	Scaridae	Intercept	3.6507	0.85078	<0.0001
		Turf	-0.049	0.02208	0.032

DISCUSSION

As all sites manifested significant differences in herbivorous fish biomass and abundance and there was no significant relationship between the reef types, it is assumed that a factor other than reef geomorphology was responsible for the observed differences in herbivorous fish populations in the region of Andavadoaka. While Nadon *et al.* (2007) found that fish abundance and diversity were higher on patch reefs, all the patch reef sites surveyed in their study were located in close vicinity to PR2 and are known to have high coral cover. The current study covered two patch reefs geographically separated from each other by a sandy lagoon, and herbivorous fish biomass was not found to differ between reef types.

Although the pomacentrid abundance was higher on patch reefs than that of other reef types, hard coral cover was found to be a more important factor than reef type. It is suggested that the higher abundance recorded on patch reefs in the Nadon *et al.* (2007) study resulted from site selection rather than reef type. A larger number of each reef type in different areas of the lagoonal system would be needed to validate this assumption.

Over-fishing and coral bleaching pose the most serious threats to the reefs of Andavadoaka (Nadon *et al.* 2007). Fishers in the study area use pirogues, on which sails are used only when conditions are appropriate. In adverse conditions, fishers are restricted to paddling. Scarinae, Siganidae and Acanthuridae are preferred food fish in

the area and are targeted when spear fishing, although fishing methods mainly consist of nets, which are indiscriminate in their catch. The biomass and abundance of herbivorous fish in this study increased with increasing distance from the village, which is probably attributable to the increased time needed for fishers to reach fishing grounds on distant reefs. These results suggest that fishing pressure may be having an adverse effect on the herbivorous fish biomass and abundance on some reefs in the region.

PR2 had a higher fish biomass and abundance than all the other sites, particularly of acanthurids and pomacentrids, despite this reef not being the furthest offshore. McClanahan *et al.* (1999) found that acanthurids were susceptible to fishing pressure on Tanzanian reefs, and are reduced in biomass and abundance as fishing pressure increases (McClanahan *et al.* 1999). Acanthurid biomass at PR2 (698.62kg ha^{-1}) was much higher than that on reefs inside or outside Tanzanian MPAs (116.1kg ha^{-1} and 32.4 kg ha^{-1} respectively; McClanahan *et al.* 1999). PR2 had a markedly higher biomass (1000.01kg ha^{-1}) compared to FR1 (75.05 kg ha^{-1}), the reef closest to the village that is known to be heavily fished. This observation can be explained by very low fishing effort at PR2, which is a small patch reef lying approximately seven km from shore in a 15-30 m deep lagoon. The small size of this reef and the depth of the surrounding lagoon make this reef difficult to locate unless the sea state is calm, with exceptional visibility. Such conditions are rare.

It is a commonly-held belief that grazing fish maintain algal turfs (Nystrom and Folke 2001; Bellwood *et al.* 2004) and, as such, a greater cover of algal turf should support a greater biomass of grazers (Graham *et al.* 2008). This study detected no increase in the herbivorous fish biomass with increased algal turf cover. Other studies have also failed to find evidence of an increase in herbivorous fish biomass or abundance with increasing turf algae (Spalding and Jarvis 2002; Russ 2003). It has been suggested that the high productivity of algal turfs, rather than their standing crop, supports a high biomass of herbivorous fish (Carpenter 1986; McCook 1999; Russ 2003). Ledlie *et al.* (2007) found that, whilst herbivorous fish are considered to play an important role in promoting coral reef recovery in the event of coral loss (Bellwood *et al.* 2003), grazing fish at Cousin Island, Seychelles, were unable to restrict macroalgae after coral loss. Abundant algal cover may exceed the ability of grazers to keep it cropped (Williams *et al.* 2001). In turn, an increased abundance of macroalgae on a reef decreases the chances of a return to coral dominance (Ledlie *et al.* 2007). Mumby (2006) highlighted the importance of managing scarid populations, since a depletion of scarids may result in a dramatic reduction in coral production and, as such, reef rugosity (Sale *et al.* 2005). The decrease in scarid biomass and abundance observed in this study as algal turf increased, suggests that scarids either avoid or are excluded from areas of high algal turf cover. While fishing has been identified as the main cause for a reduction in scarid populations (Mumby 2006; Jennings *et al.* 1995), rugosity is also known to have a positive influence (Mumby and Wabnitz 2002), in part explaining the paucity of scarids in areas of high turf algal biomass where substratum complexity is low.

Steps have been taken to reduce fishing effects on the reefs of Andavadoaka through the promulgation of MPAs. These have proven effective in reducing fishing effects at a local scale (Jennings *et al.* 1996; Halpern 2003) and maintaining a high biomass and diversity of herbivorous fish (Jennings *et al.* 1996). In Kenya, 52 of 110 fish species found in protected areas were absent on heavily-fished reefs (McClanahan 1994). Numerous studies have shown that a higher fish biomass and abundance is found in areas of low fishing intensity, or where there are adequate marine protected areas relative to harvested areas (Jennings *et al.* 1996; Russ *et al.* 2005; Newman *et al.* 2006; McClanahan *et al.* 2007). Scarids, which were low in biomass in the Andavadoaka region (81.04kg ha^{-1}), have been recorded with a much higher biomass in MPAs (247.6kg ha^{-1}) compared to fished areas (29.3kg ha^{-1}) on Tanzanian reefs (McClanahan *et al.* 1999).

Protected areas, however, are not immune from broad-scale environmental changes such as increases in sea surface temperature that cause coral bleaching (Graham *et al.* 2007, Jones *et al.* 2004). Reefs in Andavadoaka are thought to have been severely affected by the 1998 coral bleaching event (Harding *et al.* 2006). Bleached reefs can maintain abundant and diverse fish assemblages, as long as reef structure is maintained (Lindal *et al.* 2001). For example, a Tanzanian reef underwent a 39% increase in herbivore biomass in the immediate aftermath of a large coral mortality caused by the 1998 El Nino Southern Oscillation (ENSO) event (Graham *et al.* 2008, Lindal *et al.* 2001). However, dead coral skeletons are more susceptible to physical disturbances as well as biological and mechanical erosion than live coral colonies. Once dead corals have been reduced to rubble, fish abundance and diversity decrease markedly (Graham *et al.* 2007, Graham *et al.* 2006, Sano *et al.* 1987). Studies have suggested that the three-dimensional complexity of reefs with high hard coral cover favours large and diverse populations of herbivorous fish (Graham *et al.* 2008, Graham *et al.* 2007, Roberts and Ormond 1987). In the present study, herbivorous fish biomass and abundance increased with increased hard coral cover, and acanthurids and pomacentrids increased significantly in both biomass and abundance with a higher cover of hard coral. FR1, on the other hand, is a heavily degraded site which has lost a considerable amount of its three-dimensional structure (Nadon *et al.* 2007), and it displayed the lowest herbivorous fish biomass and abundance of all survey sites.

Graham *et al.* (2007) found that a loss of structural complexity due to coral bleaching posed one of the biggest threats to fish communities in the Seychelles. The protection of areas that have manifested resilience or high recovery rates from coral bleaching has been recommended (Graham *et al.* 2008, Graham *et al.* 2007). PR2, which was heavily bleached in the 1998 bleaching event, has shown unusually high recovery, suggesting it is more resilient than other reefs in the area. This may be due to its high abundance of herbivorous fish which can control algal growth and increase the chances of coral recovery (Paddack *et al.* 2006). Studies have shown that grazing fish can exclude macroalgae on reefs with 40% hard coral cover and healthy populations of other invertebrates by keeping it cropped (Williams *et al.* 2001). PR2 was the only study reef with ≥40% hard coral cover; it also had a significantly higher biomass and abundance of herbivorous fish than all other sites, including both acanthurids and pomacentrids. PR2 was protected in an MPA in 2009. This reef may prove to be an important area for protection given its high coral cover, post-bleaching recovery and high biomass and abundance of herbivorous fishes. Previous studies have also found a greater abundance and diversity of fishes at this reef, attributed to lower fishing intensity (Gillibrand *et al.* 2007; Nadon *et al.* 2007). Protection of the associated mangroves and seagrass beds is also planned to provide refugia for juvenile fish in Andavadoaka and its surrounding villages, thereby increasing recruitment to reefs (Mumby and Steneck 2008). However, it is important that the areas outside the MPAs are also managed as the MPAs in the region are small and still prone to stress from the surrounding areas.

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