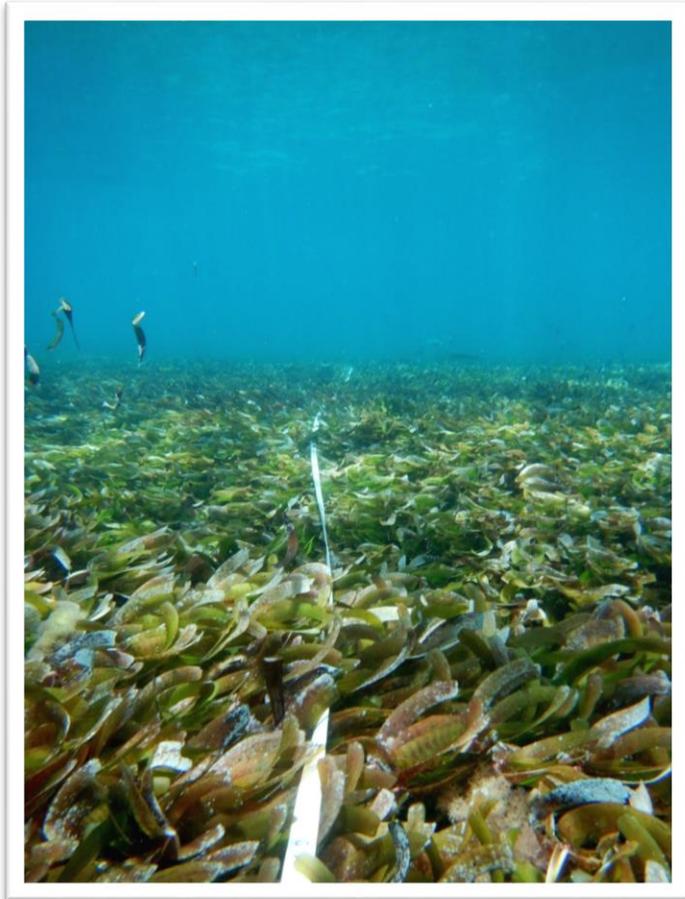


# Effects of different marine protection levels on fish communities in tropical seagrass beds and coral reefs



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## **ABSTRACT**

Overexploitation and degradation of key habitats such as seagrass meadows and coral reefs undermines the fish communities and fisheries production in tropical regions. A common way to preserve and manage ecosystem functions is to establish marine protected areas (MPAs). The protection strategies vary, but few studies have evaluated the effect of different reserve types in different habitats on fish community composition. In this study, a range of fish community variables (species richness, total biomass, mean individual fish weight and Rao's functional diversity index) were measured and compared in two different reserve types and at two different management levels, both in shallow seagrass beds and coral reefs. The survey was made in six MPAs in Tanzania and Mozambique using visual census technique. The effect of reserve type was strong in coral reefs. No-take areas (NTAs) had higher species richness, mean individual fish weight and total biomass compared with conservation areas (CAs) and open access areas (OAAs). Furthermore, the total biomass and number of fish species were higher in private managed NTAs than in areas managed by the government. Moreover, NTAs seem to work as sanctuaries for the target fish families Acanthuridae and Scaridae, which showed higher biomasses inside NTAs compared to CAs and OAAs. Seagrass meadows were not affected by reserve type or management level, except for functional diversity where CAs had higher functional diversity compared to NTAs. This might be explained by harvesting of invertebrates in CAs, reducing food competition between invertebrates and fish. Furthermore, there was a trend, however not significant, indicating that seagrass shoot density was higher in CAs, and that the number of fish species was affected by shoot density. Functional diversity in seagrass meadows might hence be explained by the combination of invertebrate fishing and seagrass shoot density. NTAs seem to work as sanctuaries for the constrained seagrass species *Siganus sutor*, which is a commercially important target species in this region. In conclusion, this study shows that the level of protection has positive effects on the fish community in coral reef, and as sanctuaries for target fisheries species, which might lead to "spillover" effects outside the boundaries of a reserve area. Even if the effect of reserve type in seagrass meadows was not as obvious as on coral reefs, potentially high fish connectivity between these two habitats suggests that protection of seagrass meadows should be of equal importance as for coral reefs.

**Keywords:** Marine protected areas, Fish community, Coral reef, Seagrass, East Africa, Tropical

## INTRODUCTION

The tropical coastal zone comprises of important marine ecosystems that provide a variety of goods and services, highly beneficial for humans in terms of e.g. fishing, tourism and protection from land erosion (Moberg & Folke, 1999; Francis et al., 2002; Donato et al., 2011; Duarte et al., 2013). Yet, the tropical seascape suffers from different types of severe threats due to abiotic and anthropogenic disturbances, where important ecosystem functions might be lost (Hoegh-Guldberg, 2006; Lotze *et al.*, 2006; Worm et al., 2006; Halpern et al., 2007; Cheung et al., 2013). Overexploitation in terms of overfishing is one of the major anthropogenic threats to marine ecosystems (Pauly et al., 2002; Dulvy et al., 2003; Halpern et al., 2007; Pontecorvo & Schrank, 2014). Overfishing affects biodiversity negatively, not only directly from outtake of target species, but also indirectly through the use of destructive fishing methods, where important habitats are destroyed (Dayton et al., 1995; Edinger et al., 1998; Pauly et al., 1998; McClanahan et al., 1999; Jackson et al., 2001; Hughes et al., 2003). In developing countries, many people are dependent on fisheries as their main income and to food security, and are therefore greatly affected by declining fish catches (Cruz-Trinidad et al., 2014). The loss of ecosystem functions from overfishing also affects habitat resilience, making these habitats more vulnerable to other stressors such as global warming (Bellwood & Hughes, 2001; Moberg & Folke, 1999; Hughes et al., 2003; Folke et al., 2004; Hooper et al., 2005; Johansen et al., 2014). Overexploitation might lead to a regime shift in an ecosystem (Folke et al., 2004). Overfishing of herbivorous fish (e.g. parrotfishes) on coral reefs, for instance, has shown to push the ecosystem to a more algae-dominated system, where corals are overgrown in absence of herbivores, which may in turn lead to an ecosystem collapse (Mumby et al., 2006; Elmhirst et al., 2009; Fox & Bellwood, 2014). Since connectivity between different habitats is high in the tropical seascape, such threats might not only affect individual habitats but also whole coastal seascapes (Ault & Johnson, 1998; Berkström et al., 2012; Berkström et al., 2013).

Marine protected areas (MPAs) have been widely established as a tool for biodiversity conservation and fisheries management (Gell & Callum, 2003; Gains et al., 2010; Maggs et al., 2013; Green et al., 2014). MPAs may often control fishing efforts inside reserve borders by gear restriction or closing of fishing grounds. This can positively affect fish community structure, resulting in an increased biomass and higher functional- and species diversity (Halpern, 2003; Claudet et al., 2008; Lester et al., 2009; Villamor & Becerro, 2012; Sheehan et al., 2013; Edgar et al., 2014). However, constructing a beneficial and successful MPA is

complex, and many issues (e.g. selection of species and habitats to protect, size and location) must be considered prior to establishment (Edgar et al., 2014, Green et al., 2014).

There is a variety of MPA strategies based on the different goals of the MPAs (Francis et al., 2002). Closed no-take areas (NTAs) are often efficient in terms of conserving target fish species and habitat protection (Halpern, 2003; Lester et al., 2009), but are often subjected to disagreement among local stakeholders since fishing grounds are closed (Jones, 2002). Fishing pressure might also increase outside the reserve borders after establishment of NTAs (Forcada et al., 2009). Moreover, NTAs could disfavor artisanal fisheries (Cinner, 2007), especially in developing countries where people are dependent on fisheries as their main income (Johnson et al., 2013) and food security (Cruz-Trinidad et al., 2014). The local actors in these coastal areas use seagrass meadows and coral reefs as their main fishing grounds and are therefore negatively affected by complete closing of shallow-water fishing grounds (De Boer et al., 2001; Johnson et al., 2013). MPAs may, however, via ‘spillover’-effects and transportation of larvae and eggs from the reserve, generate high fish biomass to adjacent fishing grounds (Rowley 1994; McClanahan & Mangi, 2000; Roberts et al., 2001; Abesamis & Russ, 2005; Brochier et al., 2013; Januchowski-Hartley et al., 2013). Partly closed or multiple use marine protected areas (e.g. conservation areas, CAs) are also established in many coastal areas. Local people in such type of reserves are allowed to restricted utilization of marine organisms inside the reserve (Lange & Jiddawi, 2009). The conflict between the government and local resource users are often less intense (Kincaid et al., 2014). However, many studies suggest the NTA approach being the most efficient way to preserve habitats and conserve biodiversity (Halpern et al., 2007; Claudet et al., 2008; Coleman et al., 2013; Edgar et al., 2014). Many reserves are established and run by the government, but also private actors could be the initiator of the establishment of MPAs (Sturner & Andersons, 1998). The private reserves often depends on preserving a pristine environment to achieve aesthetical ecosystems for tourism operations (Sturner & Andersons, 1998; Francis et al., 2002). Whatever reserve type, the incorporation of different key habitats (e.g. seagrass meadows and coral reefs), and openness for local actors’ requirements are important features for MPAs to achieve ecological conservation goals (Halpern et al., 2007; Klein et al., 2007; Edgar et al., 2014; Green et al., 2014).

The establishment of an MPA should be done based on scientific knowledge and incorporate local actors, which are the ones most affected by the establishment of MPAs, since it often leads to closing of fishing grounds. However, little is known about differences in fish community

structure among MPAs with different reserve- and management strategies. Furthermore, most of the published studies are concentrated to the Great Barrier Reef, the Caribbean and the Mediterranean. Few studies are focusing on MPAs in the Western Indian Ocean (WIO), and in particular on the East African coast. Moreover, the relative effect of an MPA on fish community structure in seagrass meadows and on coral reefs in the same reserve has been poorly evaluated.

### *Aim of study*

The aim of this study is to evaluate NTAs and multiple use areas (conservation areas, CAs) with different management levels (private- and government managed), and the possible effects on the fish community structure in shallow seagrass and coral-reef habitats, in Tanzania and Mozambique. The positive effects from a well-functioning MPA on the marine ecosystem functioning and resilience, might improve social and economic conditions for local stakeholders outside the reserve borders. This study is therefore important, to fill out knowledge gaps concerning MPAs.

## METHODS

### *Study area*

The present study was conducted in tropical/subtropical seagrass beds and coral reefs in Tanzania and Mozambique, East Africa (Fig. 1a). Sites were selected in seagrass and coral-reef habitats based on management level and included two different types of reserves; no-take areas (NTAs) and conservation areas (CAs). Each site was sampled with a matched open access area (OAA) as control site. Seagrass habitats chosen in this study were dominated by *Thalassodendron ciliatum*, which is a large seagrass species commonly found in the WIO region (Gullström et al., 2002). Coral reef habitats consisted mainly of patchy shallow reefs.

In Tanzania, three reserves were situated on Zanzibar (Chumbe, Mnemba and Fumba) and one on the mainland (Mbudya) (Fig. 1b). Chumbe Island Coral Park is a strict NTA developed in 1991. The island has no inhabitants except for the guests and staff of the lodge, and is situated approximately 5 km off the west coast of Zanzibar. This is a private managed reserve where the aim is to create a sustainable conservation financed by ecotourism (Nordlund et al., 2013). There is no fishing allowed inside the reserve and only snorkeling is allowed. Mnemba Island reserve is also a private managed strictly NTA, situated 2 km from the north east coast of

Zanzibar. Only guests of the lodge can visit the island itself, while SCUBA diving and snorkeling tourism are practiced inside the marine reserve (Sterner & Andersons, 1998). Both Chumbe and Mnemba have guards patrolling the reserve borders, protecting the reserve from utilization and destruction of the reef. Fumba is a village situated on the south coast of Zanzibar and is included in a large CA called Menai Bay Conservation Area. In this CA multiple use of the marine environment is allowed, including harvesting of invertebrates and fishing with non-destructive methods (e.g. small-mesh seine nets). Mbudya is regarded as an NTA, with guards situated on the island. During the time of this survey, however, fishing with line and hooks was ongoing inside the reserve borders. Therefore, this site was treated as CA when compared among reserve types, but considered as a government managed NTA in the management level analysis.

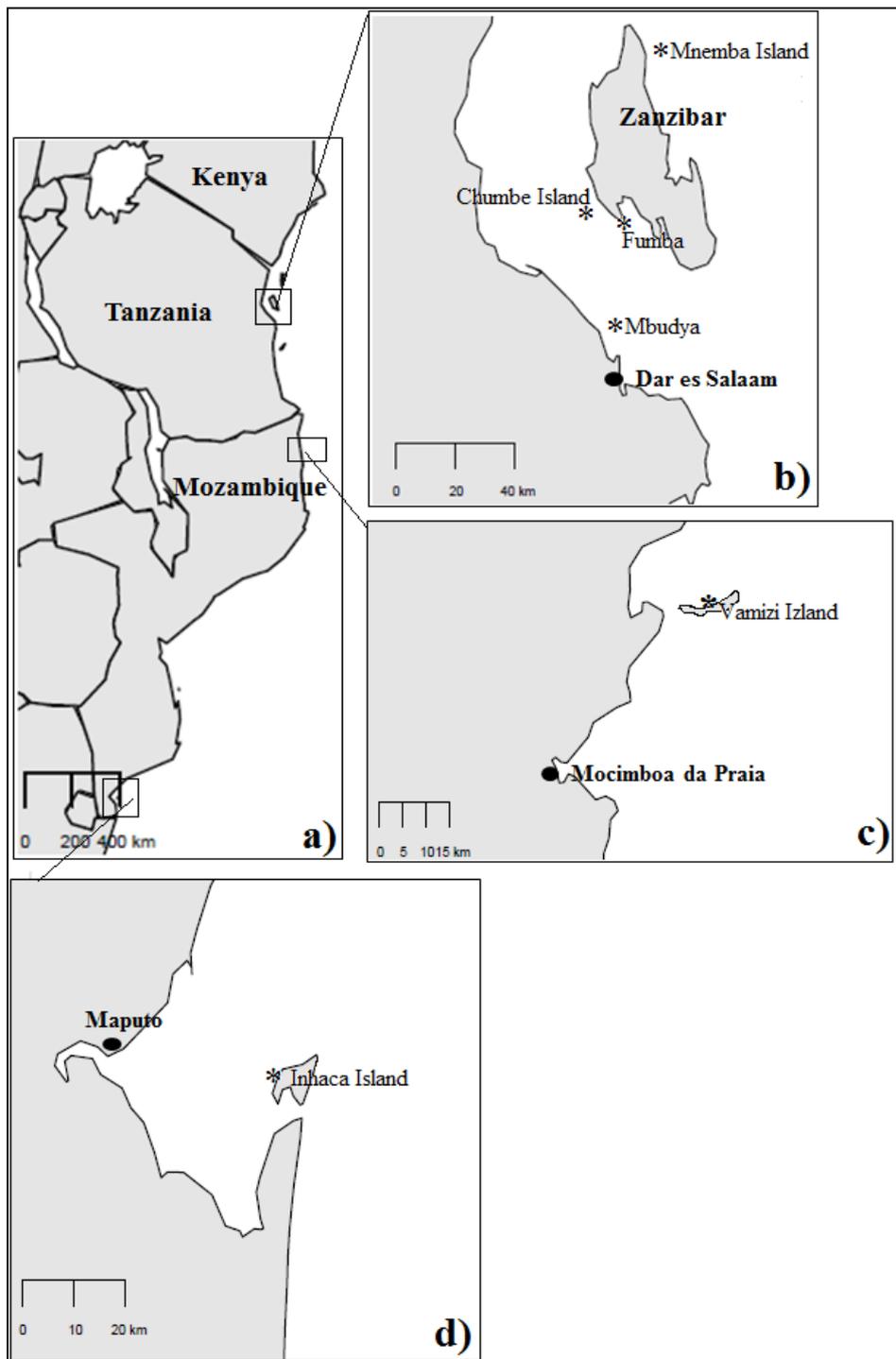
In Mozambique, two reserves were used as sampling sites, Vamizi in the north (Fig. 1c) and Inhaca Island in the south (Fig. 1d). Vamizi is an island in the Quirimbas archipelago, situated 10 km off the coast of northern Mozambique. The eastern part of the island is a protected area initiated by the local Fisheries Council. This is a reserve policed by the government, community and tourism actors. Inhaca Island is part of the Ponta do Ouro Partial Marine Reserve, where the island is separated into different areas with different levels of protection. The NTAs are protected by employed guards from the local government. However, during this survey, lines with hooks were found caught on the no-take protected reefs, indicating some level of illegal fishing.

The six MPAs varied in terms of location, type of reserve, management level, size and years of protection (Table 1). The field survey was conducted from the beginning of October to the middle of December 2013.

**Table 1)** Characteristics of the six MPAs included in this study.

<b>Site</b>	<b>Country</b>	<b>Coordinates</b>	<b>Reserve type</b>	<b>Management level</b>	<b>Reserve size (km<sup>2</sup>)</b>	<b>Years since establishment</b>
<b>Fumba</b>	Tanzania (Zanzibar)	6°19'4.60"S 39°16'58.90"E	CA	Co-managed	470	17
<b>Chumbe</b>	Tanzania (Zanzibar)	6°16'47.20"S 39°10'38.50"E	NTA	Private	0.33	20
<b>Mnemba</b>	Tanzania (Zanzibar)	5°49'14.34"S 39°23'1.72"E	NTA	Private	0.15	22
<b>Mbudya</b>	Tanzania	6°39'25.97"S 39°15'2.29"E	CA*	Government	5	39
<b>Inhaca</b>	Mozambique	26° 1'6.08"S 32°56'40.70"E	NTA	Government	1.3	5
<b>Vamizi</b>	Mozambique	11° 1'43.65"S 40°40'15.39"E	NTA	Private/ co-managed	5	13

\* Mbudya is primarily a no-take area, but due to occasionally heavy fishing inside the reserve, this site has been treated as a conservation area. Information based on local knowledge and observations during field survey.



**Figure 1.** Map of East Africa showing study sites. Sampling sites are marked with black stars.

### *Fish community survey*

Fish were counted along 25 m long line transects using snorkeling and based on common visual census technique (McCormick & Choat, 1987). All fish within 2 m on each side of the line transect were counted, and keeping an average swim speed of 2.5 m/min, the fish sampling transect took approximately 10 min, and was surveyed ones. All fish counted were identified to

species level, and the total length of individuals was estimated to the nearest 5 cm length interval (1-5 cm, 6-10 cm, 11-15 cm, etc.). Identification of fish species was made based on Liske & Myers (2002). Fish <4 cm was not included in this survey, since identification of juvenile fishes from this size category is hard using this technique. Tide amplitudes in this area vary from 1.5 to 4 m. The water depth during surveys was between 2 and 3 m. Each site included six transects in seagrass- and coral-reef habitats, both inside and outside the reserve borders, respectively (i.e. 24 transects per site, in total 144 transects), and each transect was spread at least 25 m apart from each other to be considered independent replicates. The locations of the OAA sites were chosen nearby the reserve borders to represent similar abiotic conditions (in terms of e.g. mean annual water temperature, nutrients, turbidity and exposure), but far enough to avoid “spillover” effects from the reserve (Rowley 1994; McClanahan & Mangi, 2000). Reserve transects were placed approximately 200 m from the border of the reserve, to avoid edge effects. Sites were chosen based on local knowledge from fishermen, who were hired as boat drivers during field work. The main criterion for selection of seagrass transects was a cover of at least 25 % *T. ciliatum*. Over the six areas, 137 line transects were surveyed. Seven line transects were not able to be sampled, one due to insufficient coral cover (Inhaca OAA), and six line transects in Vamizi, where there was no seagrass (*T. ciliatum*) inside the NTA.

#### *Habitat characteristics*

Habitat characteristics were measured along the same transects as mentioned above to estimate any possible influence on the fish community composition. The habitat structural complexity for coral reefs was assessed based on rugosity calculations, which were in turn based on coral reef topography measures. In seagrass habitats, the structural complexity was represented by shoot density (shoots per m<sup>2</sup>) and canopy height (cm) (Duarte & Kirkman, 2001), estimated within 0.25 m<sup>2</sup> quadrates (n = 6), which were placed at every 5 m on the line transects. The proportion (percentage cover) of live corals in coral reef habitats was also estimated using 0.25 m<sup>2</sup> quadrates (n = 6). As a complement to the above described benthic cover measurements, the proportion of live corals was estimated from the total length of live coral cover per transect. This means, that for each line transect, the length of live coral cover was measured (in cm) under the line transect, resulting in a proportion of live coral cover for each line transect. Results from the two above mentioned method were pooled, representing total cover of live coral per transect in the analysis.

### *Fish weights and total biomass*

Individual fish weights were calculated from species-specific length-weight functions extracted from Fishbase (Froese & Pauly, 2014). For species where information on length-weight relationship was unknown, data from a closely related species with similar morphology was chosen. Since fish length was estimated to the nearest 5 cm interval, the mean length for that interval was used for the weight calculation (meaning that a fish from e.g. the 6-10 cm interval was treated as 8 cm in mean length). The total fish biomass was calculated as the sum of all fish weights per line transect.

### *Functional diversity*

Functional diversity (FD) was calculated as the Rao's quadratic entropy index (Rao's Q) (Pavoine et al., 2005) using the FD function (FD package in R). Functional traits were used to reflect relevant aspects of different ecosystem functions (Table 2). Trait information of different fish species was obtained from Fishbase (Froese & Pauly 2014), and is presented in Appendix 1.

### *Data analysis*

Data were analyzed using general linear mixed models in R (v. 2.15.2) (package *lm4e*). Four fish response variables were tested separately; number of species, total fish biomass, average individual fish weight and functional diversity (FD). The predictor variables were reserve type (NTAs vs. CAs vs. OAs), management type (Private vs. Government), and habitat (seagrass meadows vs. coral reefs). Age and size of reserves were tested in models from subsets consisting of only protected sites (i.e. NTAs and CAs). For all models, site (e.g. Chumbe, Vamizi and Fumba) was used as the random factor. Normality- and variance assumptions were graphically checked using histograms and residual plots. Akaike Information Criterion corrected for infinite samples ( $AIC_c$ ) was used to choose the most parsimonious model. Chosen models for the analysis were based on  $AIC_c$  from the function *dredge* (*MuMIn* package). This function can test all possible model combinations, given the most complex model, and return a ranking of the different models based on  $AIC_c$ . To obtain p-values from the *lmer* function, the ANOVA function (*car* package) was used, which for this type of mixed effect models returns type II Wald  $X^2$  p-values. To obtain any possible differences within reserve- and management type, the significant models were further analyzed with a multiple comparison test (Tukey HSD)

from the `glht` function (`multcomp` package). This function is suited for mixed model contrast analysis.

The four response variables were further analyzed with the two habitats separated, not only to be able to assess the different habitat characteristics, but also to compare the relative effects of reserve- and management type between the two habitats.

**Table 2.** Different functional traits used in calculation of functional diversity using Rao's Q index (FD package in R). Traits based on information from Fishbase (Froese & Pauly 2014).

<b>Chosen trait</b>	<b>Traits</b>
<b>Functional group</b>	Cleaner Herbivore Invertebrates Invertebrates/Piscivore Omnivore Piscivore Planktivore
<b>Max size</b>	Max size species-specific
<b>Feeding strata</b>	Benthic Benthopelagic Pelagic
<b>Food type preferred</b>	Food item most commonly found in stomachs of the species

## RESULTS

In total, 9557 fish specimens belonging to 208 species and 42 families were observed. In general, Pomacentridae (damselfishes) was the most numerous fish family in coral reefs ( $n=4031$ ), and constituted of the highest total biomass (80 kg). In NTAs, the family with the

highest total biomass was Scaridae (parrotfishes) (52 kg). In CAs and OAAs, Pomacentridae comprised the highest total biomass (22 kg and 19 kg, respectively). Seagrass meadows were in terms of number of fish generally dominated by the fish family Labridae (wrasses) ( $n=622$ ), but the highest total biomass was shown in the family Siganidae (rabbitfishes) (32 kg). NTAs and CAs seagrass meadows biomass was dominated by Siganidae (17 and 9 kg, respectively), where OAAs was dominated by Scaridae (16 kg). In all three reserve types, the total biomass of herbivores was higher compared to other functional groups. Complete species lists with functional traits are presented in Appendix 1.

### *General effects*

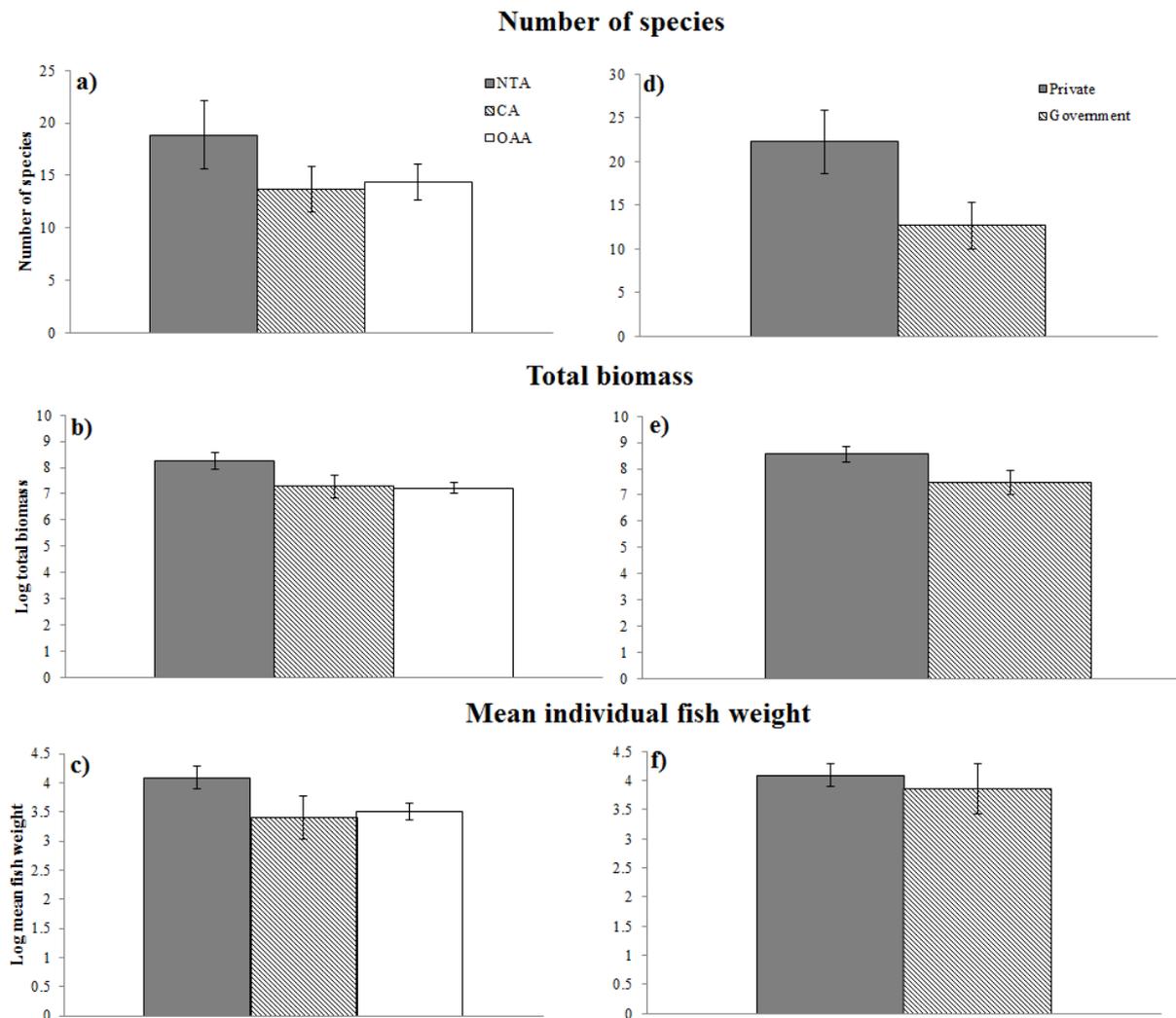
Reserve type had general effects on number of species, total biomass and individual mean weight of fish (Table 3). The number of species and total fish biomass differed between management levels. Functional diversity (measured as Rao's Q) did not differ significantly between reserve types or between management levels (Table 3). For all reserves, the age and size did not affect any fish community variable significantly (Table 3).

**Table 3.** One-way ANOVA results showing effect of reserve type, management level, reserve age and reserve size, on number of species, total fish biomass, mean individual fish weight and functional diversity ( $n=137$ ). Significant p-values indicated \*\*\*= $p<0.001$ . Not significant effects are written as actual P values.

<b>Factor</b>	<b>No. species</b>	<b>Total fish biomass</b>	<b>Mean individual fish weight</b>	<b>Rao's Q</b>
<b>Reserve type</b>	***	***	***	0.12
<b>Management level</b>	***	***	0.27	0.3
<b>Reserve age</b>	0.3	0.35	0.8	0.12
<b>Reserve size</b>	0.35	0.16	0.06	0.41

The number of fish species was higher in NTAs compared to both CAs (Tukey HSD,  $p=0.037$ ) and OAAs (Tukey HSD,  $p=0.005$ ) (Fig. 2a). NTAs also had higher total fish biomass compared to CAs (Tukey HSD,  $p=0.003$ ) and OAAs (Tukey HSD,  $p<0.001$ ) (Fig 2b). Furthermore, mean

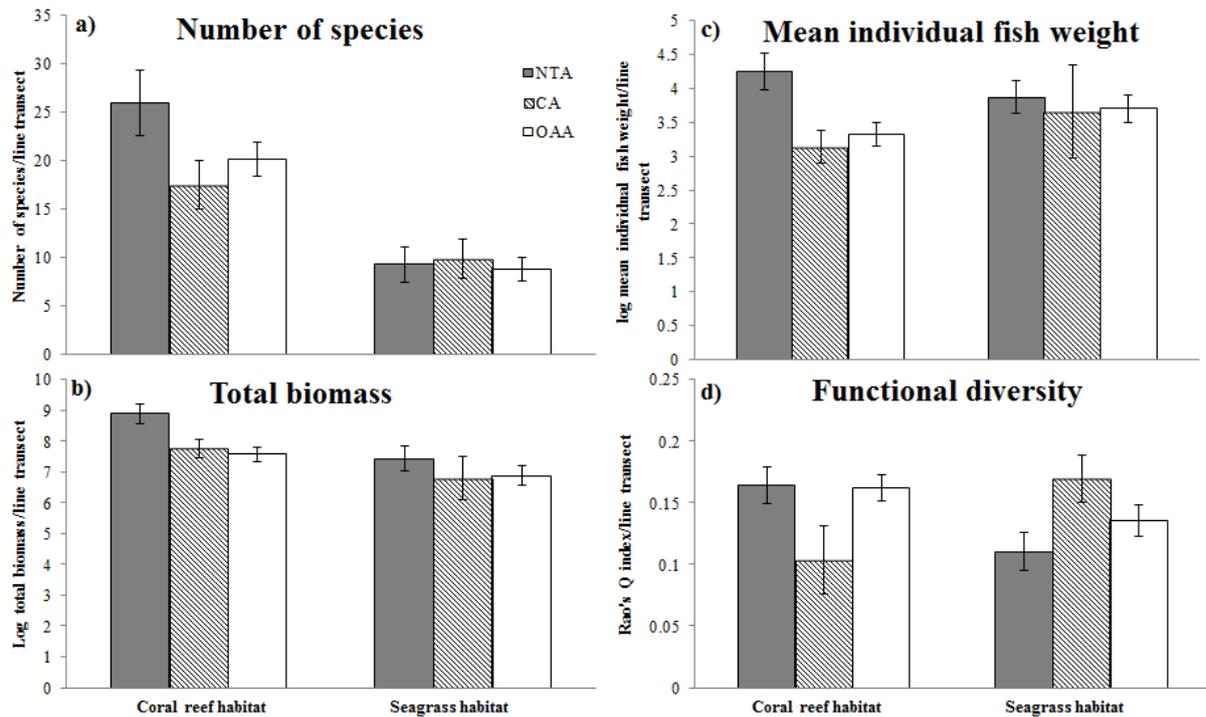
individual fish weight was higher in NTAs than it was in OAAs (Tukey HSD,  $p < 0.001$ ) (fig. 2c). There was no significant difference in any of the three fish variables tested between CAs and OAAs (Fig 2a-c). For NTAs, the private managed reserves had higher number of species (Tukey HSD,  $p < 0.001$ ) and higher biomass (Tukey HSD,  $p < 0.001$ ) compared with government managed reserves (Fig. 2d-e). There was, however, no difference in mean individual fish weight between private- and government managed protected areas.



**Figure 2.** General effects of different reserve types (a-c,  $n=137$ ), and management levels (d-f,  $n=54$ ) on fish variables in seagrass- and coral-reef habitats pooled. Bars show mean number of species (a and d), log-transformed mean total biomass (b and e), and log-transformed mean individual fish weight (c and f), for all line transects per reserve type or management level. Error bars show  $\pm 95\%$  confidence intervals.

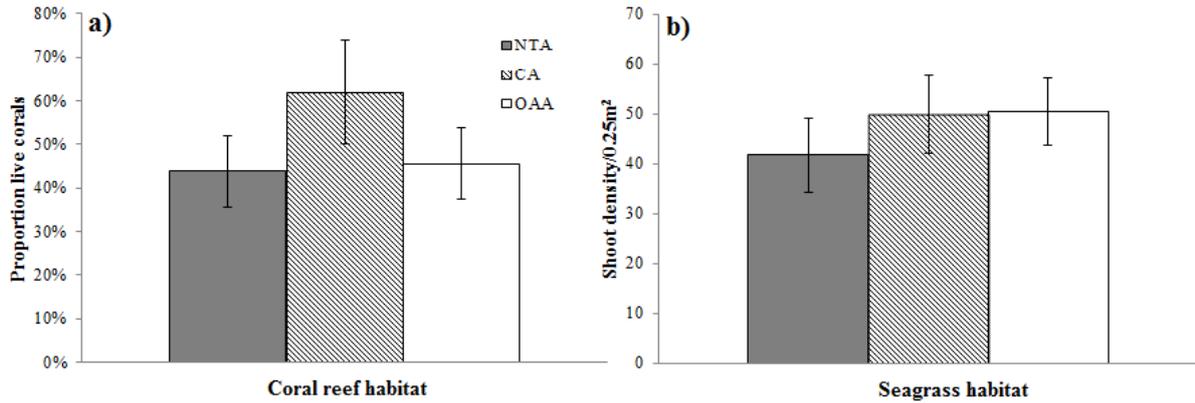
### *Effect of reserve type*

In coral-reef habitats there was a difference in number of fish species (Analysis of deviance,  $X^2=26.15$ ,  $df=2$ ,  $p<0.001$ ), total biomass (Analysis of deviance,  $X^2=49.49$ ,  $df=2$ ,  $p<0.001$ ), individual fish weight (Analysis of deviance,  $X^2=32.40$ ,  $df=2$ ,  $p<0.001$ ), and functional diversity (Analysis of deviance,  $X^2=19.01$ ,  $df=2$ ,  $p<0.001$ ) among reserve types. NTAs had higher number of species (Tukey HSD,  $p=0.003$ ), higher total biomass (Tukey HSD,  $p<0.001$ ), higher individual fish weight (Tukey HSD,  $p=0.006$ ), and higher functional diversity (Tukey HSD,  $p<0.001$ ), compared to CAs (Fig. 3a-d). NTAs also had higher number of species (Tukey HSD,  $p<0.001$ ), higher total biomass (Tukey HSD,  $p<0.001$ ) and higher individual fish weight (Tukey HSD,  $p<0.001$ ) compared to OAAs (Fig. 3a-c). There was no difference in functional diversity between NTAs and OAAs in coral-reef habitats. The functional diversity, however, was higher in coral reef OAAs compared to CAs (Tukey HSD,  $p<0.001$ ; Fig. 3d). In seagrass habitats there were no difference in any fish variable among the three reserve types (Fig. 3a-c), except for functional diversity (Analysis of deviance,  $X^2=25.72$ ,  $df=2$ ,  $p<0.001$ ), where CAs had significantly higher functional diversity than NTAs (Tukey HSD,  $p<0.001$ ), and OAAs (Tukey HSD,  $p=0.007$ ) (Fig. 3d). Furthermore, there was a higher functional diversity in OAA seagrass habitats compared to NTAs (Tukey HSD,  $p=0.006$ ; Fig. 3d).



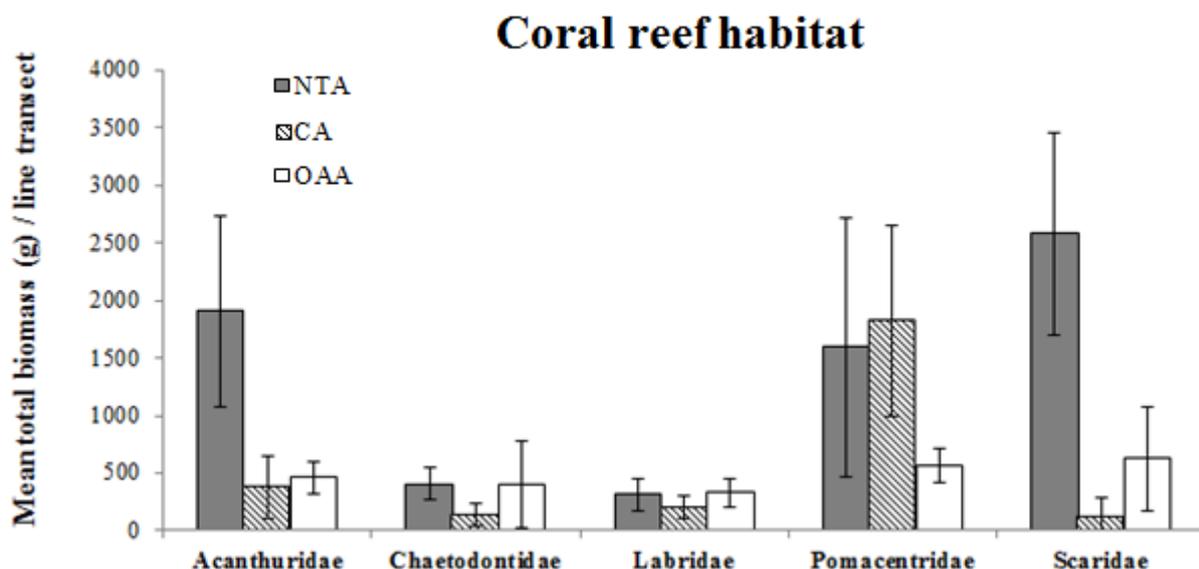
**Figure 3.** Number of fish species (a), total biomass (b), mean individual fish weight (c), and functional diversity (Rao's Q index) (d) in no-take areas (NTAs), conservation areas (CAs), and open access areas (OAAs) separated by habitat (coral reefs and seagrass meadows). Main bars show mean values per transect line (n=137). Error bars show ± 95% confidence intervals.

In coral reef sites, the proportion of live corals did affect the total fish biomass (Analysis of deviance,  $X^2=4.88$ ,  $df=1$ ,  $p=0.027$ ) and the mean individual fish weight (Analysis of deviance,  $X^2=8.21$ ,  $df=1$ ,  $p=0.004$ ). But there was no significant difference in proportion of live corals among reserve types (Analysis of deviance,  $X^2=4.39$ ,  $df=2$ ,  $p=0.11$ ; Fig. 4a), and the effect of reserve type was stronger for both total biomass (Analysis of deviance,  $X^2=49.49$ ,  $df=2$ ,  $p<0.001$ ), and mean individual fish weight (Analysis of deviance,  $X^2=32.40$ ,  $df=2$ ,  $p<0.001$ ). Functional diversity was affected by seagrass (*T. ciliatum*) shoot density (Analysis of deviance,  $X^2=8.74$ ,  $df=1$ ,  $p<0.003$ ), but even though the results indicated a trend, the shoot density did not differ significantly between reserve types (Analysis of deviance,  $X^2=5.65$ ,  $df=2$ ,  $p=0.06$ ; Fig 4b).

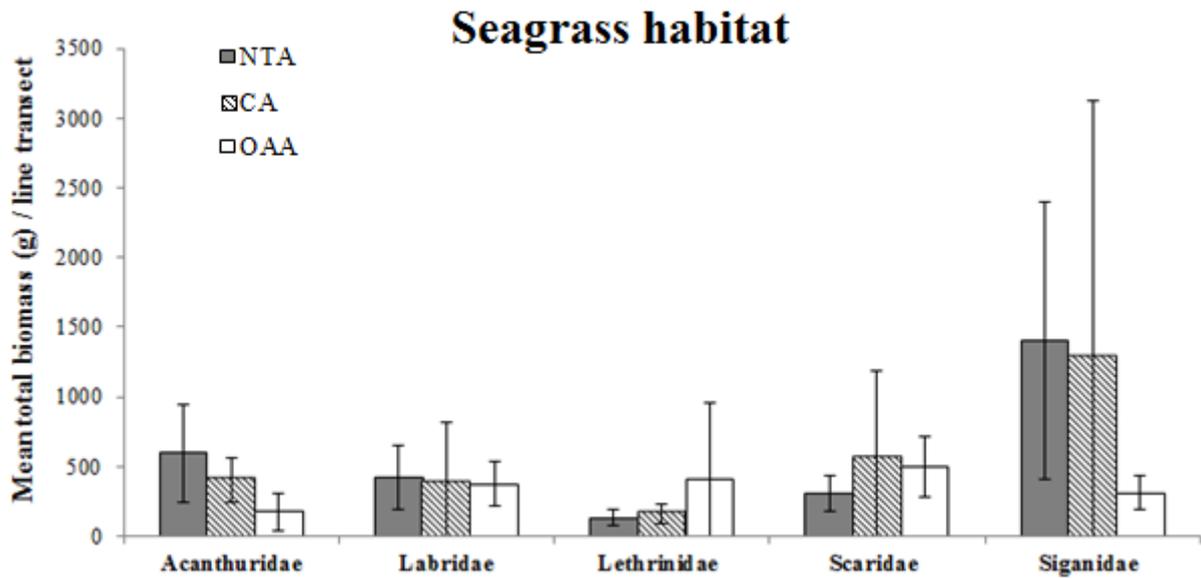


**Figure 4.** Proportion live corals (n=69) (a), and shoot density (shoots per 0.25m<sup>2</sup>) in the different reserve types. Error bars show ± 95% confidence interval.

In coral reefs, the biomass of Scaridae and Acanthuridae (surgeonfish) was significantly different comparing the three reserve types (Scaridae: Analysis of deviance,  $X^2=21.85$ ,  $df=2$ ,  $p<0.001$ ; Acanthuridae  $X^2=20.41$ ,  $df=2$ ,  $p<0.001$ ). NTAs consisted of higher biomass of Scaridae compared to CAs (TukeyHSD,  $p=0.005$ ) and OAAs (TukeyHSD,  $p<0.001$ ) (Fig. 5). NTAs also had higher biomass of Acanthuridae compared to CAs (TukeyHSD,  $p=0.003$ ) and OAAs (TukeyHSD,  $p<0.001$ ) (Fig. 5). In seagrass meadows there was no difference in fish family biomass, except for Siganidae (rabbitfish) (Analysis of deviance,  $X^2=10.82$ ,  $df=2$ ,  $p=0.004$ ), where NTAs had higher biomass of Siganidae compared to OAAs (TukeyHSD,  $p=0.003$ ) (Fig. 6).



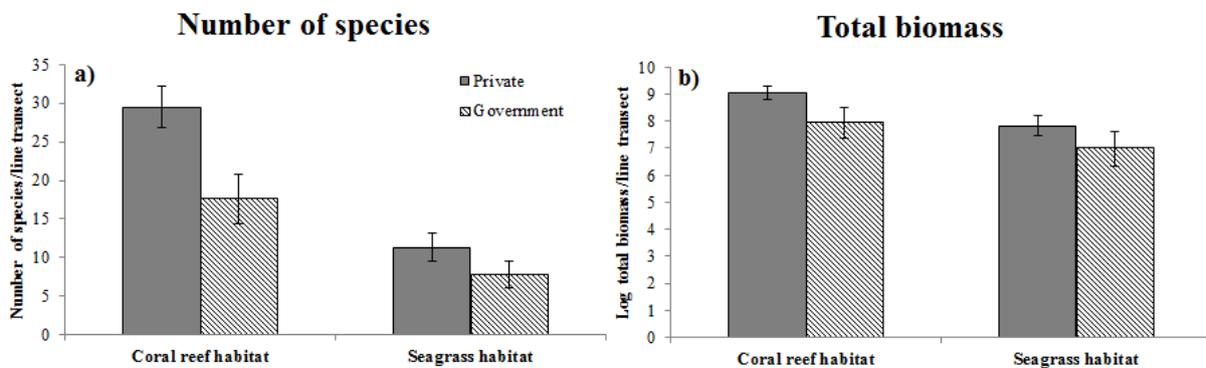
**Figure 5.** Mean total biomass for the five most common fish families in terms of total biomass per line transect in coral reefs (n=71). Error bars show ± 95% confidence interval.



**Figure 6.** Mean total biomass for the five most common fish families in terms of total biomass per line transect in seagrass meadows (n=66). Error bars show  $\pm$  95% confidence interval.

#### *Effect of management type*

The protected, private managed, coral reefs had a higher number of species (TukeyHSD,  $p=0.001$ ) and higher total biomass (TukeyHSD,  $p<0.001$ ) compared to government managed reserves (Fig. 7). There was, however, no significant difference in number of species or in total fish biomass in seagrass habitats comparing private- and government managed reserves. Mean individual fish weight and functional diversity did not differ between management levels for neither of the two habitats.



**Figure 7.** Number of species and total biomass of fish in private- and government-managed NTAs (n=54) separated by habitats. Error bars show  $\pm$  95% confidence interval.

## DISCUSSION

This study compared different types of marine reserves and management levels in seagrass- and coral-reef habitats and revealed some clear effects on fish community variables. NTAs generated more fish species, higher biomass and higher individual fish weight compared to CAs and OAAs. Furthermore, private managed reserves were more efficient in terms of conserving higher number of fish species and generate higher fish biomass compared to government managed reserves.

### *Effect of reserve type*

In coral-reef habitats, NTAs consisted of more species and higher weight of specimens compared to CA and OAA. This generated a higher total fish biomass in NTAs. High species richness together with high functional diversity in NTAs indicates that this protection strategy is more efficient in terms of conserving biodiversity and ecosystems functions compared to CAs and OAAs (Bellwood et al., 2004; Cardinale et al., 2006; Costello et al., 2010). This helps conserving vital ecosystem functions (Folke et al., 2004). Higher biomass of herbivores belonging to the Scaridae and Acanthuridae families in NTAs generates higher grazing of algae, and might improve the resilience of these coral reefs (Elmhirst et al., 2009; Fox & Bellwood, 2014), and thus reduce the risk of regime shifts from a coral-dominated to algal-dominated habitat (McClanahan et al., 1999; Mumby, 2006). Moreover, Scaridae and Acanthuridae are common target species for artisanal fisheries in the WIO region (McClanahan et al., 1999; McClanahan & Arthur, 2001; Aswani & Sabetian, 2009), and the NTAs in this study might work as sanctuaries for these two fish families. Results indicate that complete protection against fishing, even in small reserves (e.g. Chumbe), gives enough protection for these families to be more abundant. These results validate that the size of an NTA might not be the most important factor contributing to a well-functioning reserve (Halpern, 2003). Low individual fish weight in CAs and OAAs might indicate that the fisheries target preference for large fishes (Bianchi et al., 2000; Vallès & Oxenford, 2014). Hence, not only do the NTAs protect target fish families, but also large-sized fishes. High biomass of fish populations might improve reproduction success since larger and older individuals of fish generate higher recruitments (Trippel et al., 1997). A high biomass of fish inside the NTAs might also gain fisheries in adjacent fishing grounds via “spillover” effects and transportation of adult fish and fish larvae (Rowley 1994; McClanahan & Mangi, 2000; Roberts et al., 2001; Brochier et al., 2013). According to the results in this study, CAs seem not to be more efficient in protecting and conserving fish since

there were no differences in fish biomass, number of species and individual fish weight between CAs and OAAs. This reason for this might be explained by the high fishing pressure in the shallow habitats in the CAs (Lange & Jiddawi, 2009). The location of these CAs, close to local fishing villages, might result in equal high fishing pressure compared to OAAs. There was an effect of proportion live corals on number of fish species and total fish biomass, although the effect of reserve type was stronger, and there was no significant interaction between reserve type and proportion live corals. Even though not significant, the trend seems to be higher coral cover in CAs compared to NTAs and OAAs, although species richness was lower in CAs compared to NTA. Hence, increased coral cover in this study did not generate more species or higher fish biomass. This indicates that the protection against fishing directly influence the fish community variables. This study was, however, made on patchy reefs, and the positive effect of NTAs on coral cover has been shown to be stronger for fringing reefs compared to patchy reefs (McClanahan & Arthur, 2001). Moreover, NTAs in this study is relatively young (<25 years), and potential differences in coral cover might not yet be detectable, since previous studies suggest that the effect might first be noticeable after more than 25 years since closure (Magdaong et al., 2014; McClanahan et al., 2014).

In CA seagrass habitats, functional diversity was higher compared to both NTAs and OAAs. This pattern is unexpected, since there was no difference in number of fish species or total biomass among reserve types in seagrass habitats. In such case, each functional trait was occupied by more species in CAs compared to NTAs and OAAs (Pavoine et al., 2005). This means that the distribution of species over functional traits was more evenly distributed in CAs. This indicates that some utilization of fish (and also invertebrates) might in fact lead to more open functional niches that can be filled by other fish species (Connell, 1978). For instance, harvesting of intertidal invertebrates in CAs of this region is common and mainly done in seagrass habitats (Nordlund et al., 2010; Nordlund & Gullström, 2013). This might reduce possible effects from competition between fish and invertebrates sharing the same food niche (McClanahan et al., 1996). The variation of fish species in seagrass meadows due functional diversity was also affected by *T. ciliatum* shoot density, but the effect from reserve type was stronger. There was, however, a trend indicating that CAs generate higher shoot density of *T. ciliatum* compared to OAAs and NTAs. Gullström et al. (2008) suggest that seagrass structural complexity (canopy height and shoot density) can explain fish assemblage structure. This might also explain the higher functional diversity index in CA seagrass meadows in the present study. In NTA seagrass meadows, the biomass of the Siganidae family was higher compared to OAAs,

where *Siganus sutor* is the dominant species. This is also one of the most commercially important fish species in seagrass meadows in this region (McClanahan & Mangi, 2000; Gell & Whittington, 2002; Eklöf et al., 2006; Hicks & McClanahan, 2012). The NTAs might work as sanctuaries, protecting target fish species from fishing in seagrass habitats. Even though the number of species, total biomass and mean individual fish weight did not differ among reserve types in seagrass habitats, the value of protecting seagrass meadows should not be neglected. Connectivity between seagrass meadows and coral reefs is high, and the effect inside NTA coral reefs might be influenced by the protection of adjacent seagrass meadows, since ontogenetic and feeding migrations between these two habitats are extensive (Ault & Johnson, 1998; Dorenbosch et al., 2005; Verweij et al., 2009; Berkström et al., 2013).

### *Management effects*

Private managed reserves had more species and higher total biomass compared with government managed NTAs in coral reef habitats. Chumbe, Mnemba and Vamizi Island are to some extent private managed reserves, and are dependent on a pristine marine ecosystem as their main income, from tourism (Sternér & Andersson, 1998). Therefore, a proper protection of these reefs should be of high value for these reserves (Francis et al., 2002). The three reserves had guarding boats patrolling the reserve during this study, indicating higher level of protection compared to the government managed NTAs. In contrast, on Mbudya, extensive fishing was seen during the time of this field survey, where people unhindered could practice fishing with line and hook, and at the protected coral reef of Inhaca Island many lines with hooks attached to the reef was found during this study. This indicates higher frequency of illegal fishing inside the government managed NTAs. Hence, management level may not directly be the driving force of the differences in biomass and number of species, but rather the level of protection and guarding of the reserves, and/or the presence/absence of illegal fishing inside the reserves. Consistent to previous studies, this study stresses the importance of enforcement and high protection of MPAs to be efficient in conserving biodiversity in coral-reef habitats (McClanahan et al., 1999; Edgar et al., 2014). Perception by the public on the MPA conservation goals, and possible positive effects on adjacent fishing grounds, could generate a more accepted and further reduce illegal fishing (McClanahan et al., 2006; Kincaid & Rose, 2014). Currently, the understanding of MPA effects in reserve of this study is of low character (Rosendo et al., 2011). This indicates that the local actors did not see the potential advantage from MPAs, and the closing of their fishing grounds. The income from guarding and ecotourism

from MPAs could also generate alternative income sources for people that lose their rights to fish on their formal fishing grounds (Russ et al., 2004; Hind et al., 2010).

No difference in fish community variables between different management levels was detected in seagrass habitats. This indicates that management- or protection level is not as important in generating high species richness and biomass of fish in seagrass meadows as coral reefs. But as mentioned above, the connectivity between these two habitats is high (Ault & Johnson, 1998; Berkström et al., 2012; Berkström et al., 2013), and the high species richness and biomass in coral reefs inside private managed reserves might be influenced by the protection of the seagrass habitats (Verweij et al., 2009). This is an important stress since seagrass habitats seem to be of low interest when establishing MPAs, having a lower recreational value for tourism compared to coral reefs (Milazzo et al., 2002).

#### *Future studies*

McClanahan (2014) suggests that it might take more than 35 years for a protected area to fully recover after enclosure. Hence, the effect of reserve type might be different in the future. Therefore, studies of the same character as this study might be appropriate in the future to evaluate long-term effects of different MPA strategies. Combining invertebrate data from the same region could be of interest to be able to evaluate the relative effect of different species and trophic interactions between fish and invertebrates inside the different reserve types. Many fish species interact with invertebrates, partly as food source but also in terms of competition for food (McClanahan et al., 1996). In future studies, the direct potential “spillover” effects from different MPAs would be interesting to evaluate, by placing OAA sites inside the potential spillover-range, and by that compare which reserve type that generates the highest biomass of fish in this spillover-range.

#### *Conclusion*

High protection of coral-reef habitats influenced the fish community variables positively, and the effect of fishing protection was stronger than the indirect effect of habitat protection. Strictly no-take reserves, governed by private managers, generated higher species richness and biomass of fish compared to government managed reserves. Private reserves in this study had higher levels of guarding and by that potentially reduced illegal fishing inside the reserves compared to government managed reserves. This indicates that the level of guarding is the main reason

for the positive effect on fish community variables, and not the actual reserve- and management types. Total biomass of target fishes belonging to the Scaridae- and Acanthuridae families was higher in NTA coral reefs, indicating sanctuary effects on these two families. This might gain these ecosystems with higher recruitment of fish and more resilient ecosystem functions. Functional diversity was the only variable affected by reserve type in seagrass habitats, where CAs generated a higher functional diversity. This pattern might be explained by harvesting of competitive invertebrates by local people in low- or no protected areas, opening empty functional niches to be filled by fish. Even though species richness and fish biomass did not differ among reserve types in seagrass habitats, the high level of connectivity between seagrass- and coral-reef habitats suggests that protection of seagrass meadows is of high importance. NTAs generate sanctuaries for *S. sutor* in seagrass habitats. This is a commercially important fish species in the WIO region. Scientific indications of positive effects of MPAs, such as “spillover” effects, on adjacent fishing grounds indicate that fisheries outside the reserve borders might gain from a well-functioning MPA.

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**Appendix 1.** All fish species found during the field survey, and functional traits extracted from Fishbase.

<b>Species</b>	<b>Functional group</b>	<b>Max size</b>	<b>Feeding strata</b>	<b>Food type preferred</b>
<i>Abudefduf sexfasciatus</i>	Omnivore	19	Benthopelagic	Zooplankton/algae
<i>Abudefduf sparoides</i>	Omnivore	16	Benthopelagic	Algae/crust
<i>Abudefduf vaigiensis</i>	Omnivore	20	Benthopelagic	Zooplankton/algae
<i>Acanthurus dussumieri</i>	Herbivore	54	Benthic	Algae
<i>Acanthurus leucosternon</i>	Herbivore	54	Benthic	Algae
<i>Acanthurus lineatus</i>	Omnivore	38	Benthic	Algae/crust
<i>Acanthurus nigricauda</i>	Omnivore	40	Benthic	Algae/crust/mol
<i>Acanthurus nigrofuscus</i>	Herbivore	21	Benthic	Algae
<i>Acanthurus tennentii</i>	Herbivore	31	Benthic	Algae
<i>Acanthurus triostegus</i>	Herbivore	27	Benthic	Algae
<i>Acreichthys tomentosus</i>	Omnivore	12	Benthic	Algae/inv
<i>Aethaloperca rogaa</i>	Invertebrates/Piscivore	30	Benthopelagic	Fish/zoobent
<i>Amphiprion akallopisos</i>	Omnivore	11	Benthopelagic	Algae/plank
<i>Amphiprion allardi</i>	Omnivore	15	Benthopelagic	Algae/plank
<i>Anampses caeruleopunctatus</i>	Invertebrates	42	Benthic	Mol/crust
<i>Anampses melanurus</i>	Invertebrates	12	Benthic	Mol/crust
<i>Anampses twistii</i>	Invertebrates	18	Benthic	Mol/crust
<i>Apogon nigripes</i>	Invertebrates	7	Benthopelagic	Crust/plank
<i>Archamia mozambiquensis</i>	Invertebrates	9	Benthopelagic	Crust/plank
<i>Arothron nigropunctatus</i>	Omnivore	33	Benthic	Algae/crust/mol/coral
<i>Aulostomus chinensis</i>	Piscivore	80	Pelagic	Fish
<i>Balistapus undulatus</i>	Omnivore	30	Benthic	Algae/crust/mol/ech
<i>Bodianus axillaris</i>	Invertebrates/Piscivore	20	Benthic	Crustaceans
<i>Caesio caerulea</i>	Planktivore	35	Pelagic	Plankton
<i>Caesio xanthonota</i>	Planktivore	40	Pelagic	Plankton
<i>Calotomus carolinus</i>	Herbivore	54	Benthic	Algae
<i>Calotomus spinidens</i>	Herbivore	30	Benthic	Algae/seagrass
<i>Cantherhines dumerilii</i>	Omnivore	38	Benthic	Algae/crust/mol/ech
<i>Cantherhines fronticintus</i>	Omnivore	25	Benthic	Algae/crust/mol/ech
<i>Cantherhines pardalis</i>	Invertebrates	25	Benthic	Zoobenthos
<i>Canthigaster bennetti</i>	Omnivore	10	Benthic	Algae/inv
<i>Canthigaster solandri</i>	Omnivore	12	Benthic	Algae/crust/mol/ech
<i>Canthigaster valentini</i>	Omnivore	11	Benthic	Algae/crust/mol/ech
<i>Caranx melampygus</i>	Piscivore	117	Pelagic	Fish
<i>Centropyge multispinis</i>	Omnivore	14	Benthic	Algae/Coral
<i>Cephalopholis argus</i>	Invertebrates/Piscivore	60	Benthopelagic	Fish
<i>Cephalopholis boenak</i>	Invertebrates/Piscivore	30	Benthopelagic	Fish
<i>Cephalopholis leopardus</i>	Invertebrates/Piscivore	24	Benthopelagic	Fish/crust
<i>Cephalopholis miniata</i>	Invertebrates/Piscivore	50	Benthopelagic	Fish/crust
<i>Cephalopholis sexmaculata</i>	Invertebrates/Piscivore	50	Benthopelagic	Fish

<i>Cetoscarus bicolor</i>	Herbivore	90	Benthic	Algae
<i>Chaetodon auriga</i>	Omnivore	23	Benthic	Algae/Coral
<i>Chaetodon falcula</i>	Omnivore	20	Benthic	Algae/inv
<i>Chaetodon guttatissimus</i>	Omnivore	12	Benthic	Algae/Coral
<i>Chaetodon interruptus</i>	Omnivore	20	Benthic	Algae/Coral
<i>Chaetodon kleinii</i>	Omnivore	15	Benthic	Algae/Coral/zoopl
<i>Chaetodon lunula</i>	Omnivore	20	Benthic	Algae/Coral/inv
<i>Chaetodon melannotus</i>	Invertebrates	18	Benthic	Corals
<i>Chaetodon meyeri</i>	Invertebrates	20	Benthic	Corals
<i>Chaetodon trifascialis</i>	Invertebrates	18	Benthic	Corals
<i>Chaetodon trifasciatus</i>	Invertebrates	15	Benthic	Corals
<i>Chaetodon vagabundus</i>	Omnivore	23	Benthic	Algae/Coral
<i>Chaetodon xanthocephalus</i>	Omnivore	20	Benthic	Algae/inv
<i>Chaetodon zanzibarensis</i>	Invertebrates	12	Benthic	Corals
<i>Cheilinus chlorourus</i>	Invertebrates	45	Benthic	Corals
<i>Cheilinus fasciatus</i>	Invertebrates	40	Benthic	Mol/crust
<i>Cheilinus oxycephalus</i>	Invertebrates	17	Benthic	Mol/crust
<i>Cheilinus trilobatus</i>	Invertebrates/Piscivore	45	Benthopelagic	Fish/crust/mol
<i>Cheilio inermis</i>	Invertebrates/Piscivore	50	Benthopelagic	Mol/crust/echi
<i>Cheilodipterus arabicus</i>	Invertebrates	18	Benthic	Crustaceans
<i>Cheilodipterus artus</i>	Invertebrates/Piscivore	19	Benthopelagic	Fish
<i>Cheilodipterus quinquelineatus</i>	Invertebrates/Piscivore	13	Benthopelagic	Fish/crust
<i>Chlorurus sordidus</i>	Herbivore	40	Benthic	Algae
<i>Chromis agilis</i>	Omnivore	8	Benthopelagic	Algae/plank
<i>Chromis dimidiata</i>	Omnivore	9	Benthopelagic	Algae/inv
<i>Chromis nigroanalis</i>	Omnivore	12	Benthopelagic	Algae/inv
<i>Chromis nigrura</i>	Planktivore	6	Pelagic	Plankton
<i>Chromis ternatensis</i>	Planktivore	11	Pelagic	Plankton
<i>Chromis weberi</i>	Planktivore	14	Pelagic	Plankton
<i>Chromis viridis</i>	Omnivore	10	Benthopelagic	Algae/plank
<i>Chrysiptera annulata</i>	Omnivore	8	Benthopelagic	Algae/plank
<i>Chrysiptera unimaculata</i>	Omnivore	10	Benthopelagic	Algae/plank
<i>Cirrhitichthys oxycephalus</i>	Invertebrates/Piscivore	10	Benthopelagic	Fish/crust
<i>Cirripectes castaneus</i>	Herbivore	9	Benthic	Algae
<i>Cirripectes stigmaticus</i>	Herbivore	10	Benthic	Algae
<i>Coris aygula</i>	Invertebrates	120	Benthic	Mol/crust/echi
<i>Coris caudimacula</i>	Invertebrates	20	Benthic	Mol/crust/echi
<i>Coris formosa</i>	Invertebrates	60	Benthic	Mol/crust/echi
<i>Corythoichthys flavofasciatus</i>	Invertebrates/Piscivore	12	Benthic	N.A.
<i>Ctenochaetus binotatus</i>	Herbivore	22	Benthic	Algae/detritus
<i>Ctenochaetus striatus</i>	Herbivore	26	Benthic	Algae/cyano
<i>Ctenochaetus truncatus</i>	Herbivore	16	Benthic	Algae
<i>Dascyllus aruanus</i>	Omnivore	10	Benthopelagic	Algae/plank/inv
<i>Dascyllus carneus</i>	Omnivore	7	Benthopelagic	Algae/plank
<i>Dascyllus trimaculatus</i>	Omnivore	11	Benthopelagic	Algae/plank
<i>Diodon liturosus</i>	Invertebrates	65	Benthic	Mol/crust

<i>Echidna nebulosa</i>	Invertebrates/Piscivore	100	Benthic	Crustaceans
<i>Epibulus insidiator</i>	Invertebrates/Piscivore	54	Benthic	Fish/crust
<i>Epinephelus merra</i>	Invertebrates/Piscivore	32	Benthopelagic	Fish
<i>Fistularia commersonii</i>	Invertebrates/Piscivore	160	Benthopelagic	Fish/crust/mol
<i>Forcipiger longirostris</i>	Invertebrates	22	Benthic	Crustaceans
<i>Gerres oyena</i>	Invertebrates	30	Benthic	Mol/crust
<i>Gobiidae sp.</i>	Omnivore	9	Benthic	N.A.
<i>Gomphosus caeruleus</i>	Invertebrates	32	Benthic	N.A.
<i>Grammistes sexlineatus</i>	Invertebrates/Piscivore	30	Benthopelagic	Fish
<i>Gunnelichthys curiosus</i>	Omnivore	12	Benthopelagic	Algae/plank
<i>Halichoeres hortulanus</i>	Invertebrates	27	Benthic	Mol/crust/echi
<i>Halichoeres nebulosus</i>	Invertebrates	12	Benthic	Zoobenthos
<i>Halichoeres nigrescens</i>	Invertebrates	14	Benthic	N.A.
<i>Halichoeres scapularis</i>	Invertebrates	20	Benthic	Crustaceans
<i>Hemigymnus fasciatus</i>	Invertebrates	80	Benthic	Mol/crust/echi
<i>Hemigymnus melapterus</i>	Invertebrates	90	Benthic	Mol/crust/echi
<i>Heniochus acuminatus</i>	Omnivore	25	Benthopelagic	N.A.
<i>Hipposcarus harid</i>	Herbivore	75	Benthic	Algae
<i>Hyporhamphus dussumieri</i>	Invertebrates/Piscivore	38	Pelagic	Fish/crust
<i>Labrichthys unilineatus</i>	Invertebrates	18	Benthic	Corals
<i>Labroides bicolor</i>	Cleaner	15	Bentic	Fishparasites
<i>Labroides dimidiatus</i>	Cleaner	14	Bentic	Fishparasites
<i>Leptoscarus vaigiensis</i>	Herbivore	35	Benthic	Seagrass
<i>Lethrinus harak</i>	Invertebrates/Piscivore	50	Benthopelagic	Fish/crust/mol/ech
<i>Lethrinus lentjan</i>	Invertebrates/Piscivore	52	Benthopelagic	Fish/crust/mol/ech
<i>Lethrinus mahsena</i>	Invertebrates/Piscivore	65	Benthopelagic	Fish/crust/mol/ech
<i>Lethrinus microdon</i>	Invertebrates/Piscivore	80	Benthopelagic	Fish/crust/mol/ech
<i>Lethrinus nebulosus</i>	Invertebrates/Piscivore	87	Benthopelagic	Fish/crust/mol/ech
<i>Lethrinus obsoletus</i>	Invertebrates	60	Benthic	Mol/crust/echi
<i>Lethrinus variegatus</i>	Invertebrates	20	Benthic	Invertebrates
<i>Lutjanus bohar</i>	Invertebrates/Piscivore	90	Benthopelagic	Fish/crust
<i>Lutjanus fulviflamma</i>	Invertebrates/Piscivore	35	Benthopelagic	Fish/crust
<i>Lutjanus gibbus</i>	Invertebrates/Piscivore	50	Benthopelagic	Fish/crust/mol
<i>Lutjanus kasmira</i>	Omnivore	40	Benthopelagic	Plankton
<i>Macolor niger</i>	Invertebrates/Piscivore	75	Benthopelagic	Fish/crust
<i>Macropharyngodon bipartitus</i>	Invertebrates	13	Benthic	Invertebrates
<i>Meiacanthus mossambicus</i>	Omnivore	10	Benthopelagic	Algae/plank
<i>Monotaxis grandoculis</i>	Invertebrates	60	Benthic	Mol/crust/echi
<i>Mulloidichthys flavolineatus</i>	Invertebrates/Piscivore	43	Benthic	Mol/crust/echi
<i>Myrichthys maculosus</i>	Invertebrates/Piscivore	100	Benthic	N.A.
<i>Myripristis murdjan</i>	Planktivore	60	Pelagic	Plankton/crust
<i>Myripristis violacea</i>	Planktivore	35	Pelagic	Plankton/crust
<i>Naso annulatus</i>	Omnivore	100	Benthopelagic	Algae/plank
<i>Naso elegans</i>	Herbivore	45	Benthic	Algae
<i>Naso unicornis</i>	Herbivore	70	Benthic	Leathary algae
<i>Neoglyphidodon melas</i>	Omnivore	18	Benthopelagic	Detritus

<i>Neopomacentrus azysron</i>	Planktivore	8	Pelagic	Plankton
<i>Neopomacentrus fuliginosus</i>	Planktivore	11	Pelagic	Plankton
<i>Novaculichthys taeniourus</i>	Invertebrates	30	Benthic	Mol/crust/echi
<i>Novaculooides macrolepidotus</i>	Invertebrates	16	Benthic	Crustaceans
<i>Ostorhinchus aureus</i>	Invertebrates	15	Benthic	Crustaceans
<i>Ostracion cubicus</i>	Omnivore	45	Benthic	Algae/mol/ech
<i>Ostracion meleagris</i>	Omnivore	25	Benthic	Algae/mol/ech
<i>Oxycheilinus bimaculatus</i>	Invertebrates	15	Benthopelagic	Invertebrates
<i>Oxycheilinus digramma</i>	Invertebrates/Piscivore	40	Benthic	Mol/crust/echi
<i>Oxymonacanthus longirostris</i>	Invertebrates	12	Benthic	Corals
<i>Paracanthurus hepatus</i>	Planktivore	31	Pelagic	Plankton
<i>Paracirrhites arcatus</i>	Invertebrates/Piscivore	20	Benthic	Fish/crust
<i>Paracirrhites forsteri</i>	Invertebrates/Piscivore	22	Benthic	Fish/crust
<i>Parapercis hexophthalma</i>	Invertebrates	29	Benthic	Zoobenthos
<i>Parupeneus barberinus</i>	Invertebrates	60	Benthic	Zoobenthos
<i>Parupeneus ciliatus</i>	Invertebrates/Piscivore	38	Benthic	Crustaceans
<i>Parupeneus cyclostomus</i>	Invertebrates/Piscivore	50	Benthopelagic	Fish/crust
<i>Parupeneus macronemus</i>	Invertebrates	40	Benthic	Crust/worms
<i>Parupeneus rubescens</i>	Invertebrates	43	Benthic	Crust/worms
<i>Parupeneus trifasciatus</i>	Invertebrates/Piscivore	35	Benthopelagic	Fish/crust
<i>Pelates quadrilineatus</i>	Invertebrates/Piscivore	30	Benthopelagic	Fish/crust
<i>Plagiotremus rhinorhynchos</i>	Cleaner	12	Bentic	Fishparasites
<i>Platax teira</i>	Invertebrates/Piscivore	70	Benthopelagic	Fish/crust
<i>Plectorhinchus flavomaculatus</i>	Invertebrates/Piscivore	60	Benthopelagic	Fish/crust
<i>Plectorhinchus gaterinus</i>	Invertebrates/Piscivore	50	Benthopelagic	Fish/crust
<i>Plectorhinchus playfairi</i>	Invertebrates/Piscivore	90	Benthopelagic	Fish/crust
<i>Plectorhinchus vittatus</i>	Invertebrates/Piscivore	72	Benthopelagic	Fish/crust/mol
<i>Plectroglyphidodon dickii</i>	Omnivore	11	Benthopelagic	Algae/plank
<i>Plectroglyphidodon lacrymatus</i>	Omnivore	10	Benthic	Algae/plank
<i>Pomacanthus imperator</i>	Omnivore	40	Benthic	Sponges
<i>Pomacanthus semicirculatus</i>	Omnivore	40	Benthic	Sponges
<i>Pomacentrus aquilus</i>	Omnivore	12	Benthopelagic	Algae/plank
<i>Pomacentrus baenschi</i>	Omnivore	10	Benthopelagic	Algae/plank
<i>Pomacentrus caeruleus</i>	Omnivore	10	Benthopelagic	Algae/plank
<i>Pomacentrus pavo</i>	Omnivore	9	Benthopelagic	Algae/plank
<i>Pomacentrus sulfureus</i>	Omnivore	11	Benthopelagic	Algae/plank
<i>Pomacentrus trichrourus</i>	Omnivore	11	Benthopelagic	Algae/plank
<i>Pomacentrus trilineatus</i>	Omnivore	10	Benthopelagic	Algae/plank
<i>Pseudanthias squamipinnis</i>	Planktivore	15	Pelagic	Plankton
<i>Pseudocheilinus hexataenia</i>	Invertebrates	10	Benthic	Crustaceans
<i>Pseudojuloides argyreogaster</i>	Invertebrates	13	Benthic	N.A.
<i>Pteragogus flagellifer</i>	Omnivore	20	Benthopelagic	Invertebrates
<i>Ptereleotris evides</i>	Planktivore	14	Pelagic	Plankton
<i>Pterocaesio chrysozona</i>	Planktivore	21	Pelagic	Plankton
<i>Pterocaesio tile</i>	Planktivore	30	Pelagic	Plankton
<i>Pygoplites diacanthus</i>	Invertebrates	25	Benthic	Sponges

<i>Rhabdamia gracilis</i>	Invertebrates	6	Pelagic	N.A.
<i>Rhinecanthus rectangulus</i>	Omnivore	30	Benthic	Algae/crust/mol/ech
<i>Sargocentron diadema</i>	Invertebrates/Piscivore	17	Benthic	Mol/crust
<i>Saurida gracilis</i>	Invertebrates/Piscivore	32	Benthic	Fish
<i>Scarus falcipinnis</i>	Herbivore	60	Benthic	Algae
<i>Scarus frenatus</i>	Herbivore	47	Benthic	Algae
<i>Scarus ghobban</i>	Herbivore	90	Benthic	Algae
<i>Scarus niger</i>	Herbivore	40	Benthic	Algae
<i>Scarus psittacus</i>	Herbivore	30	Benthic	Algae
<i>Scarus rubroviolaceus</i>	Herbivore	70	Benthic	Algae
<i>Scarus scaber</i>	Herbivore	37	Benthic	Algae
<i>Scarus tricolor</i>	Herbivore	27	Benthic	Algae
<i>Scarus viridifucatus</i>	Herbivore	45	Benthic	Algae
<i>Scolopsis ghanam</i>	Invertebrates/Piscivore	30	Benthopelagic	Fish/crust/mol/ech
<i>Siganus stellatus</i>	Omnivore	40	Benthopelagic	Algae/plank
<i>Siganus sutor</i>	Herbivore	45	Benthic	Seagrass
<i>Sphyræna flavicauda</i>	Invertebrates/Piscivore	60	Benthopelagic	Fish/crust
<i>Stegastes nigricans</i>	Omnivore	14	Benthopelagic	Algae/plank
<i>Stethojulis albobittata</i>	Invertebrates	14	Benthic	Mol/crust
<i>Stethojulis strigiventer</i>	Invertebrates	15	Benthic	Zoobenthos
<i>Sufflamen chrysopterum</i>	Invertebrates	30	Benthic	Zoobenthos
<i>Thalassoma amblycephalum</i>	Planktivore	16	Pelagic	Plankton
<i>Thalassoma hardwicke</i>	Invertebrates/Piscivore	20	Benthopelagic	Fish/crust
<i>Thalassoma hebraicum</i>	Invertebrates	23	Benthic	Zoobenthos
<i>Thalassoma lunare</i>	Invertebrates	45	Benthic	Fish egg
<i>Thryssa baelama</i>	Invertebrates	11	Pelagic	Zooplankton
<i>Tylosurus crocodilus crocodilus</i>	Piscivore	150	Pelagic	Fish
<i>Zanclus cornutus</i>	Omnivore	23	Benthopelagic	Algae/sponge
<i>Zebrasoma desjardini</i>	Herbivore	40	Benthic	Algae
<i>Zebrasoma scopas</i>	Herbivore	40	Benthic	Algae