



## Protection outcomes for fish trophic groups across a range of management regimes

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### ABSTRACT

Understanding how Marine Protected Areas (MPAs) improve conservation outcomes across anthropogenic pressures can improve the benefits derived from them. Effects of protection for coral reefs in the western and central Indian Ocean were assessed using size-spectra analysis of fish and the relationships of trophic group biomass with human population density. Length-spectra relationships quantifying the relative abundance of small and large fish (slope) and overall productivity of the system (intercept) showed inconsistent patterns with MPA protection. The results suggest that both the slopes and intercepts were significantly higher in highly and well-protected MPAs. This indicates that effective MPAs are more productive and support higher abundances of smaller fish, relative to moderately protected MPAs. Trophic group biomass spanning piscivores and herbivores, decreased with increasing human density implying restoration of fish functional structure is needed. This would require addressing fisher needs and supporting effective MPA management to secure ecosystem benefits for coastal communities.

### 1. Introduction

Reef fishes play critical roles in community dynamics within coral reef habitats where they regulate reef benthic composition by performing different inter-related functional roles. These roles support coral reef ecosystem functions (Pratchett et al., 2011), and importantly, can alter depending on fish size (Bellwood et al., 2019). In the presence of continuing over-exploitation through fishing and habitat degradation through climate change (Hoegh-Guldberg et al., 2018; Reynolds et al., 2005), protection of functionally important fish species is an increasingly prevalent aspect of reef conservation efforts.

Fish assemblages are fundamentally influenced by the resources and shelter provided by coral reefs (Richardson et al., 2018). These bottom-up control mechanisms mean that healthy coral habitats support high fish abundance including juveniles of large-bodied species (Graham et al., 2007), which recruit to become fishable stocks over time. Similarly, high fish productivity is expected where the ecosystem is in better condition, which can be achieved through high levels of protection. Conversely, fishing has a top-down control on reef fishes and continuous

harvesting reduces fish size, abundance and biomass (Zgliczynski and Sandin, 2017; Robinson et al., 2020). High fishing pressure lowers abundance of large-bodied fishes and increases the relative abundance of small-bodied fishes (Graham et al., 2007), causing significant impacts on the size structure of reef fish assemblages (McClanahan et al., 2011). The identification of factors such as reef productivity that influence the size structure of reef fish populations could allow for fisheries management initiatives, which identify specific reef zones for protection (Ojea et al., 2017).

No-take zones in Marine Protected Areas (MPAs) are a widely applied management and conservation measure used to mitigate human associated disturbances, such as fishing, and improve resilience of reefs to climate change (Mellin et al., 2016; Roberts et al., 2017). MPAs can increase fish diversity, biomass, and the number of exploited species in adjacent fishing grounds (Russ et al., 2004; Kough et al., 2019). A network of MPAs ensures different fish sizes and life history stages are protected (Green et al., 2014) and this is critical in the recovery and maintenance of fish biodiversity and productivity, which refers to the rate of generation of biomass in an aquatic system (Halpern, 2003;

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Lester and Halpern, 2008; McClanahan et al., 2007).

Assessing the effectiveness of MPAs in achieving desired objectives requires information from highly protected MPAs, or those in remote locations. This is essential for determining the maximum potential abundance and biomass of fishes or ocean systems (McClanahan et al., 2019; McClanahan et al., 2020; MacNeil et al., 2020). It is now established that the benefits of protected areas depend on their size, age, level of protection, distance to fish markets, levels of compliance, number of staff and budget capacity (Molloy et al., 2009; Gill et al., 2017; Cinner et al., 2018). Yet, it remains unclear how varying levels of protection impact the relative abundance of different fish sizes and overall fish productivity.

Examining the size-spectra of fishes can inform the decision-making process when comparing areas in different geographical locations or management levels (Graham et al., 2007; Polishchuk and Blanchard, 2019). Size-spectra descriptors of slope and intercept are considered robust indicators, able to show fish population structure at different spatial scales (Petchey and Belgrano, 2010; Zgliczynski and Sandin, 2017). These indicators quantify the relative abundance of small and large fish (slope) and the overall productivity of the system (intercept) (Shin et al., 2005). Slope becomes steeper (more negative) when small fish are more abundant than large fish, while intercepts become greater where fish community productivity is high. Due to these properties, size-spectra analysis is a useful tool in evaluating the ecosystem effects of fishing and guiding the management of tropical multi-species and multi-gear fisheries (Graham et al., 2005; Shin et al., 2005; Guiet et al., 2016; Zgliczynski and Sandin, 2017).

Here we use fish density and size data collected from a consistent reef morphology (ocean exposed fringing coral reefs: Andréfouët et al., 2009, Samoily et al., 2019) in the western and central Indian Ocean, to compare size spectra indicators and biomass of trophic groups across a range of management regimes. Trophic groups were selected to represent a wide range of functional roles on coral reefs (Osuka et al., 2018; Parravicini et al., 2020). The study tested the hypotheses that the abundance of both small and large fish is higher in protected areas than unprotected areas and that local human population density influences this protection outcome.

## 2. Methods

### 2.1. Study area

Reefs in the western Indian Ocean (WIO) exhibit a range of geomorphologies, which have been categorised as: ocean-exposed fringing reefs, coastal barrier reef complexes, inner seas patch reef complexes, inner seas exposed fringing reefs, lagoon exposed fringing reef, and bank barrier or bank lagoon reefs (Andréfouët et al., 2009; Samoily et al., 2019). Reef geomorphology strongly influences coral reef fish communities and biomass (Taylor et al., 2015; Samoily et al., 2019). Therefore, this study only focused on fish assemblages within the consistent geomorphology of ocean-exposed fringing reefs (Fig. 1). Fish data were collated from two published studies based on surveys carried out between 2009 and 2015 in the western and central Indian Ocean (Table 1), which rapidly assessed sites that were selected haphazardly to maximize a range of protection levels occurring in the Indian Ocean. A site refers to a reef surveyed on two dives, where fish were counted in two or three replicate transects, with each transects measuring 50 m × 5 m (250 m<sup>2</sup>). Data from WIO were sourced from Samoily et al. (2019). This included data from 24 sites across four countries: Tanzania – seven sites, Mozambique – seven, Comoros – six, and Madagascar – four (Fig. 1). An additional dataset was collected from eight sites in the Chagos Archipelago (Samoily et al., 2018; Fig. 1). These sites were grouped into four protection levels based on the existence and effectiveness of management rules as determined from IUCN protected area categories (IUCN, 2004), consultations with managers, personal knowledge and literature: highly protected, well-protected, moderately protected and unprotected

(fished) (Table 1). Highly protected sites came from the Chagos Archipelago (IUCN category I - strict nature reserve). Well-protected included sites from Mafia Marine National Park (IUCN category VI - protected area with sustainable use of natural resources), Metundo and Vamizi Islands (no assigned IUCN category but considered as effective in-situ conservation areas, due to high awareness and adherence to informal management practices). Moderately protected sites from Mnazi Bay-Ruvuma Estuary Marine Park (IUCN category VI) and Mnemba Island Marine Conservation Area (IUCN category VI) (Supporting information Table S1). Fished sites were drawn from Comoros and Ambodivahibe and Loky in Madagascar. Data on human population counts and reef area (km<sup>2</sup>) in 2015 and within a radius of 20 km of site geographic coordinates, were derived from the Marine Socio-Environmental Covariates dataset (Yeager et al., 2017). Human population counts at each site were divided by reef area and log transformed to calculate local population density. Highly protected areas had zero human population values yielding a minimal population category. This was followed by well-protected, moderate protection and fished areas that were categorised as lightly, moderately, and heavily populated, respectively (Table 1). Highly protected areas were located in remote areas with very low human population and also showed relatively high compliance with no-take zone (NTZ) management rules (Sheppard et al., 2012), therefore the reef system was considered as a remote highly protected area.

### 2.2. Fish surveys

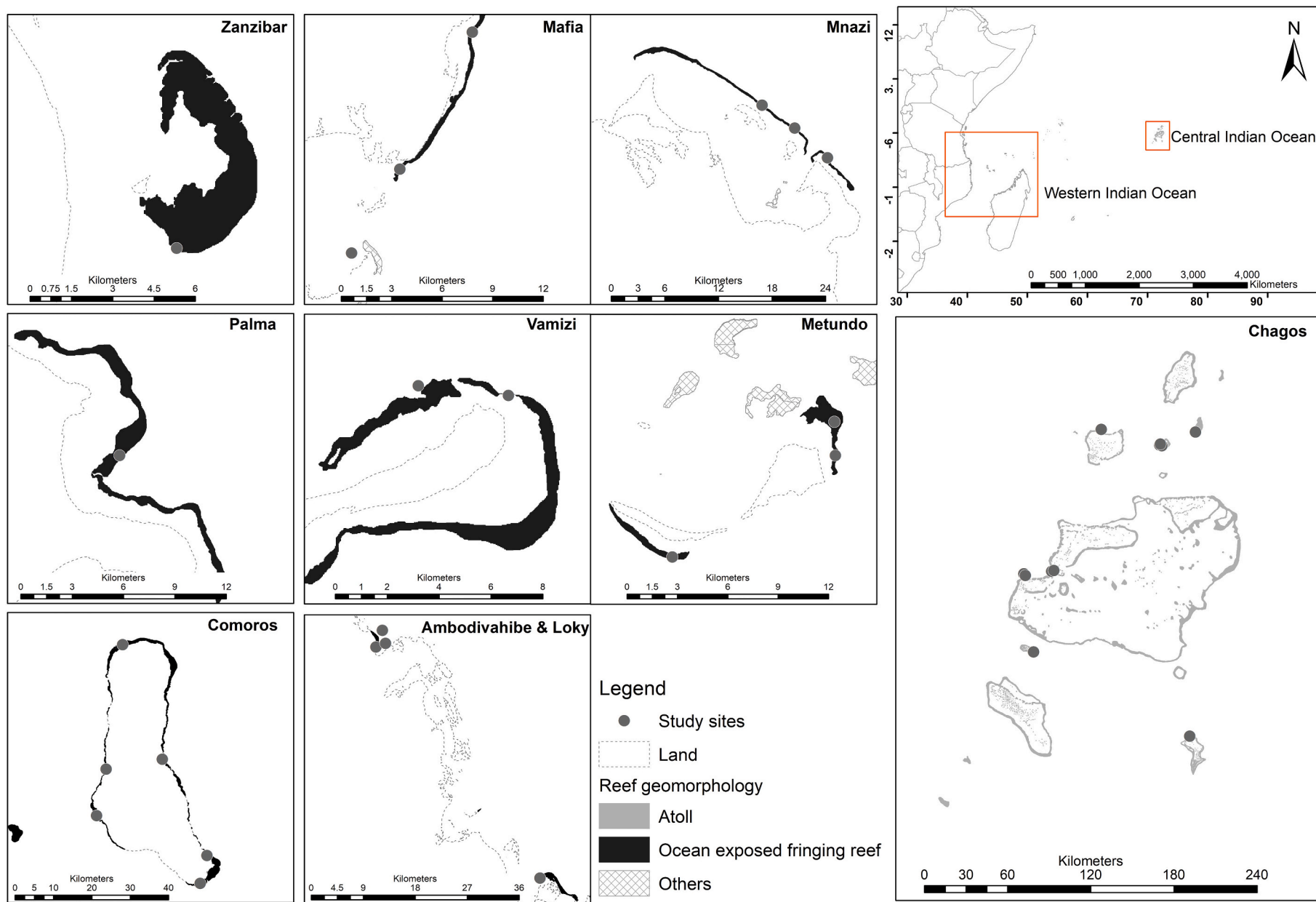
Fish surveys were conducted based on methods detailed in Samoily et al. (2019). The surveys involved estimating fish species densities and total lengths (TL) in 5 cm size classes from 6 cm, by an experienced diver (M.A.S) with over 20 years' experience of conducting Underwater Visual Census (UVC) surveys.

A total of 155 fish species from 11 families (Acanthuridae, Balistidae, Caesionidae, Chaetodontidae, Haemulidae, Lethrinidae, Lutjanidae, Pomacanthidae, Serranidae, Scarinae (Labridae) and Siganidae) were surveyed. The families and species were chosen because they are good indicators of disturbance effects across all trophic levels (Samoily and Randriamanantsoa, 2011). The biomass of each species was calculated based on length–weight relationships presented in Samoily et al. (2018). Species were assigned to the following trophic groups: piscivores, omnivores, corallivores, invertivores, planktivores, detritivores and herbivores (Osuka et al., 2018; Samoily et al., 2019; Parravicini et al., 2020). The herbivores included six sub-groups composed of: large excavators, small excavators, scrapers, browsers, grazers and grazers-detritivores (Bellwood et al., 2019).

### 2.3. Data analysis

Multivariate dimensional scaling (MDS) analyses based on Bray-Curtis similarity index were performed on log (x + 1) transformed fish density and biomass data with an assumption that the influence of protection outweighed site differences. This was after performing MDS based on location and a combined factor of location and protection (Supplementary material Fig. S1a–d). A permutation-based hypothesis testing analysis of similarities (ANOSIM) was used to compare fish density and biomass across the four protection levels (Clarke and Gorley, 2006).

Size-spectra analysis was performed for each site based on fish densities in each of the 19 size classes ranging from 11 to 105 cm. This involved determining the slope and intercept of a linear regression of log transformed midpoint of size classes and log<sub>10</sub> (x + 1) transformed count data. Prior to analysis, the midpoint lengths were centred across the size range at a site, thereby removing the correlation between slope and intercept (Daan et al., 2005). The mean slopes and intercepts of protection levels were compared using One-way ANOVA (Zar, 1999). Tukey's post-hoc tests were then performed to determine significant pairwise protection differences.



**Fig. 1.** Map of the survey sites from the western Indian Ocean (WIO) and central Indian Ocean (CIO). WIO survey sites comprised reefs sampled in Tanzania (Zanzibar, Mafia and Mnazi), Mozambique (Palma, Vamizi and Metundo), Comoros and Madagascar (Ambodivahibe and Loky). CIO survey sites were sampled from the Chagos Archipelago.

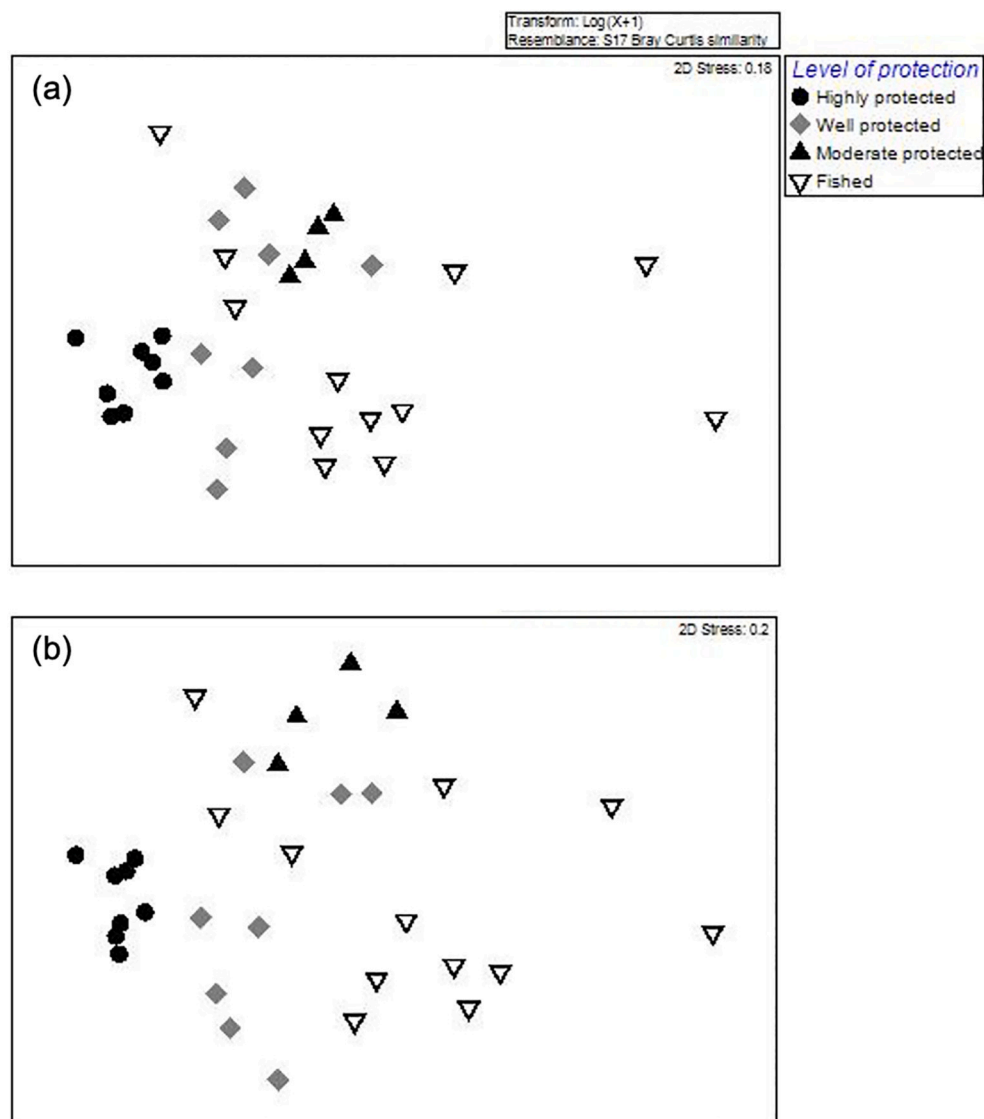
**Table 1**

Details of fish survey sites in ocean exposed fringing reefs and atolls with their depths, reef type, protection index and local human population density derived from the Marine Socio-Environmental Covariates data set (Yeager et al., 2017). Protection levels are defined as: high protection - a gazetted no-take marine protected area (MPA) in remote location with strict enforcement; well-protected - a gazetted MPA or a tourism zone with informal rules and good enforcement; moderate protection - a gazetted MPA established though effectiveness weak due to poor enforcement; Fished – reef with no management in place at all. (Data sources: Samoilyls et al., 2018; Samoilyls et al., 2019).

Protection level	Location (sites)	Max - Min depth (m)	Reef type	Local human population density (log <sub>10</sub> persons per km <sup>2</sup> of reef)	
				Mean (±SE)	Population category
High protection	Chagos (8)	3 - 23	Forereef and terrace	0.00 (0.00)	Minimal
Well protected	Mozambique (4), Tanzania (3)	3 - 22	Forereef and deep terrace	1.58 (0.21)	Lightly populated
Moderate protection	Tanzania (4)	5 - 22	Forereef and deep terrace	2.62 (0.10)	Moderately populated
Fished	Madagascar (4), Comoros (6), Mozambique (3)	3 - 20	Forereef	2.98 (0.17)	Heavily populated

Reef area is an important variable controlling fish productivity (Williams et al., 2015), therefore biomass data were divided by reef area derived from the Marine Socio-Environmental Covariates dataset (Yeager et al., 2017) before comparing protection levels. Differences in fish trophic group biomass among protection levels were tested using a One-way Kruskal-Wallis test after failing both normality and homogeneity of variance tests using Shapiro-Wilk and Levene tests respectively,

even after log-transformations (Zar, 1999). Mann-Whitney post-hoc tests were then performed to determine significant pairwise differences. Differences in the human population densities were only compared between three protection levels (well-protected, moderately protected and fished areas) using one-way ANOVA followed by Tukey’s post-hoc tests after passing normality and homogeneity tests. Highly protected areas showed no variance in human population density. The relationship



**Fig. 2.** Multi-dimensional scaling plots based on Bray-Curtis similarity statistic on fish species: a) density and b) biomass between four protection levels from five countries in western and central Indian Ocean.

between trophic groups, and human population density was then assessed using generalised additive models (GAMs) using the *mgcv* package in R ([www.r-project.org](http://www.r-project.org)). Contribution of the predictors to the model was assessed from GAMs effective degrees of freedom (edf), which represents the complexity of the smoothing term. An edf of 1 represents a straight line or a linear effect while an edf of  $\geq 2$  describes a non-linear effect. To validate the influence of human population on the biomass of trophic groups, effect of spatial autocorrelation was checked using Moran's I test (Supplementary material Table S2). Where spatial autocorrelation was detected, generalised least squares regression models were fitted using five different types of spatial correlation structures (exponential, gaussian, spherical, linear, and rational quadratic). Akaike information criterion (AIC) model selection method was thereafter applied to select the best model in comparison to a model without spatial autocorrelation structure.

### 3. Results

#### 3.1. Fish community structure

MDS plot of fish community biomass and density showed that sites separated out largely in relation to the four protection levels (Fig. 2). However, a few of the fished sites particularly in Mozambique overlapped in multivariate space with well and moderately protected sites. ANOSIM results revealed a clearer protection pattern in fish biomass ( $R = 0.435$ ;  $p < 0.001$ ) than in fish density ( $R = 0.315$ ;  $p < 0.001$ ). All protection levels showed significant differences in fish biomass; but with fish density, only highly protected areas differed significantly from well-protected, moderately protected and fished areas (Table 2).

#### 3.2. Size-spectra and protection

The mean slope differed considerably across protection levels (Fig. 3; ANOVA  $F_{3, 28} = 9.87$ ,  $p < 0.001$ ). Post-hoc Tukey's tests showed that slopes in the highly protected areas were similar to well-protected areas but significantly more negative than moderately protected and fished areas (Table 3a). The means of intercepts also varied considerably across protection levels (Fig. 3; ANOVA  $F_{3, 28} = 12.00$ ,  $p < 0.001$ ). Post-hoc Tukey's tests showed overall productivity in the highly protected areas was greater than moderately protected and fished areas while well-protected areas showed greater intercepts than fished areas (Table 3b).

#### 3.3. Influence of protection on fish biomass

The median biomass of trophic groups showed significant differences across the four levels of protection except for detritivores, browsers and grazer detritivores (Table 4). Mann-Whitney post-hoc tests showed that in all trophic groups except invertivores, the highest biomass, more than 2.6 fold, was seen in highly protected areas compared to all other

**Table 2**

Results from ANOSIM tests showing global and pairwise tests on fish density and biomass between protection levels. Bolded *p*-values indicate significant comparisons.

	Density		Biomass	
	R value	<i>P</i> value	R value	<i>P</i> value
Global test	0.315	<b>0.001</b>	0.435	<b>0.001</b>
Pairwise tests				
High protection, Well-protected	0.568	<b>0.002</b>	0.575	<b>0.001</b>
High protection, Moderate protection	0.998	<b>0.002</b>	1.000	<b>0.002</b>
High protection, Fished	0.403	<b>0.001</b>	0.527	<b>0.002</b>
Well-protected, Moderate protection	0.165	0.121	0.331	<b>0.030</b>
Well-protected, Fished	0.120	0.089	0.241	<b>0.011</b>
Moderate protection, Fished	0.002	0.473	0.251	<b>0.050</b>

protected or fished areas (Fig. 4). Scrapers, invertivores and large excavators had higher biomass in fished areas than moderately protected or well-protected areas (Fig. 4). The biomass of piscivores, omnivores, planktivores, small excavators and grazers was similar across well-protected, moderately protected and fished areas, while scrapers showed higher biomass in well-protected areas compared to moderately protected areas (Fig. 4).

#### 3.4. Influence of local human population on fish biomass

Comparisons of local human population density excluding zero data from remote highly protected areas, revealed significant differences across protection levels (ANOVA  $F_{2, 21} = 5.61$ ,  $p = 0.011$ ). A pairwise Tukey's test showed that only well-protected areas were located in areas with low human density ( $1.58 \pm 0.21(\text{se}) \log_{10}$  persons per  $\text{km}^2$  of reef) compared to fished areas ( $2.98 \pm 0.17(\text{se}) \log_{10}$  persons per  $\text{km}^2$  of reef).

A significant nonlinear relationship signified by an edf  $\geq 2$  was evident in nine trophic groups notably: piscivores, omnivores, planktivores, detritivores, large excavators, small excavators, scrapers, grazers and grazer-detritivores (Table 5). Overall, biomass decreased with increasing human density except for detritivores, grazers and grazer-detritivores (Fig. 5). Detritivores and grazers showed high biomass in both minimal and heavily populated areas and low biomass in moderately populated areas (Fig. 5). Grazer-detritivores showed no apparent pattern although elevated biomass was observed in moderately populated areas. Relationships within the other four trophic groups were not significant. Models without spatial autocorrelation effects showed significant decrease in biomass with increasing human population density for piscivores, planktivore, large- and small excavators (Table 6).

### 4. Discussion

This study revealed three key findings. Firstly, size spectra analysis showed fish community size structure on coral reefs in the western and central Indian Ocean varied according to protection level. However, similar fish community size structure was found between highly protected and well-protected areas. Secondly, effects of protection on fish trophic groups differed but were highest between remote highly protected areas and other protection levels. Moderately protected areas showed no apparent benefits in biomass for any of the trophic groups. Thirdly, the biomass of nine trophic group showed significant non-linear relationships with human population density. However, clearer linear biomass reductions with increasing human population were only evident four trophic groups spanning piscivores to herbivores. This indicates protected and fished areas in close proximity to high human population densities are likely to have low biomass of key trophic groups, particularly piscivores, planktivores, large- and small excavators (Cinner et al., 2013; Robinson et al., 2017). These results illustrate the value of remote highly protected areas (Graham et al., 2013; Samoilys et al., 2018; Cinner et al., 2020) in illuminating the effects of protection of coral reefs in the WIO region.

#### 4.1. Implications of size-spectra indicators

A high proportion of small fish was found in highly protected areas, inconsistent with expected size spectra slopes of minimally populated areas. This potentially reflects removal of meso-predators by top-predators or previous fishing effects leading to prey release (Stallings, 2009; Sandin et al., 2010). Indeed, a previous study in the Chagos Archipelago noted fewer large-sized *Epinephelus* spp. groupers in 2014, which was attributed to lag effects of a previous handline fishery that closed in 2010 (Samoilys et al., 2018). Given a four-year period may not be adequate to allow recovery, this could explain why high and well-protected sites showed similar results. While relatively larger fish occurred in highly protected areas compared to moderately protected and fished areas, their influence on shallowing the size-spectra slopes

**Table 3**

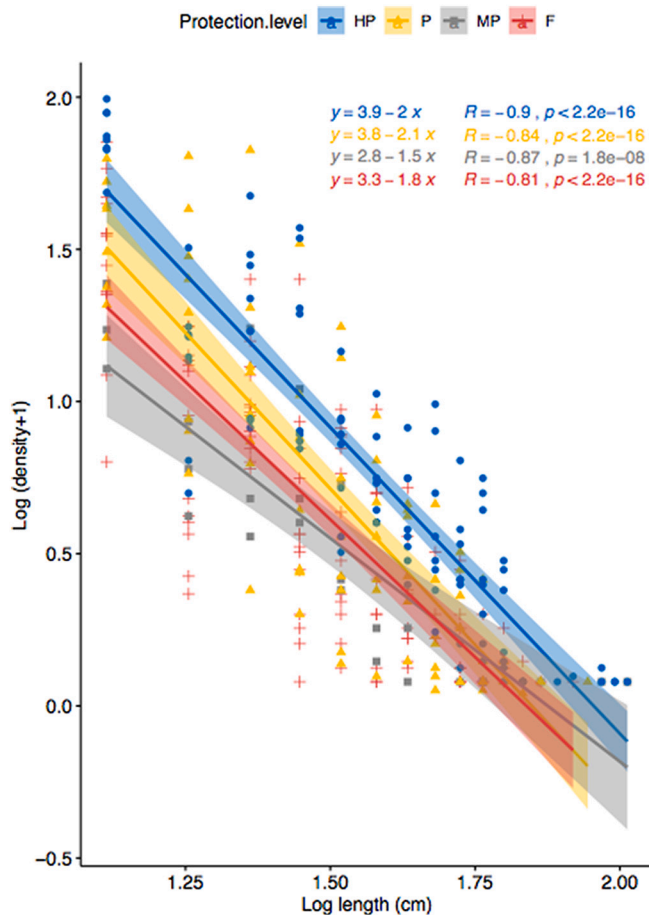
Tukey post-hoc pairwise test results with F values (unshaded) and p-values (shaded) for size spectra slopes and size intercepts. Significant comparisons are bold.

a) Slope

	Fished	Moderate-protection	Well-protected	High protection
Fished		0.8763	0.104	<b>0.001</b>
Moderate-protection	1.060		0.377	<b>0.007</b>
Well-protected	3.369	2.309		0.234
High protection	6.116	5.057	2.747	

b) Intercept

	Fished	Moderate-protection	Well-protected	High protection
Fished		0.997	<b>0.010</b>	<b>0.001</b>
Moderate-protection	0.300		0.153	<b>0.001</b>
Well-protected	3.385	3.085		0.125
High protection	6.625	6.324	3.239	



**Fig. 3.** Relationships between fish length and density for four protection levels in western and central Indian Ocean. HP = high protection, P = well-protected, MP = moderate protection and F = fished. Shaded area around the line is 95% confidence interval.

was overwhelmed by the exceptionally high abundance of small fish. This suggests that processes other than exploitation, may be driving fish abundance and increasing the proportions of small fish.

Steeper size-spectra slopes reflect fewer large-sized individuals, more small fish, or a combination of both (Wilson et al., 2010). In this study, steeper size-spectra slopes were seen in highly and well-protected areas and were due to relatively high densities of small fish, which occurs when the majority of small fish that would usually be composed of juveniles of larger fish species are protected (Russ et al., 2018). While the

size spectra result in this study represented the community level processes, it is possible that the proportion of large individuals acting as parental stocks in highly and well-protected areas is sufficient to support and maintain a high abundance of small fish. This could indicate that processes such as recruitment rates, are propelling fish abundance (Russ et al., 2018) thereby increasing the densities of small fish. Accordingly, the shallower slopes in moderately protected and fished areas could suggest lower rates of juvenile recruitment, which is a concern for sustainability of the fish populations in these areas (Graham et al., 2007; Russ et al., 2018). Therefore, implementation of well-enforced MPAs will be critical in enhancing recruitment and supporting the long-term viability of reef fish populations in the WIO region.

Greater fish productivity overall also occurred in highly and well-protected areas. This can be linked to several key factors in these areas: high compliance to management rules, remoteness, low human population densities and reef condition. Fishing removes target species, changing community size structure and overall fish biomass (Zgliczynski and Sandin, 2017). High exploitation rates are expected in densely populated areas such as those next to moderately protected sites in Tanzania, and fished sites in Madagascar and Comoros, posing a management challenge, particularly where the use of destructive and indiscriminate fishing methods and poaching occurs (Mwaipopo, 2008). Interestingly, some fished sites in Mozambique grouped with sites under well- and moderately protected regimes suggesting their potential to support high fish productivity possibly due to use of low-technology and sustainable artisanal fishing gears (Osuka et al., 2020).

Collectively, the size-spectra results suggest that fisheries may not influence the slope as expected but could reduce overall productivity. This could either be because the fisheries target all fish and not only larger fish, or the fisheries have impacted ecosystem condition and productivity by removing key species or using destructive methods.

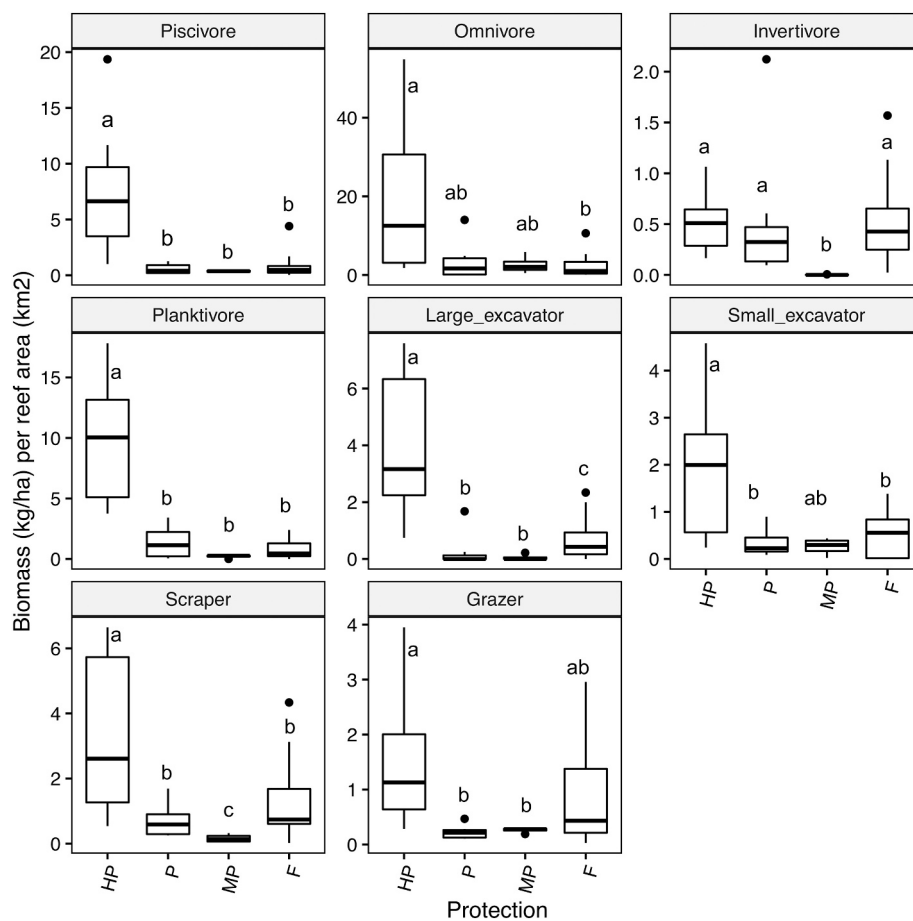
#### 4.2. Influence of protection on trophic groups

Moderately protected areas showed low biomass within a wide range of trophic groups, which is a conservation concern for the MPAs in the WIO. Indeed, moderately protected areas exhibited no significant benefits to any fish trophic groups. This is important and alarming, as it indicates that the lack of effective management regulations in well-protected areas can drastically reduce the biomass to levels equivalent or lower than those found in fished areas. Since larger fish in moderately protected areas are generally fished out first (McClanahan and Mangi, 2000), overall fish productivity is also expected to reduce.

Highly protected areas were effective in sustaining high biomass of piscivores, which can exert top-down control on fish of lower trophic levels. Similarly, highly protected areas had higher biomass of omnivores than fished areas. The lack of apparent differences in the biomass of two key fishery target trophic groups (piscivores and omnivores)

**Table 4**  
Tabulated medians and interquartile range (IR) and one-way Kruskal-Wallis tests on trophic group biomass compared between four protection levels.

Variable	High protection		Well protected		Moderate protection		Fished		Kruskal-Wallis	
	Median	IR	Median	IR	Median	IR	Median	IR	H-value	p-value
Trophic group biomass (kg/ha) per reef area (km <sup>2</sup> )										
Piscivores	6.63	3.45, 11.0	0.40	0.17, 1.19	0.36	0.25, 0.43	0.47	0.21, 1.12	15.44	<0.001
Omnivores	12.52	2.61, 37.3	1.66	0.05, 4.86	2.07	0.76, 5.02	1.02	0.30, 3.35	7.96	0.047
Invertivores	0.50	0.23, 0.70	0.32	0.10, 0.60	0.00	0.00, 0.00	0.42	0.24, 0.75	10.89	0.012
Planktivores	10.03	4.79, 15.91	1.13	0.11, 2.26	0.26	0.06, 0.28	0.45	0.21, 1.3	19.12	<0.001
Detritivores	0.56	0.36, 1.02	0.14	0.07, 0.27	0.12	0.02, 0.19	0.30	0.17, 1.32	1.42	0.231
Large excavators	3.16	1.94, 6.36	0.00	0.00, 0.24	0.00	0.00, 0.16	0.42	0.16, 1.20	19.76	<0.001
Small excavators	1.99	0.36, 2.8	0.22	0.09, 0.62	0.29	0.07, 0.42	0.55	0, 0.84	8.36	0.039
Scrapers	2.60	0.88, 6.08	0.58	0.27, 1.07	0.13	0.06, 0.29	0.74	0.56, 1.76	12.52	0.006
Browsers	0.67	0.11, 1.65	1.14	0.12, 2.03	0.29	0.14, 0.55	0.52	0.15, 1.00	2.33	0.506
Grazers	1.12	0.47, 2.23	0.21	0.11, 0.28	0.27	0.21, 0.29	0.43	0.17, 1.47	9.86	0.020
Grazer detritivores	0.35	0.06, 0.56	0.03	0.00, 0.29	0.00	0.00, 0.37	0.31	0.13, 0.8	6.74	0.080



**Fig. 4.** Median biomass of trophic groups that showed significant differences across protection levels from western and central Indian Ocean. The lowercase letters above each box show Mann-Whitney posthoc test with unique letters indicating significant differences and duplicated letters showing no statistical significance. HP = high protection, P = well-protected, MP = moderate protection and F = fished.

between well-protected, moderately protected and fished areas suggest that these groups may require highly protected MPAs to thrive (Edgar et al., 2014; MacNeil et al., 2020).

The biomass of planktivorous fish was also particularly high in highly protected areas compared to other protection levels within the WIO. Planktivorous fish rely on allochthonous planktonic food materials including pelagic zooplankton, and are more abundant in exposed reef areas, where suspended food levels are high (McLachlan and Defeo, 2017). The high biomass in highly protected areas in this study may have been driven by the high abundance of pelagic zooplankton resulting from upwelling along the Seychelles-Chagos ridge (Sheppard

et al., 2012). Significant inter-atoll differences in planktivores have been reported in these areas (Samoilys et al., 2018) and such localised processes coupled with fishing effects are important in understanding the dynamics in abundance of planktivorous fishes.

The overall biomass of herbivorous fish was consistently low in moderately protected areas. In particular, scrapers were more than four-fold lower in moderately protected than well-protected areas. Since herbivores are critical for enhancing reef resilience through regulating competition between algae and corals, their loss in moderately protected areas may increase algal dominance and associated ecological phase shifts and reef-scale productivity (Hughes et al., 2007). Such a risk can

**Table 5**

Generalised additive model results for the biomass (kg per ha per km<sup>2</sup> of reef) of 11 trophic groups showing effective degrees of freedom (edf), deviance explained by the model for their relationships with human population from five locations in western and central Indian Ocean. Bolded p-values indicate significant relationships.

Trophic group	edf	p-value	Deviance explained (%)
Piscivores	2.8	<0.001	50.7
Omnivores	2.3	<b>0.016</b>	31.8
Invertivores	1.8	0.209	14.0
Planktivores	2.9	<0.001	67.2
Detritivores	4.7	<0.001	73.5
Large excavators	2.9	<0.001	56.0
Small excavators	2.0	<b>0.003</b>	37.0
Scrapers	2.3	<b>0.014</b>	33.2
Browsers	1.0	0.642	0.7
Grazers	3.6	<0.001	54.7
Grazer-detritivores	7.0	<b>0.047</b>	48.5

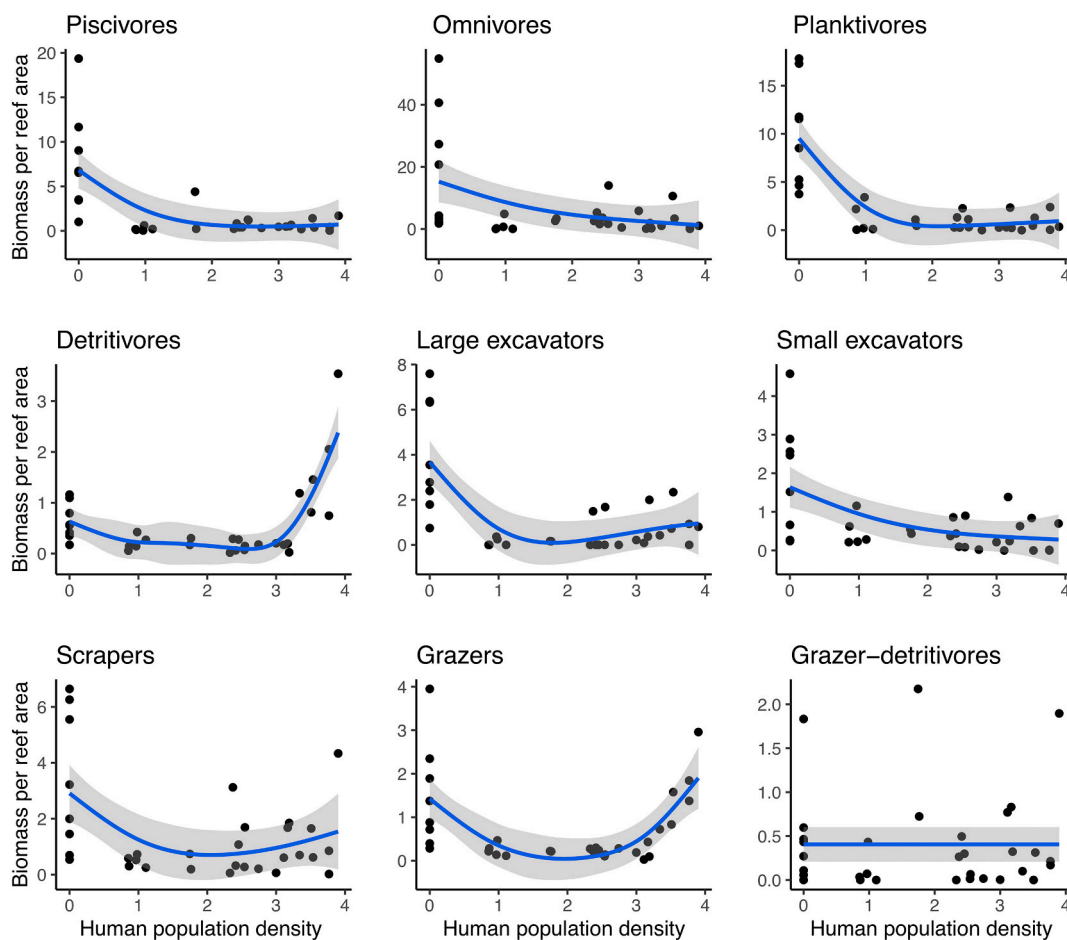
be counteracted through management measures that protect and increase the abundance and biomass of small-bodied herbivores (Kuempel and Altieri, 2017).

**4.3. Influence of human population on trophic groups**

Local human population densities appear to be a key driver of the coral reef fish biomass patterns found in the WIO. Fisheries target trophic groups such as piscivores and omnivores are sensitive to fishing pressure, and where human population density is high, their biomass

can reduce significantly, leading to cascading impacts on ecosystem functioning and triggering loss of functional roles (Zgliczynski and Sandin, 2017). The ultimate outcome of a reduction in biomass of piscivores can be changes in food web interactions that result in prey release (Sandin et al., 2010). Equally, in populated areas, planktivorous fishes experience increased fishing pressure (McClure et al., 2021) and would need protection to maintain a high biomass especially when ecological drivers such as upwelling shift or fail (Jacobs et al., 2020).

Within herbivorous fishes, large- and small excavators showed a significant decrease in biomass with increasing human population density. This demonstrates susceptibility of herbivores to fishing, though in heavily populated areas, various sub-trophic groups particularly detritivores, scrapers and grazers can show increased biomass per reef area. The different patterns reflect the importance of both physical (such as reef type and reef area) and human (such as fishing pressure and market demand) factors (Cinner et al., 2013; McClure et al., 2021) in shaping herbivorous fish biomass. The high biomass of detritivores in heavily populated areas points to a reef system in an altered ecosystem condition having a high cover of rubble and organic matter in sediment and reef surface (Tebbett et al., 2017). Taken together, our findings suggest that maintenance and in turn restoration of key trophic groups requires high levels of protection while ensuring fishers livelihood needs are met (Cinner et al., 2013; MacNeil et al., 2020). This can be challenging as many locations become more populated therefore calling for effective multiple-use zones that could balance protection goals and human uses.



**Fig. 5.** Relationship using generalised additive model (GAM) smoothing method between local human population density (log persons per km<sup>2</sup>) and biomass (kg/ha) per reef area (km<sup>2</sup>) of nine fish trophic groups sampled from western and central Indian Ocean.



**Table 6**

Coefficients of the best generalised least squares models showing the relationship between human population density and biomass of 11 trophic groups from five locations in central and western Indian Ocean. Models were selected from different types of spatial autocorrelation structures (exponential, gaussian, spherical, linear, and rational quadratic) using the Akaike Information Criterion (AIC) model selection process. Bolded *p*-values indicate significant relationships.

Trophic group	Autocorrelation structure	Coefficient	Estimate	se	t-value	<i>p</i> -value
Piscivores	Gaussian	Intercept	5.763	1.484	3.882	<b>0.001</b>
		Human population	-1.748	0.653	-2.679	<b>0.012</b>
Omnivores	Spherical	Intercept	11.795	4.765	2.475	<b>0.019</b>
		Human population	-2.861	2.167	-1.320	0.197
Invertivores	Gaussian	Intercept	0.356	0.143	2.495	<b>0.018</b>
		Human population	0.059	0.061	0.956	0.347
Planktivores	Gaussian	Intercept	7.671	1.734	4.425	<b>0.000</b>
		Human population	-2.480	0.787	-3.152	<b>0.004</b>
Detritivores	Gaussian	Intercept	0.381	0.246	1.545	0.133
		Human population	0.156	0.108	1.438	0.161
Large excavators	Spherical	Intercept	2.402	0.898	2.675	<b>0.012</b>
		Human population	-0.540	0.362	-1.492	<b>0.046</b>
Small excavators	Gaussian	Intercept	1.521	0.265	5.745	<b>0.000</b>
		Human population	-0.386	0.114	-3.390	<b>0.002</b>
Browsers	Gaussian	Intercept	1.060	0.349	3.038	0.005
		Human population	-0.071	0.150	-0.470	0.642
Scrapers	Rational quadratic	Intercept	2.377	0.670	3.549	0.001
		Human population	-0.420	0.300	-1.403	0.171
Grazers	Exponential	Intercept	0.850	0.386	2.203	<b>0.035</b>
		Human population	-0.082	0.174	-0.473	0.640
Grazer detritivores	Exponential	Intercept	0.392	0.173	2.272	<b>0.030</b>
		Human population	0.007	0.074	0.096	0.924

#### 4.4. Role of MPAs and no-take zones

Small-sized fish may be responsible for fuelling reef trophodynamics and maintaining high community biomass (Brandl et al., 2019). A high biomass of small-sized trophic groups, notably planktivores, small-excavators, grazers and scrapers occurred in remote highly protected areas, indicating the benefits of well-enforced MPAs in protecting small fish. These benefits were also visible in well-protected areas where human population density was relatively low. Moderately protected areas were less effective in supporting high biomass of most invertivores, large excavators and scrapers. Invertivores feed on coral competitors such as soft corals and invertebrates (Kramer et al., 2015), while large excavators and scrapers play considerable roles in bioerosion and removal of algae, sediment and other material from reef substrate. Therefore, the low biomass of invertivores and herbivorous fishes in moderately protected areas is a concern for reef resilience (Jouffray et al., 2015) given feeding on coral competitors can prevent the substrate from being overgrown by macroalgae thus allowing coral recruits to settle. The low biomass in moderately protected areas is similar to a study in Kenya that found Reserve MPAs (where fishing using traditional gears is allowed) were inadequate for maintaining or restoring reef fishes compared with no-take Park MPAs (Samoilys et al., 2017). Indeed, moderately protected areas in Mnazi Bay have experienced dynamite fishing in the past (Mwaiopopo, 2008), which caused coral reef destruction and overexploitation of fishes (Wells, 2009). Thus, recovery of parental fish stocks from such historic pressures is likely to take several years.

Overall, our results highlight the ever-greater need to invest in MPAs and strengthen and support management regimes, particularly for the moderately protected MPAs, and within areas of high human population density. As more MPAs are expected to be established to meet the Convention of Biodiversity (CBDs) 30% by 2030 targets (CBD, 2021), our findings suggest that biodiversity conservation targets are more likely not to be met unless an expansion of MPAs in populated areas, is accompanied by changes in human behaviour reducing impacts on marine resources. Ensuring high levels of protection and effective MPA networks in the WIO region can help realise the benefits observed in highly protected areas. Coral reefs occurring in well-protected and in lightly populated locations in the WIO are associated with high fish biomass of key trophic groups which in turn support coastal fishing

communities (Chirico et al., 2017; Ban et al., 2019). Increasing community support for MPAs through measures that encourage compliance to management rules and addressing fish demand aspects related to high fishing pressure can help improve effectiveness of MPAs and also restore the functional roles played by different trophic groups. This will increase the resilience of coral reef fish communities and contribute towards sustainable livelihood security.

#### CRediT authorship contribution statement

Kennedy E. Osuka - Conceptualization, methodology, formal analysis, visualisation, writing - original draft. Bryce D. Stewart - Supervision, writing - review & editing. Melita A. Samoilys - funding acquisition, field sampling, writing - review & editing. Ronan C. Roche - Field sampling, writing - review & editing. John Turner - Funding acquisition, writing - review. Colin McClean - Supervision, writing - review & editing.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2021.113010>.

## References

- Andréfouët, S., Chagnaud, N., Kranenburg, C.J., 2009. Atlas of Western Indian Ocean Coral Reefs. Centre IRD de Nouméa, New-Caledonia.
- Ban, N.C., Gurney, G.G., Marshall, N.A., Whitney, C.K., Mills, M., Gelcich, S., Bennett, N. J., Meehan, M.C., Butler, C., Ban, S., Tran, T.C., 2019. Well-being outcomes of marine protected areas. *Nat.Sustain.* 2 (6), 524–532. <https://doi.org/10.1038/s41893-019-0306-2>.
- Bellwood, D.R., Streit, R.P., Brandl, S.J., Tebbett, S.B., 2019. The meaning of the term 'function' in ecology: a coral reef perspective. *Funct. Ecol.* 33 (6), 948–961. <https://doi.org/10.1111/1365-2435.13265>.
- Brandl, S.J., Tornabene, L., Goatley, C.H., Casey, J.M., Morais, R.A., Côté, I.M., Baldwin, C.C., et al., 2019. Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning. *Science* 364 (6446), 1189–1192. <https://doi.org/10.1126/science.aav3384>.
- Chirico, A.A., McClanahan, T.R., Eklóf, J.S., 2017. Community-and government-managed marine protected areas increase fish size, biomass and potential value. *PLoS one* 12 (8), e0182342. <https://doi.org/10.1371/journal.pone.0182342>.
- Cinner, J.E., Graham, N.A., Huchery, C., MacNeil, M.A., 2013. Global effects of local human population density and distance to markets on the condition of coral reef fisheries. *Conserv. Biol.* 27 (3), 453–458. <https://doi.org/10.1111/j.1523-1739.2012.01933.x>.
- Cinner, J.E., Maire, E., Huchery, C., MacNeil, M.A., Graham, N.A., Mora, C., McClanahan, T.R., et al., 2018. Gravity of human impacts mediates coral reef conservation gains. *Proc. Natl. Acad. Sci.* 115 (27), E6116–E6125. <https://doi.org/10.1073/pnas.1708001115>.
- Cinner, J.E., Zamborain-Mason, J., Gurney, G.G., Graham, N.A., MacNeil, M.A., Hoey, A. S., Mora, C., Villéger, S., et al., 2020. Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. *Science* 368 (6488), 307–311.
- Clarke, K., Gorley, R., 2006. Plymouth Marine Laboratory, Plymouth, UK.
- Convention on Biological Diversity, 2021. In: First Draft of the Post-2020 Global Biodiversity Framework CBD/WG2020/3/3, p. 12.
- Daan, N., Gislason, H., G. Pope, J., C. Rice, J., 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES J. Mar.Sci.* 62 (2), 177–188. <https://doi.org/10.1016/j.icesjms.2004.08.020>.
- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., et al., 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506 (7487), 216–220. <https://doi.org/10.1038/nature13022>.
- Gill, D.A., Mascia, M.B., Ahmadi, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., et al., 2017. Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* 543 (7647), 665–669. <https://doi.org/10.1038/nature21708>.
- Graham, N.A.J., Dulvy, N.K., Jennings, S., Polunin, N.V.C., 2005. Size-spectra as indicators of the effects of fishing on coral reef fish assemblages. *Coral Reefs* 24 (1), 118–124. <https://doi.org/10.1007/s00338-004-0466-y>.
- Graham, N.A., Wilson, S.K., Jennings, S., Polunin, N.V., Robinson, J.A.N., Bijoux, J.P., Daw, T.M., 2007. Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conserv. Biol.* 21 (5), 1291–1300. <https://doi.org/10.1111/j.1523-1739.2007.00754.x>.
- Graham, N.A., Pratchett, M.S., McClanahan, T.R., Wilson, S.K., 2013. The status of coral reef fish assemblages in the Chagos Archipelago, with implications for protected area management and climate change. In: Sheppard, C.R.C. (Ed.), *Coral reefs of the United Kingdom overseas territories*. Springer, Dordrecht, pp. 253–270.
- Green, A.L., Fernandes, L., Almamy, G., Abesamis, R., McLeod, E., Aliño, P.M., White, A. T., et al., 2014. Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. *Coast. Manag.* 42 (2), 143–159. <https://doi.org/10.1080/08920753.2014.877763>.
- Guiet, J., Poggiale, J.C., Maury, O., 2016. Modelling the community size-spectrum: recent developments and new directions. *Ecol. Model.* 337, 4–14. <https://doi.org/10.1016/j.ecolmodel.2016.05.015>.
- Halpern, B.S., 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecol. Appl.* 13 (supl), 117–137.
- Hoegh-Guldberg, O., Kennedy, E.V., Beyer, H.L., McClennen, C., Possingham, H.P., 2018. Securing a long-term future for coral reefs. *Trends Ecol. Evol.* 33 (12), 936–944. <https://doi.org/10.1016/j.tree.2018.09.006>.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschanivskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* 17 (4), 360–365.
- IUCN, 2004. IUCN Eastern African Regional Programme, Nairobi.
- Jacobs, Z.L., Jebri, F., Srokosz, M., Raitos, D.E., Painter, S.C., Nencioli, F., Osuka, K., Samoilys, M., Sauer, W., Roberts, M., Taylor, S.F., 2020. A major ecosystem shift in coastal East African waters during the 1997/98 Super El Niño as detected using remote sensing data. *Remote Sens.* 12 (19), 3127. <https://doi.org/10.3390/rs12193127>.
- Jouffray, J.B., Nyström, M., Norström, M., Williams, I.D., Wedding, L.M., Kittinger, J. N., Williams, G.J., 2015. Identifying multiple coral reef regimes and their drivers across the Hawaiian archipelago. *Philos.Trans.R.Soc.B Biol.Sci.* 370 (1659), 20130268. <https://doi.org/10.1098/rstb.2013.0268>.
- Kough, A.S., Belak, C.A., Paris, C.B., Lundy, A., Cronin, H., Gnanalingam, G., Hagedorn, S., et al., 2019. Ecological spillover from a marine protected area replenishes an over-exploited population across an island chain. *Conserv.Sci.Pract.* 1 (3), e17. <https://doi.org/10.1111/csp2.17>.
- Kramer, M.J., Bellwood, O., Fulton, C.J., Bellwood, D.R., 2015. Refining the invertivore: diversity and specialisation in fish predation on coral reef crustaceans. *Mar. Biol.* 162 (9), 1779–1786. <https://doi.org/10.1007/s00227-015-2710-0>.
- Kuempel, C.D., Altieri, A.H., 2017. The emergent role of small-bodied herbivores in pre-empting phase shifts on degraded coral reefs. *Sci. Rep.* 7, 39670.
- Lester, S.E., Halpern, B.S., 2008. Biological responses in marine no-take reserves versus partially protected areas. *Mar. Ecol. Prog. Ser.* 367, 49–56. <https://doi.org/10.3354/meps07599>.
- MacNeil, M.A., Chapman, D.D., Heupel, M., Simpfendorfer, C.A., Heithaus, M., Meekan, M., Harvey, E., et al., 2020. Global status and conservation potential of reef sharks. *Nature* 583 (7818), 801–806. <https://doi.org/10.1038/s41586-020-2519-y>.
- McClanahan, T.R., Mangi, S., 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecol. Appl.* 10 (6), 1792–1805. [https://doi.org/10.1890/1051-0761\(2000\)010\[1792:SOEFFA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[1792:SOEFFA]2.0.CO;2).
- McClanahan, T.R., Graham, N.A., Calnan, J.M., MacNeil, M.A., 2007. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecol. Appl.* 17 (4), 1055–1067.
- McClanahan, T.R., Graham, N.A., MacNeil, M.A., Muthiga, N.A., Cinner, J.E., Bruggemann, J.H., Wilson, S.K., 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proc. Natl. Acad. Sci.* 108 (41), 17230–17233. <https://doi.org/10.1073/pnas.1106861108>.
- McClanahan, T.R., Schroeder, R.E., Friedlander, A.M., Vigliola, L., Wantiez, L., Caselle, J. E., Graham, N.A., et al., 2019. Global baselines and benchmarks for fish biomass: comparing remote reefs and fisheries closures. *Mar. Ecol. Prog. Ser.* 612, 167–192. <https://doi.org/10.3354/meps12874>.
- McClanahan, T.R., Friedlander, A.M., Graham, N.A., Chabanet, P., Bruggemann, J.H., 2020. Variability in coral reef fish baseline and benchmark biomass in the central and western Indian Ocean provinces. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* <https://doi.org/10.1002/aqc.3448>.
- McClure, E.C., Hoey, A.S., Sievers, K.T., Abesamis, R.A., Russ, G.R., 2021. Relative influence of environmental factors and fishing on coral reef fish assemblages. *Conserv. Biol.* 35 (3), 976–990. <https://doi.org/10.1111/cobi.13636>.
- McLachlan, A., Defeo, O., 2017. The ecology of sandy shores. UK, Academic Press, London, p. 572.
- Mellin, C., MacNeil, A.M., Cheal, A.J., Emslie, M.J., Caley, J.M., 2016. Marine protected areas increase resilience among coral reef communities. *Ecol. Lett.* 19 (6), 629–637. <https://doi.org/10.1111/ele.12598>.
- Molloy, P.P., McLean, I.B., Cote, I.M., 2009. Effects of marine reserve age on fish populations: a global meta analysis. *J.Appl.Ecol.* 46, 743–751. <https://doi.org/10.1111/j.1365-2664.2009.01662.x>.
- Mwaiopopo, N.R., 2008. International Collective in Support of Fishworkers, Dar es Salaam, Tanzania.
- Ojea, E., Pearlman, I., Gaines, S.D., Lester, S.E., 2017. Fisheries regulatory regimes and resilience to climate change. *Ambio* 46 (4), 399–412. <https://doi.org/10.1007/s13280-016-0850-1>.
- Osuka, K., Kochzius, M., Vanreusel, A., Obura, D., Samoilys, M., 2018. Linkage between fish functional groups and coral reef benthic habitat composition in the Western Indian Ocean. *J. Mar. Biol. Assoc. U. K.* 98 (2), 387–400. <https://doi.org/10.1017/S0025315416001399>.
- Osuka, K., Rosendo, S., Riddell, M., Huet, J., Daide, M., Chauque, E., Samoilys, M., 2020. Applying a social-ecological systems approach to understanding local marine management trajectories in Northern Mozambique. *Sustainability* 12 (9), 3904.
- Parravicini, V., Casey, J.M., Schiettekatte, N.M., Brandl, S., Pozas-Schacre, C., Carlot, J., Edgar, G., et al., 2020. Global Gut Content Data Synthesis and Phylogeny Delineate Reef Fish Trophic Guilds. *bioRxiv*. <https://doi.org/10.1101/2020.03.04.977116>.
- Petchey, O.L., Belgrano, A., 2010. Body-size distributions and size-spectra: universal indicators of ecological status? *Biol. Lett.* <https://doi.org/10.1098/rsbl.2010.0240>.
- Polishchuk, L.V., Blanchard, J.L., 2019. Uniting discoveries of abundance-size distributions from soils and seas. *Trends Ecol. Evol.* 34 (1), 2–5. <https://doi.org/10.1016/j.tree.2018.10.007>.
- Pratchett, M.S., Hoey, A.S., Wilson, S.K., Messmer, V., Graham, N.A., 2011. Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity* 3 (3), 424–452. <https://doi.org/10.3390/d3030424>.
- Reynolds, J.D., Dulvy, N.K., Goodwin, N. B., Hutchings, J.A., 2005. Biology of extinction risk in marine fishes. *Proc. Royal Soc. B* 272 (1579), 2337–2344.
- Richardson, L.E., Graham, N.A., Pratchett, M.S., Eurich, J.G., Hoey, A.S., 2018. Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Glob. Chang. Biol.* 24 (7), 3117–3129. <https://doi.org/10.1111/gcb.14119>.
- Roberts, C.M., O'Leary, B.C., McCauley, D.J., Cury, P.M., Duarte, C.M., Lubchenco, J., Worm, B., 2017. Marine reserves can mitigate and promote adaptation to climate change. *Proc. Natl. Acad. Sci.* 114 (24), 6167–6175. <https://doi.org/10.1073/pnas.1701262114>.
- Robinson, J.P., Williams, I.D., Edwards, A.M., McPherson, J., Yeager, L., Vigliola, L., Baum, J.K., 2017. Fishing degrades size structure of coral reef fish communities. *Glob. Chang. Biol.* 23 (3), 1009–1022. <https://doi.org/10.1111/gcb.13482>.
- Robinson, J.P., McDevitt-Irwin, J.M., Dajka, J.C., Hadj-Hammou, J., Howlett, S., Graba-Landry, A., Hoey, A.S., et al., 2020. Habitat and fishing control grazing potential on coral reefs. *Funct. Ecol.* 34 (1), 240–251. <https://doi.org/10.1111/1365-2435.13457>.
- Russ, G.R., Alcala, A.C., Maypa, A.P., Calumpong, H.P., White, A.T., 2004. Marine reserve benefits local fisheries. *Ecol. Appl.* 14 (2), 597–606. <https://doi.org/10.1890/03-5076>.

- Russ, G.R., Payne, C.S., Bergseth, B.J., Rizzari, J.R., Abesamis, R.A., Alcalá, A.C., 2018. Decadal-scale response of detritivorous surgeonfishes (family Acanthuridae) to no-take marine reserve protection and changes in benthic habitat. *J. Fish Biol.* 93 (5), 887–900. <https://doi.org/10.1111/jfb.13809>.
- Samoilys, M., Randriamanantsoa, B., 2011. Reef fishes of northeast Madagascar. In: Obura, D., Carlo, G. Di, Rabearisoa, A. (Eds.), *A Rapid Marine Biodiversity Assessment of the coral reefs of northeast Madagascar*. RAP Bull Biol Assessment, 61. Conservation International, Arlington, VA, pp. 29–39.
- Samoilys, M.A., Osuka, K., Maina, G.W., Obura, D.O., 2017. Artisanal fisheries on Kenya's coral reefs: decadal trends reveal management needs. *Fish. Res.* 186, 177–191. <https://doi.org/10.1016/j.fishres.2016.07.025>.
- Samoilys, M., Roche, R., Koldewey, H., Turner, J., 2018. Patterns in reef fish assemblages: insights from the chagos archipelago. *PLoS one* 13 (1), e0191448. <https://doi.org/10.1371/journal.pone.0191448>.
- Samoilys, M.A., Halford, A., Osuka, K., 2019. Disentangling drivers of the abundance of coral reef fishes in the Western Indian Ocean. *Ecol. Evol.* 9 (7), 4149–4167. <https://doi.org/10.1002/ece3.5044>.
- Sandin, S.A., Walsh, S.M., Jackson, J.B., 2010. Prey release, trophic cascades, and phase shifts in tropical nearshore marine ecosystems. In: Terborgh, J., Estes, J.A. (Eds.), *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*. Island Press, Washington, DC, pp. 71–90.
- Sheppard, C.R., Ateweberhan, M., Bowen, B.W., Carr, P., Chen, C.A., Clubbe, C., Gaither, M.R., 2012. Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 22 (2), 232–261. <https://doi.org/10.1002/aqc.1248>.
- Shin, Y.J., Rochet, M.J., Jennings, S., Field, J.G., Gislason, H., 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* 62 (3), 384–396. <https://doi.org/10.1016/j.icesjms.2005.01.004>.
- Stallings, C.D., 2009. Predator identity and recruitment of coral-reef fishes: indirect effects of fishing. *Mar. Ecol.-Prog. Ser.* 383, 251–259. <https://doi.org/10.3354/meps08004>.
- Taylor, B.M., Lindfield, S.J., Choat, J.H., 2015. Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. *Ecography* 38 (5), 520–530. <https://doi.org/10.1111/ecog.01093>.
- Tebbett, S.B., Goatley, C.H., Bellwood, D.R., 2017. Clarifying functional roles: algal removal by the surgeonfishes *Ctenochaetus striatus* and *Acanthurus nigrofuscus*. *Coral Reefs* 36 (3), 803–813. <https://doi.org/10.1007/s00338-017-1571-z>.
- Wells, S., 2009. Dynamite fishing in northern Tanzania—pervasive, problematic and yet preventable. *Mar. Pollut. Bull.* 58 (1), 20–23. <https://doi.org/10.1016/j.marpolbul.2008.09.019>.
- Williams, I.D., Baum, J.K., Heenan, A., Hanson, K.M., Nadon, M.O., Brainard, R.E., 2015. Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS One* 10 (4), e0120516. <https://doi.org/10.1371/journal.pone.0120516>.
- Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A.J., Dulvy, N.K., Turner, R.A., Cakacaka, A., et al., 2010. Habitat degradation and fishing effects on the size structure of coral reef fish communities. *Ecol. Appl.* 20 (2), 442–451. <https://doi.org/10.1890/08-2205.1>.
- Yeager, L.A., Marchand, P., Gill, D.A., Baum, J.K., McPherson, J.M., 2017. Marine socio-environmental covariates: queryable global layers of environmental and anthropogenic variables for marine ecosystem studies. *Ecology* 98 (7), 1976. <https://doi.org/10.1002/ecy.1884>.
- Zar, J.H., 1999. *Biostatistical Analysis*, 4th ed. Prentice-Hall Inc., New Jersey.
- Zgliczynski, B.J., Sandin, S.A., 2017. Size-structural shifts reveal intensity of exploitation in coral reef fisheries. *Ecol. Indic.* 73, 411–421. <https://doi.org/10.1016/j.ecolind.2016.09.045>.