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

Osuka, Kennedy E.; Stewart, Bryce D.; Samoilys, Melita A.; Roche, Ronan; Turner, John; McClean, Colin

Marine Pollution Bulletin

DOI:
https://doi.org/10.1016/j.marpolbul.2021.113010

Published: 01/12/2021

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

Kennedy E. Osuka[1, 2], Bryce D. Stewart[1], Melita A. Samoilys[2], Ronan C. Roche[3], John Turner[3] and Colin Mcclean[1]

Institutional affiliation:

[1] Department of Environment and Geography, University of York (York, UK)

[2] CORDIO East Africa (Mombasa, Kenya)

[3] School of Ocean Sciences, Bangor University (Bangor, UK)

Corresponding author email: koe503@york.ac.uk

Abstract

Understanding how Marine Protected Areas (MPAs) improve conservation outcomes across a range of 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 the overall productivity of the system (intercept) did not show consistent patterns with MPA protection. Highly-protected areas contained high biomass of seven trophic groups spanning piscivores, herbivores and detritivores, while well-protected only contained elevated biomass of scraper and detritivores. Piscivores, omnivores, planktivores and herbivores showed negative relationships with human population suggesting restoration of fish functional roles require addressing fisher demands. The high biomass in highly-protected and well-protected areas underscores the need to support effective MPA management to secure ecosystem benefits for the coastal communities.

Keywords: Marine Protected Areas, size-spectra, fish biomass, fishing effects, compliance.

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.*, 2004). In the presence of continuing over-exploitation through fishing and habitat degradation through climate change (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. Conversely, fishing has a top-down control on reef fishes and continuous harvesting reduces fish size, abundance and biomass (Zgliczynski & 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 that influence the size structure of reef fish populations could allow for specific fisheries management initiatives and designation of 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; White *et al.*, 2017) 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; McClanahan *et al.*, 2007; Lester and Halpern, 2008).

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 MPAs 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, distance to fish markets and levels of compliance (Molloy, McLean & Cote, 2009; Cinner et al., 2018). Yet, it remains unclear how different 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 & Belgrano, 2010; Zgliczynski & 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 (Shin et al. 2005; Zgliczynski & Sandin 2017).

Here we use fish density and size data collected from a consistent reef morphology (ocean exposed fringing coral reefs: Andréfouët, Chagnaud & Kranenburg, 2009, Samoilys, Halford and Osuka 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

Reef geomorphology refers to reef type and structure and incorporates an understanding of the processes driving historical reef growth as well as future structural development (Hopley *et al.,* 2007). 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; Samoilys et al. 2019). Reef geomorphology strongly influences coral reef fish communities and biomass (Taylor, Lindfield & Choat, 2015; Samoilys, Halford & Osuka, 2019). Therefore, this study only focused on fish assemblages within the consistent geomorphology of ocean-exposed fringing reefs (Figure 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. Data from WIO were sourced from Samoilys, Halford & Osuka (2019). This included data from 24 sites across four countries: Tanzania – seven sites, Mozambique - seven, Comoros – six, and Madagascar – four (Figure 1). Another set of data collected from eight sites in the Chagos Archipelago was sourced from Samoilys *et al.*, (2018; Figure 1). These sites were grouped into four protection levels based on 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). 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 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 Samoilys, Halford & Osuka (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 (Samoilys & Randriamanantsoa, 2011). The biomass of each species was calculated based on length–weight relationships presented in Samoilys *et al.* (2018). Species were assigned to the following trophic groups: piscivores, omnivores, corallivores, invertivores, planktivores, detritivores and herbivores (Osuka *et al.*, 2018; Samoilys, Halford & Osuka*,* 2019; Parravicini et al., 2020). The herbivores included six sub-groups composed of: large excavators, small excavators, scrapers, browsers, grazers and grazers-detritivores.

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. A permutation-based hypothesis testing analysis of similarities (ANOSIM) was used to compare fish density and biomass across the four protection levels (Clarke & Gorley, 2006).

Size-spectra analysis was performed for each site based on fish densities in each of the 19 size classes ranging from 11–105 cm. This involved determining the slope and intercept of a linear regression of log transformed midpoint of size classes and $\log_{10}$ (x+1) transformed count data. Prior to analysis, the midpoint lengths were centred across the size range, thereby removing the correlation between slope and intercept

(Daan *et al.*, 2003). 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.

Differences in fish trophic group biomass protection levels were tested using a One-way Kruskal-Wallis test after failing both normality and homogeneity of variance test, even after log-transformations (Zar, 1999). Mann-Whitney post-hoc tests were then performed to determine significant pairwise differences. Since highly protected areas showed no variance in human population density, differences in the variable were only compared across three protection levels (well-protected, moderately protected and fished areas) using one-way ANOVA followed by Tukey post-hoc tests. The relationship between trophic groups, and human population density was then assessed using ordinary least squares regression.

3. RESULTS

Fish community structure

MDS plot of fish community biomass and density showed that sites separated out largely in relation to the four protection levels (Figure 2). However, a few of the fished sites overlapped in multivariate space with well and moderately protected sites. ANOSIM results revealed 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 (Figure 2; ANOVA $F_{3, 31} = 9.87$, $p < 0.001$). 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 S2a). The means of intercepts also varied considerably across protection levels (Figure 3; ANOVA $F_{3, 31} = 12.00$, $p < 0.001$). 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 S2b).

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 omnivores, browsers and grazer detritivores (Table 3). Mann-Whitney post-hoc tests showed that in all trophic groups except invertivores, the highest biomass, more than 1.7 fold, was seen in highly protected areas compared to all other protected or fished areas (Figure 4). For some trophic groups, fished areas had higher biomass than moderately protected or well-protected areas such as scrapers, detritivores, invertivores and large excavators (Figure 4). The biomass of small excavators and grazers was similar across well-protected, moderately protected and fished areas, while piscivores and planktivores showed higher biomass in well-protected areas compared to fished areas and moderately protected areas respectively.

3.3 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 $F_{2, 23} = 5.61$, p 0.011). A pairwise Tukey's test showed that only well-protected areas were located in less populated areas compared to fished areas.

A significant linear relationship ($p<0.05$) between human population density and fish biomass was found in seven trophic groups: piscivores, omnivores, planktivores, large excavators, small excavators, scrapers and grazers (Table 4). A linear decrease in biomass ranging from 10 kg/ha in grazers to 180 kg/ha in plankivores was found for every log unit increase in human population density (Figure 5). Relationships within the other four trophic groups were not significant.

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 levels. 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 clearer differences were evident between remote highly protected areas and other protection levels. Moderately protected areas showed no apparent biomass benefits to any of the trophic groups. Thirdly, the biomass of seven trophic groups (piscivores, omnivores, plankivores, large- and small excavators, scrapers and grazers) showed strong negative relationships with human population density. This indicates protected and fished areas in close proximity to high human population densities are likely to have low biomass of key trophic groups (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) 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 remotely populated areas, but potentially reflecting removal of meso-predators by top-predators or previous fishing effects leading to prey release (Stallings 2009; Sandin Walsh & Jackson, 2010). Indeed, a previous study in these areas noted fewer large-sized *Epinephelus* spp. groupers in 2014, which was potentially attributed to lag effects of a previous handline fishery that closed in 2010 (Samoilys *et al.,* 2018). While relatively larger fish occurred in highly protected areas compared to moderately protected and fished areas, their influence on shallowing the size-spectra slopes was overwhelmed by the exceptionally high abundance of small fish. This clearly suggests that processes other than exploitation, may be driving fish abundance and increasing 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 juveniles are protected (Russ et al., 2018). This suggests 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 indicates 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 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 and low human population densities. Fishing selectively removes target species, changing population size structure and overall fish biomass (Zgliczynski & Sandin 2017). High exploitation rates are expected in densely populated areas like 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 fishing methods and poaching occurs (Mwaipopo, 2008). Interestingly, some fished sites particularly 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).

4.2 Influence of protection on trophic groups

In the lower protection spectrum, moderately protected areas showed low biomass of key trophic groups, which is a conservation concern for the MPAs in the WIO. Indeed, moderately protected areas exhibited no considerable benefits to any fish trophic groups. This is important and alarming, as it indicates that protection benefits can drastically be lost to biomass levels equivalent or even lower than those found in fished areas under poor compliance to management rules. Since big fish in moderate protection are generally fished out first (McClanahan & Mangi, 2000), overall fish productivity is also expected to reduce.

Highly protected areas were important at sustaining high biomass of piscivores, which can exert top-down control on fish of lower trophic levels. Similarly, well-protected areas had higher biomass of piscivores than fished areas. The lack of apparent differences in piscivore biomass between moderately protected and fished areas suggest that piscivores may require fully protected MPAs to thrive (Edgar *et al.*, 2014; MacNeil et al., 2020).

The biomass of planktivorous fish was also particularly high in highly protected area 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 & 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 trophic groups have been reported for planktivores in these areas (Samoilys et al., 2018) and such localised processes 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 higher in well-protected than moderately 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 (Hughes et al 2007). Such a risk can be counteracted through management measures that protect and increase the abundance and biomass of small-bodied herbivores (Kuempel & Altieri, 2017).

4.3 Influence of human population on trophic groups

In coral reefs of the WIO, local human population densities appear to be a key driver of the biomass patterns found herein. Fishery 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 & 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, Walsh & Jackson, 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.

Of the herbivorous fishes, only the large- and small excavators, scrapers and grazers showed a significant decrease in biomass with increasing human population density. This clearly demonstrates susceptibility of herbivores to fishing, though various sub trophic groups show different rates of decline with increasing fishing pressure and market demand (Cinner et al., 2013; McClure et al 2021). Taken together, our findings suggest that restoration of key trophic groups requires high levels of protection while addressing fisher demands (Cinner et al 2013; MacNeil et al., 2020).

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 invertivores and detritivores. Invertivores feed on coral competitors such as soft corals and invertebrates (Kramer *et al.*, 2015), while detritivores feed on organic matter in sediment and reef surface (Tebbett et al., 2017). This coupled with the low biomass of herbivorous fishes in moderately protected area is a concern for reef resilience (Jouffrays et al., 2015). 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 previously experienced dynamite fishing in the past (Mwaipopo, 2008), which may have caused habitat destruction and overexploitation of large fishes (Wells, 2009) that serve as an important parental stock in coral reef ecosystems.

Overall, our results highlight the ever-greater need to invest in MPAs and support management regimes, acutely for the moderately protected MPAs, and particularly in areas of high human population density. 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 (Chiroco 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 in the face of on-going anthropogenic threats.

ACKNOWLEDGEMENTS

We are grateful to different grants to CORDIO East Africa and Bangor University that funded the field surveys including the Marine Science for Management Programme of the Western Indian Ocean Marine Science Association (WIOMSA: MASMA/OR/2008/05), Conservation International (CI) in Madagascar, the European Union's Biodiversity Management Programme in Mozambique (DCI-ENV/2013/323-897) and DEFRA Darwin Initiative grant 19-027 in Chagos Archipelago. KO was funded by CORDIO East Africa through grants from the SOLSTICE-WIO project and Norwegian agency for development cooperation (Norad). We are grateful to Callum Roberts for his critical review of an early draft.

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.

REFERENCES

Andréfouët, S., Chagnaud, N., & Kranenburg, C. J. (2009). Atlas of Western Indian Ocean coral reefs. New-Caledonia: Centre IRD de Nouméa.

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. *Nature Sustainability*, *2*(6), pp.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. *Functional Ecology*, *33*(6), 948-961. https://doi.org/10.1111/1365-2435.13265

Blanchard, J. L., Dulvy, N. K., Jennings, S., Ellis, J. R., Pinnegar, J. K., Tidd, A., & Kell, L. T. (2005). Do climate and fishing influence size-based indicators of Celtic Sea fish community structure?. *ICES Journal of Marine Science*, *62*(3), 405-411. https://doi.org/10.1016/j.icesjms.2005.01.006

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., & Eklöf, 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

Clarke, K., & Gorley, R. (2006). PRIMER: *Pymouth Routine in Multivariate Ecologica Research: Getting Started with v6*. Plymouth, UK: Plymouth Marine Laboratory.

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. *Conservation Biology*, *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. *Proceedings of the National Academy of Sciences*, *115*(27), E6116-E6125. https://doi.org/10.1073/pnas.1708001115

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 Journal of marine Science*, *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

Fernandes, L., Day, J. O. N., Lewis, A., Slegers, S., Kerrigan, B., Breen, D.A.N., Cameron, D., et al. (2005). Establishing representative no-take areas in the Great Barrier Reef: large-scale implementation of theory on marine protected areas. *Conservation biology*, *19*(6), 1733-1744. https://doi.org/10.1111/j.1523-1739.2005.00302.x

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. Conservation biology, 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: C.R.C. Sheppard (Ed.) *Coral reefs of the United Kingdom overseas territories.* Dordrecht: Springer pp. 253-270.

Green, A. L., Fernandes, L., Almany, 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. *Coastal Management*, *42*(2), 143-159. https://doi.org/10.1080/08920753.2014.877763

Hoegh-Guldberg, O., Kennedy, E. V., Beyer, H. L., McClennen, C., & Possingham, H. P. (2018). Securing a long-term future for coral reefs. *Trends in ecology & evolution*, *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., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S. and Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current biology*, *17*(4), pp.360-365.

IUCN. (2004). Managing Marine Protected Areas: A Toolkit for the Western Indian Ocean. Nairobi: IUCN Eastern African Regional Programme.

Jouffray, J. B., Nyström, M., Norström, A. V., 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. *Philosophical Transactions of the Royal Society B:*

Biological Sciences, *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. *Conservation Science and Practice*, *1*(3), e17. https://doi.org/10.1111/csp2.17

Kuempel CD, Altieri AH, (2017) The emergent role of small-bodied herbivores in pre-empting phase shifts on degraded coral reefs. *Scientific reports*, *7*, 39670.

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. *Marine biology*, *162*(9), 1779-1786. https://doi.org/10.1007/s00227-015-2710-0

Lester, S.E. & Halpern, B.S. (2008). Biological responses in marine no-take reserves versus partially protected areas. *Marine Ecology Progress Series*, 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. *Ecological applications*, 10(6), 1792-1805. https://doi.org/10.1890/1051-0761(2000)010[1792:SOEFFA]2.0.CO;2

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. *Marine Ecology Progress Series*, *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. *Aquatic Conservation: Marine and Freshwater Ecosystems*. https://doi.org/10.1002/aqc.3448

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. *Proceedings of the National Academy of Sciences*, *108*(41), 17230-17233. https://doi.org/10.1073/pnas.1106861108

McClure, E. C., Hoey, A. S., Sievers, K. T., Abesamis, R. A., & Russ, G. R. (2020). Relative influence of environmental factors and fishing on coral reef fish assemblages. *Conservation Biology*.

McLachlan, A. & Defeo, O., 2017. Surf-zone zooplankton and nekton. *The ecology of sandy shores*. London:UK, Academic Press.

Mellin, C., MacNeil, A.M., Cheal, A.J., Emslie, M.J. & Caley, J.M. (2016). Marine protected areas increase resilience among coral reef communities. *Ecology letters*, 19(6) 629-37. 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. *Journal Appllied Ecology* 46: 743−751. https://doi.org/10.1111/j.1365-2664.2009.01662.x

Mwaipopo, N. R. (2008). *The social dimensions of marine protected areas: a case study of the Mafia Island Marine Park in Tanzania.* Dar es Salaam, Tanzania: International Collective in Support of Fishworkers

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. *Journal of the Marine Biological Association of the United Kingdom*, *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? *Biology Letters*, 434–437. 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 in ecology & evolution*, *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

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. *Global*

Change Biology, *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. *Proceedings of the National Academy of Sciences*, *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. *Global Change Biology*, *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. *Functional Ecology*, *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. *Ecological applications*, *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., & Alcala, A. C. (2018). Decadal-scale response of detritivorous surgeonfishes (family Acanthuridae) to no-take marine reserve protection and changes in benthic habitat. *Journal of fish biology*, *93*(5), 887-900. https://doi.org/10.1111/jfb.13809

Sandin, S. A., Walsh, S. M. & Jackson, J. B. (2010). Prey release, trophic cascades, and phase shifts in tropical nearshore marine ecosystems. In: J. Terborgh, J. A. Estes (Eds.) *Trophic cascades: predators, prey, and the changing dynamics of nature*: Washington, DC: Island Press, pp. 71–90.

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., Osuka, K., Maina, G. W., & Obura, D. O. (2017). Artisanal fisheries on Kenya's coral reefs: Decadal trends reveal management needs. *Fisheries Research*, *186*, 177-191. https://doi.org/10.1016/j.fishres.2016.07.025

Samoilys, M. A., Halford, A., & Osuka, K. (2019). Disentangling drivers of the abundance of coral reef fishes in the Western Indian Ocean. *Ecology and evolution*, *9*(7), 4149-4167. https://doi.org/10.1002/ece3.5044

Samoilys, M. & Randriamanantsoa, B. (2011). Reef fishes of northeast Madagascar. In: D. Obura, G. Di Carlo, A., Rabearisoa, (Eds.). *A Rapid Marine Biodiversity Assessment of the coral reefs of northeast Madagascar.* RAP Bull Biol Assessment 61 Arlington, VA: Conservation International, pp. 29–39.

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. *Aquatic Conservation: marine and freshwater ecosystems*, *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. I*CES Journal of marine Science*, 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), pp.803-813. https://doi.org/10.1007/s00338-017-1571-z

Wedding, L. M. & Friedlander, A. (2008). Determining the influence of seascape structure on coral reef fishes in Hawaii using a geospatial approach. *Marine Geodesy*, 31(4), 246–266. https://doi.org/10.1080/01490410802466504

Wells, S. (2009). Dynamite fishing in northern Tanzania–pervasive, problematic and yet preventable. *Marine Pollution Bulletin*, *58*(1), 20-23. https://doi.org/10.1016/j.marpolbul.2008.09.019

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. *Ecological Applications*, *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), 1976-1976. https://doi.org/10.1002/ecy.1884

Zar, J. H. (1999). Biostatistical analysis (4th ed,) New Jersey: Prentice-Hall Inc.

Zgliczynski, B. J., & Sandin, S. A. (2017). Size-structural shifts reveal intensity of exploitation in coral reef fisheries. *Ecological Indicators*, *73*, 411-421. https://doi.org/10.1016/j.ecolind.2016.09.045

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 define as: high protection - a gazetted marine protected area (MPA) in remote location with strong 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.

Protection level	Location (sites)	Max – Min depth (m)	Reef type	Local human population density (log_{10} persons per km^2 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

Table 2: Results from ANOSIM tests showing global and pairwise tests on fish density and biomass across protection levels. Bolded p-values indicate significant comparisons.

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

Table 3: Tabulated medians and interquartile range (IR) and one-way Kruskal-Wallis tests on trophic group biomass compared across four protection levels. HP = high protection, P = Well-protected, MP = moderate protection and F = Fished.

Variable	High protection		Well protected		Moderate protection		Fished		Kruskal-Wallis	
	Median	IR	Median	IR	Median	IR	Median	IR	H-value	p-value
a) Trophic group biomass										
Piscivores	273.60	108.30, 727.33	47.92	14.13, 93.72	5.96	0.00, 63.69	13.12	0.00, 40.74	39.59	<0.001
Omnivores	290.79	22.86, 1000.19	57.87	0.00, 630.18	161.10	16.33, 538.83	36.01	5.72, 176.07	5.777	0.123
Invertivores	22.19	16.03, 50.75	24.12	3.93, 78.82	0.00	0.00, 0.00	25.24	7.03, 50.49	35.31	<0.001
Planktivores	465.60	158.92, 1028.98	33.81	0.00, 269.63	0.71	0.00, 30.06	14.37	0.00, 72.50	51.62	<0.001
Detritivores	60.09	13.14, 82.72	34.60	11.19, 53.69	8.39	0.60, 25.85	28.63	17.10, 48.93	17.33	<0.001
Large excavators	232.12	23.82, 417.87	0.00	0.00, 0.00	0.00	0.00, 0.00	0.00	0.00, 47.65	53.61	<0.001
Small excavators	81.41	34.92, 133.61	29.63	7.12, 87.67	17.76	0.00, 62.45	19.24	0.00, 81.04	18.98	<0.001
Scrapers	152.72	55.55, 270.76	71.10	26.94, 131.00	16.22	0.00, 50.77	39.54	4.29, 145.31	29.47	<0.001
Browsers	11.16	0.00, 77.61	60.89	0.00, 320.01	18.12	0.00, 78.24	11.16	0.00, 31.45	7.52	0.057
Grazers	75.44	52.34, 106.94	34.67	15.61, 59.21	27.33	17.95, 64.24	30.14	15.03, 49.78	33.42	<0.001
Grazer detritivores	2.27	0.00, 38.36	0.00	0.00, 26.62	0.00	0.00, 1.70	0.00	0.00, 38.03	4.651	0.199

Table 4: Relationship between human population and mean biomass of 11 trophic groups from five locations in western and central Indian Ocean. Bolded p-values indicate significant relationships.

Trophic group	**Slope**	**SE**	**Intercept**	**SE**	**R**	***p***
Piscivores	-96.902	19.168	343.900	44.518	-0.678	**0.001**
Omnivores	-166.010	55.916	740.870	129.870	-0.477	**0.006**
Invertivores	0.205	6.462	37.169	15.007	0.006	0.975
Planktivores	-179.880	34.118	597.010	79.238	-0.694	**0.001**
Detritivores	-4.481	3.670	47.097	8.523	-0.218	0.232
Large excavators	-55.647	13.829	200.900	32.118	-0.592	**0.001**
Small excavators	-28.005	8.594	120.670	19.960	-0.511	**0.003**
Scrapers	-33.464	11.728	175.210	27.238	-0.462	**0.008**
Browsers	-3.355	15.377	90.566	35.712	-0.040	0.829
Grazers	-10.276	3.029	67.070	7.034	-0.527	**0.002**
Grazer-detritivores	-5.938	8.448	51.733	19.621	-0.127	0.488

Figure legends

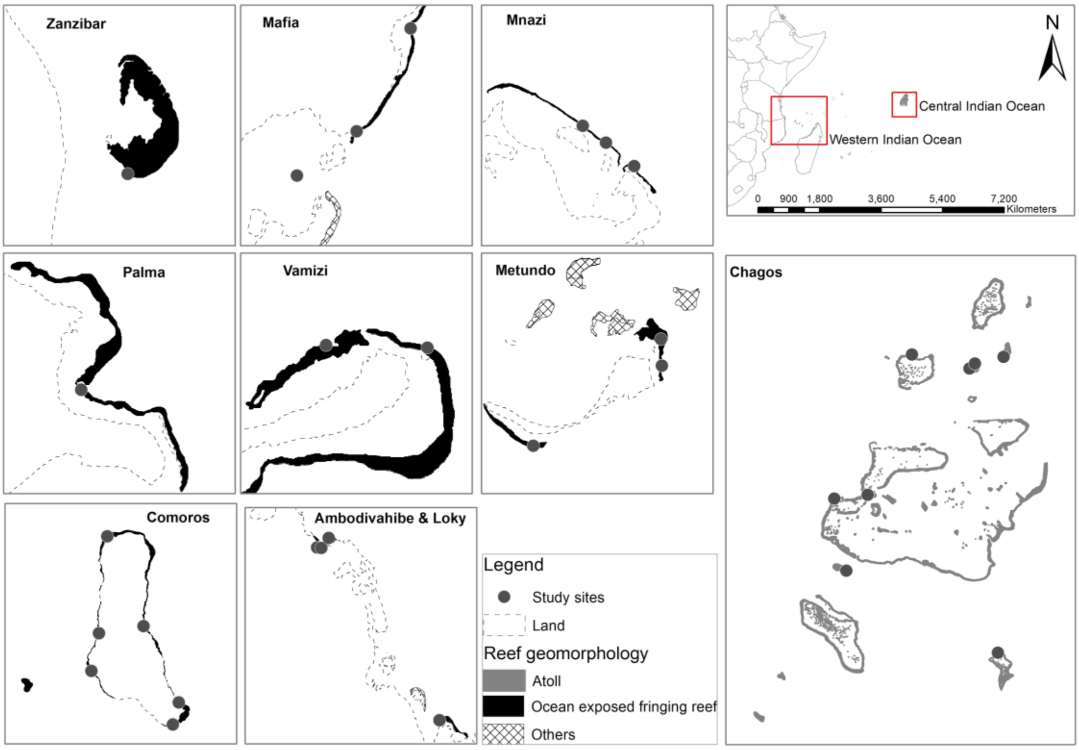

Figure 1: Map of the survey sites from the western Indian Ocean (WIO) and central Indian Ocean (CIO). WIO survey sites comprised reefs sampled in Tanzania (Zanzibar, Mafia and Mnazi), Mozambique (Palma, Vamizi and Metundo), Comoros and Madagascar (Ambodivahibe and Loky). CIO survey sites were sampled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

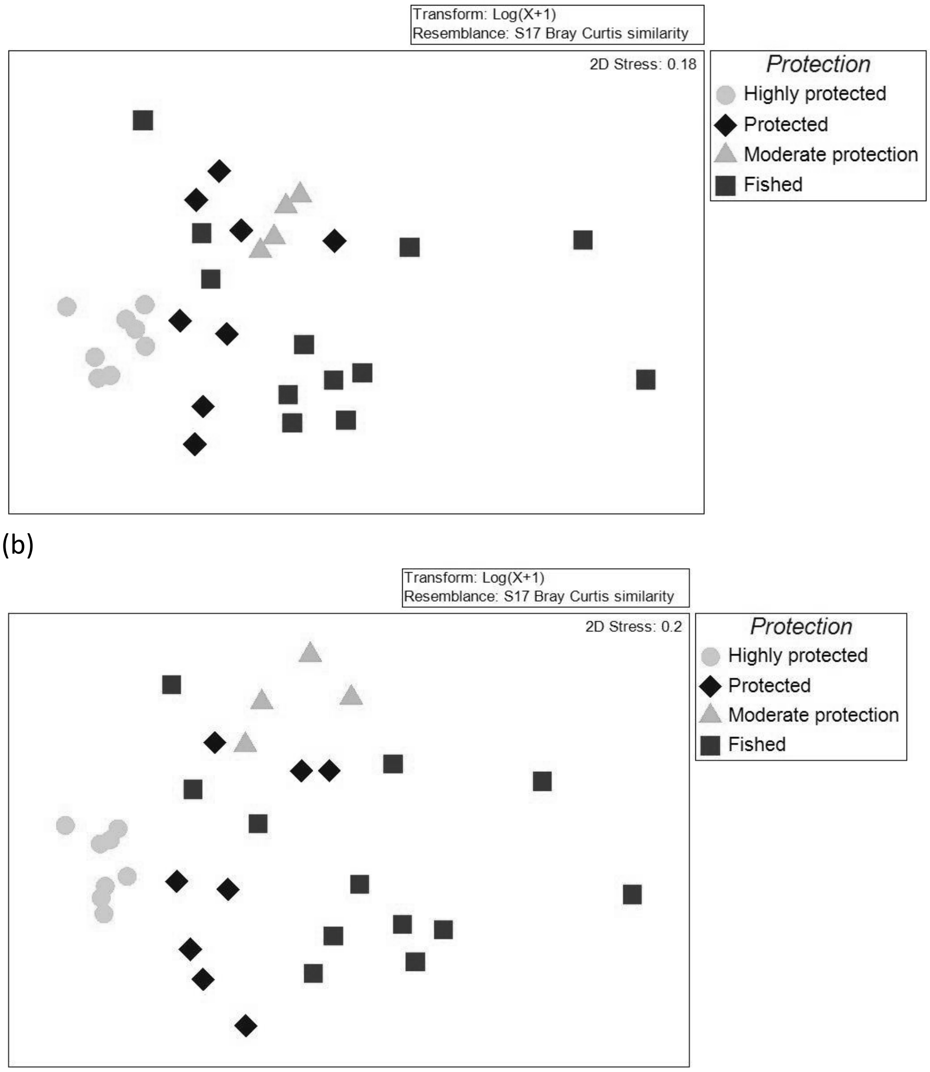

Figure 2: Multi-dimensional scaling plots based on Bray-Curtis similarity statistic on fish species: a) density and b) biomass across seven combinations of location and protection from five countries in western and central Indian Ocean. HP = high protection, P = Well-protected, MP = moderate protection and F = Fished.

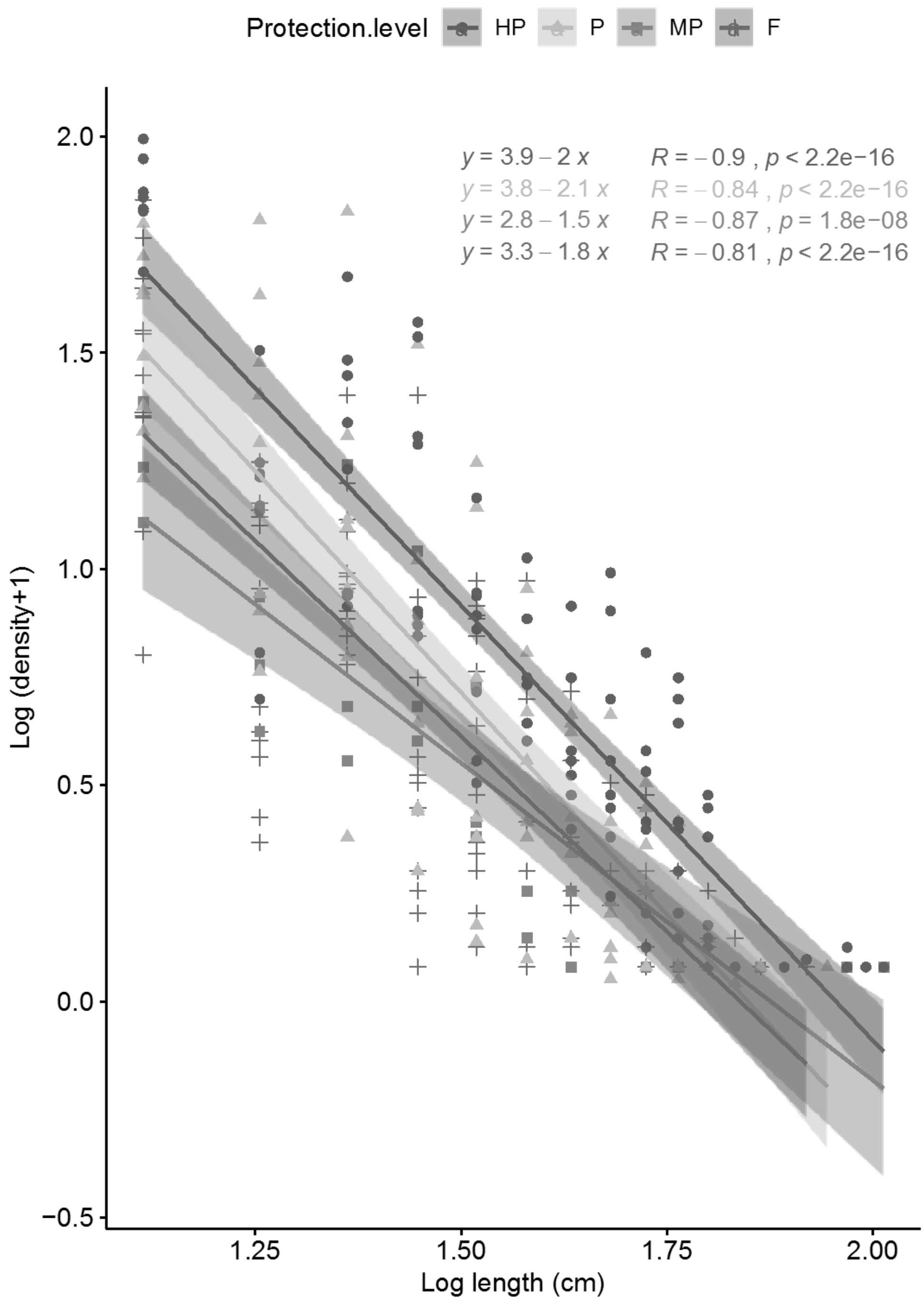

Figure 3: Relationships between fish length and density for four protection levels in western and central Indian Ocean. HP = high protection, P = well-protected, MP = moderate protection and F = fished.

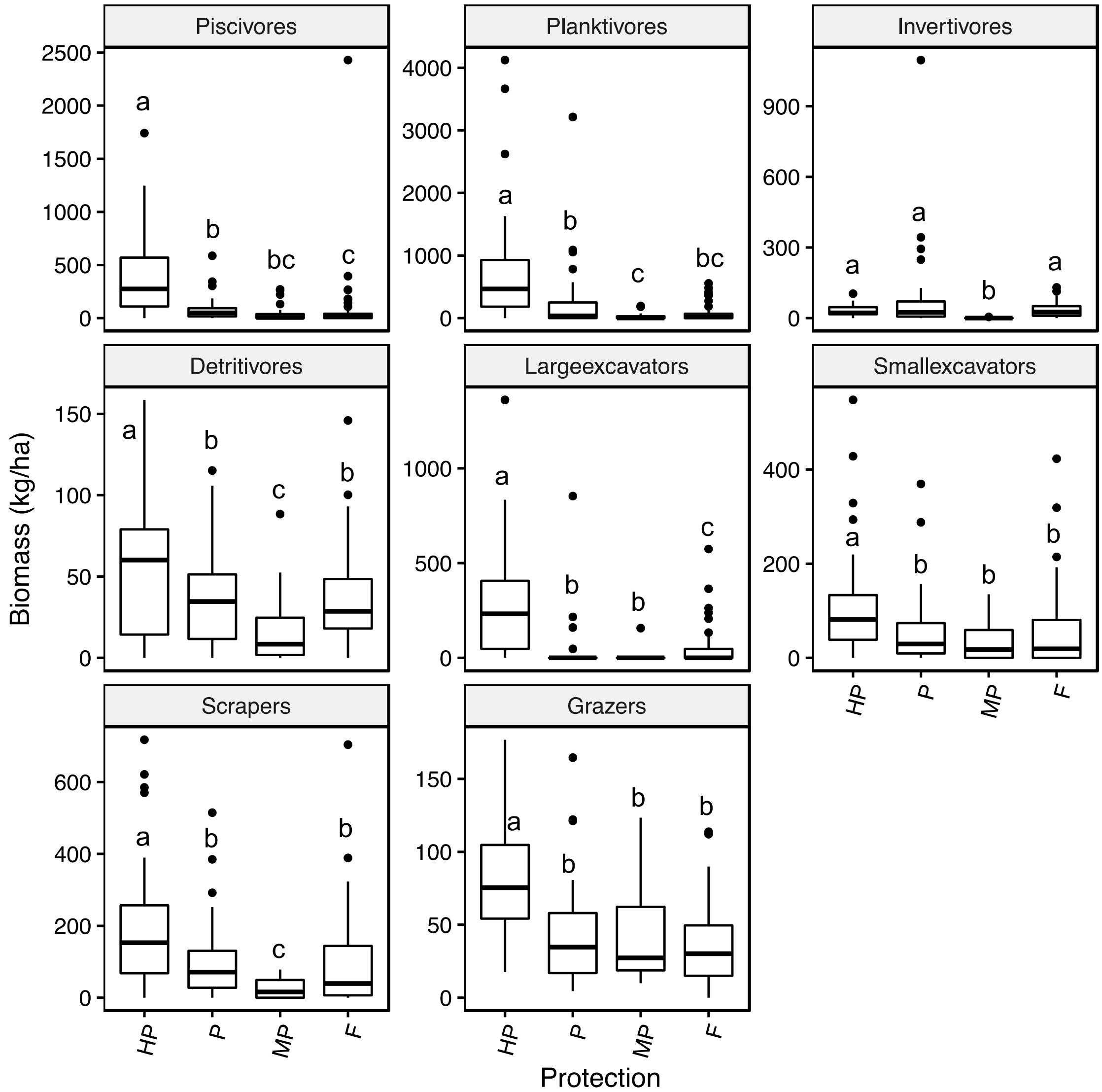

Figure 4: Median biomass of trophic groups that showed significant differences across protection levels from western and central Indian Ocean. The lowercase letters show Mann-Whitney posthoc test with the identical lowercase letters showing no statistical significance. HP = high protection, P = well-protected, MP = moderate protection and F = fished.

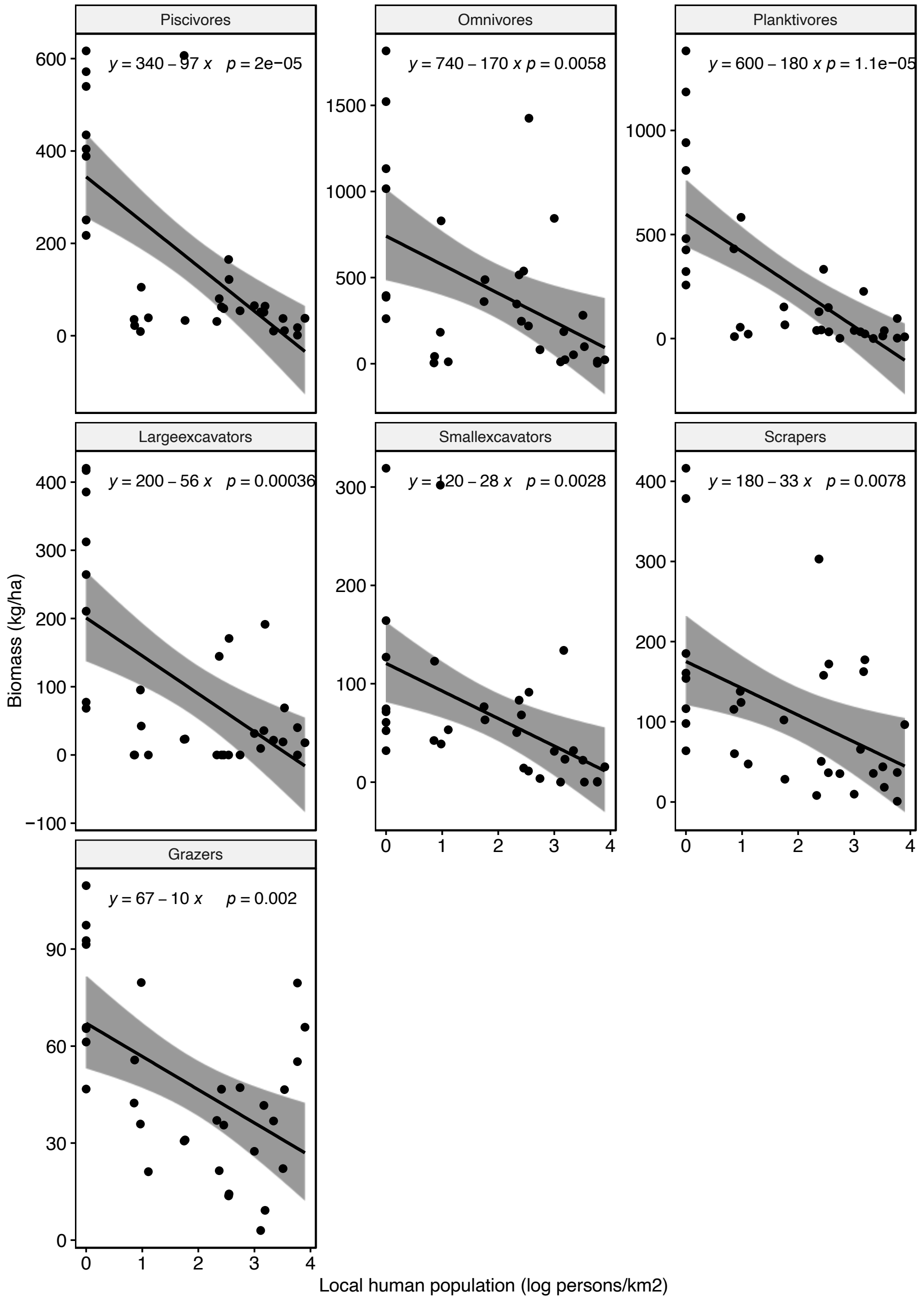

Figure 5: Relationship between local human population and biomass of seven fish trophic groups sampled from western and central Indian Ocean.

Declaration of Interest Statement
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.