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Effects of protection on large-bodied reef fishes in the western Indian Ocean

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Abstract

Predatory and large-bodied coral reef fishes have fundamental roles in the functioning and biodiversity of coral reef ecosystems, but their populations are declining, largely due to overexploitation in fisheries. These fishes include sharks, groupers, Humphead wrasse (*Cheilinus undulatus*), and Green Humphead parrotfish (*Bolbometopon muricatum*). In the western Indian Ocean, this situation is exacerbated by limited population data on these fishes, including from conventional visual census methods, which limit the surface area surveyed. We developed a rapid timed scuba swim survey approach for application over large areas for estimation of the abundance of large-bodied reef fishes and assessment of the effectiveness of marine protected areas (MPAs) in maintaining these species' populations. Using this method, we sampled 7 regions in the western central Indian Ocean and Gulf of Aden, including 2 remote reference locations where fishing is prohibited. Eight families were selected for the surveys from across 3 categories: pelagic, demersal, and large-bodied single species. Sharks (Carcharhinidae) were absent in 5 of the 7 regions, observed only in Mozambique and the Chagos Archipelago. Tunas (Scombridae) and barracudas (Sphyraenidae) were rarely observed (none in Madagascar, Djibouti, and Iles Glorieuses). The Giant grouper (*Epinephelus lanceolatus*) was absent in all regions, Humphead wrasse was absent in Comoros and Iles Glorieuses, and Green Humphead parrotfish was observed at only one site in Tanzania. The MPAs were not effective in protecting these single large-bodied species or the 4 pelagic families, except for sharks in the highly protected reference locations. However, MPAs with medium levels of protection were effective in maintaining the abundance of some demersal families, notably large-bodied groupers. Our results support the hypothesis of local extirpation of these large-bodied fishes on many coral reefs in the western Indian Ocean.

KEYWORDS
coral reefs, endangered species, Indian Ocean, large-bodied fishes, marine parks, predatory fishes

INTRODUCTION

Large-bodied and predatory fishes that associate with coral reefs are declining (Hammerschlag et al., 2018; Osuka et al., 2022; Richards et al., 2012). Primary causes are overexploitation in fisheries due to poor management or lack of enforcement and destructive fishing gears (Graham et al., 2017; Sadovy et al., 2003; Samoilys et al., 2017). Biological vulnerability due to the life-history strategies of some of these species, particularly sharks and groupers (Sadovy de Mitcheson et al., 2020; Sherman et al., 2023), exacerbates these issues. However, long-term quantitative data on the population status of large-bodied reef fish populations are scant, particularly in the western Indian Ocean (WIO). This region contains globally significant

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biodiversity hotspots (Myers et al., 2000) and faces challenges in monitoring and protecting marine ecosystems due to a lack of human, institutional, and technical capacity (Samoilys et al., 2022; Stefanoudis et al., 2022; Veech, 2003; Wafar et al., 2011). There is therefore an urgent need for species-level population data in the WIO to improve understanding of how the coral reef ecosystems are functioning.

Ecological importance of large-bodied reef fishes

Fish biomass is often used as a proxy for estimating energy flow, which can be loosely termed as ecosystem functioning or productivity of a reef (Mora et al., 2011; Morais et al., 2020). Large-bodied fishes, such as sharks, barracuda, trevally, tunas, and groupers, play a critical role in reef ecosystem productivity (Kulbicki et al., 2015) and represent a significant energy store as piscivorous species at a high trophic level (Hammerschlag et al., 2019; Hussey et al., 2013). Top-level predatory reef fishes associate with high coral cover and structural complexity (Sartori et al., 2021), and their absence releases lower trophic taxonomic groups, thereby disrupting fish community trophic structure (Heithaus et al., 2008; Hixon, 2015; Robinson et al., 2019). The importance of predatory reef fishes is also evidenced in their use as a metric in ecosystem extinction risk assessments for coral reef ecosystems (Obura et al., 2021).

IUCN Red List

The International Union for Conservation of Nature (IUCN) Red List is the most comprehensive standardized data source on the extinction risk of species and is widely used by governments, nongovernmental organizations (NGOs), researchers, and donors to inform and catalyze action for biodiversity conservation, policy change, and awareness raising (Betts et al., 2020). Three of the large-bodied reef-associated species we surveyed are threatened (IUCN, 2023): 2 Labridae—the endangered (EN) Humphead wrasse (*Cheilinus undulatus*) and the vulnerable (VU) Green Humphead parrotfish (*Bolbometopon muricatum*)—while the Giant grouper (*Epinephelus lanceolatus*), the largest bony fish in the world (Craig & Hastings, 2007), previously classified as vulnerable, is now classified as Data Deficient (DD). Despite this global recognition of the vulnerability of these 3 species, no published population surveys from the WIO were available to the IUCN when these assessments were conducted (Chan et al., 2012; Fennessy et al., 2018; Russell, 2004), largely because of limited funding and human capacity for in situ research surveys on coral reefs in this region (Samoilys et al., 2022; Stefanoudis et al., 2022; K.O., personal observation). Population data from the WIO are critical to raising awareness in the region of vulnerable species that are taken in fisheries and to assist member states in reporting progress toward international multilateral agreements on biodiversity conservation.

Fishing and economic value

Fishing is one of the key threats to coral reefs globally (Andrello et al., 2022; Hughes et al., 2017; Letessier et al., 2019). Large-bodied reef fishes are often target fishery species because of their high market value (Sadovy de Mitcheson et al., 2020), though this is less so in the WIO, where artisanal fisheries dominate and are characterized by the use of gears that capture a wide range of species (McClanahan & Mangi, 2004; Samoilys et al., 2017). However, large-bodied reef fishes in the WIO face increasing threats because the region is experiencing faster warming than other ocean basins (Hermes et al., 2019), has a rapidly growing and hence youthful human population (Davis & Balls, 2022; United Nations, 2011), and faces varying levels of technical and management capacity (Wafar et al., 2011).

Populations of reef sharks have been declining worldwide for decades (Jackson et al., 2001) and are now highly depleted, except in areas where gill net fishing is excluded, large marine sanctuaries are in place, or both (MacNeil et al., 2020), such as in New Caledonia and Palau (Ward-Paige, 2017). In the WIO, Seychelles is the only country that actively protects sharks and where abundant reef sharks are reported (MacNeil et al., 2020). Understanding of natural population levels of shark species associated with coral reefs is poor. For example, even in the Chagos Archipelago, reef shark populations have declined by 75% from the 1970s to 2012 (Ferretti et al., 2018). However, in most countries in the WIO, there is no active management of sharks, and quantitative information on reef shark populations is lacking (Bennett et al., 2022). For example, many WIO fisheries reports to the Food and Agricultural Organization simply provide an aggregate value for “sharks and rays,” making targeted species management difficult.

Rapid underwater census methods

Insufficient data on large-bodied reef-associated fishes in the WIO are partly due to the difficulties in surveying these species underwater because many are shy and highly mobile or have naturally low population densities and are not often observed in commonly employed belt transect surveys with relatively small surface area (~250 m^2). Consequently, they are often not selected for regular coral reef monitoring (Samoilys & Carlos, 2000; Samoilys et al. 2019; Usseglio, 2015), such as in Global Coral Reef Monitoring Network (GCRMN) surveys (Obura et al., 2017; Wilkinson, 2008). Therefore, we developed a rapid, timed, long scuba swim approach to assess the population status of predatory and large-bodied (attain >55 cm total length [TL]) reef fishes and to determine whether this method can be usefully added to the standard 250-m^2 belt transect surveys by GCRMN teams in the WIO. We deployed the timed swim method across 7 countries in the western and central Indian Ocean and Gulf of Aden. We then assessed the effects of protected areas on these selected taxonomic groups and hypothesized that the 2 remote regions (Chagos, Iles Glorieuses) support high populations of these species, possibly representing close to unfished natural populations, compared with reefs in the other 5 locations that are fished or less protected.

METHODS

Study area

Surveys of large-bodied reef fishes were conducted in 27 locations that ranged from 11.8°N to 14.7°S to 42.5°–72.7°E and were spread across 7 countries (hereafter referred to as regions) (Figure 1; Appendix S1). Five regions were in the WIO: Comoros, Madagascar, Mozambique, Tanzania, and Iles Glorieuses (France). One was in the central Indian Ocean, Chagos Archipelago, and one was in Djibouti in the Gulf of Aden. Surveys were all conducted from 2009 to 2015, except in Comoros, where additional surveys were conducted in 2018 to supplement the limited survey in 2009.

Marine protected area indices

Reference locations for unfished populations (Chabanet et al., 2016; Samoilys et al., 2018) were in 2 marine protected areas (MPAs) that are protected from fishing and have highly restricted access because they are military zones: the Chagos Archipelago and Iles Glorieuses (Figure 1). Sites were assigned one of 4 protection indices based on the management and enforcement in place (Appendix S1), following previous criteria for the region (Osuka et al., 2021): none, no management in place; low, MPA gazetted and established but enforcement considered poor; medium, MPA gazetted and established with some no-take-zone (NTZ) restrictions and good enforcement; and high, MPA with NTZs and strong enforcement. Survey sites were spread as much as possible across these protection levels in each location to maximize comparisons across the study area; however, high-protection sites were present in only 2 reference locations. This index is relatively simple and does not incorporate the size or age of the MPA, which varied considerably across the study regions (Appendix S1).

Taxonomic groups

We estimated the density and size of a preselected group of reef-associated fishes that attain a large body size (>55 cm TL) and are either high-trophic-level species (~4.0; Hussey et al., 2013) or threatened by extinction (IUCN, 2023). These taxonomic groups spanned 8 families and one subfamily and fell into 3 types: pelagic, demersal, and single large-bodied species (Table 1). Pelagic taxa included highly mobile or wide-ranging reef-associated predators: sharks (Carcharhinidae), tunas (Scombridae), trevally (Carangidae), and barracuda (Sphyraenidae). Demersal large-bodied taxa included grouper (Epinephelidae, piscivores), snapper and emperor combined (Lutjanidae and Lethrinidae), largely omnivores, pooled for analyses), and parrotfishes (Scarinae [subfamily of Labridae]), herbivores). Single IUCN Red List threatened species included wrasse (Labridae): EN Humphead wrasse (*C. undulatus*), VU Green Humphead parrotfish (*B. muricatum*), and the DD Giant grouper (*E. lanceolatus*). The 4 demersal families are frequently surveyed in standard underwater visual census (UVC) belt transect surveys, but here we surveyed only those species that attain maximum length ($L_{\max}$) of greater than 55 cm Total Length (TL) (Paxton et al., 2020).

UVC method

A timed long swim (LS) of 10 min on scuba (Choat & Pears, 2003; Robbins et al., 2006) was used to estimate densities and fish sizes of the 10 preselected taxonomic groups (Table 1). All species ($TL_{\max}$ >55 cm, where $TL_{\max}$ is the maximum size the species attains) in each of the pelagic and demersal families were searched for; thus, missing species from sites represented zero observations. The UVC survey consisted of a timed swim parallel to the reef crest ranging over the depth of the reef but ≤30 m while counting fish within a ~20-m-wide swathe (Appendix S2). Mean visibility was 14.7 m; no swims were conducted in <7-m visibility. The swim was designed to cover as much distance as possible underwater parallel to the reef edge. At each reef site, 2 LS replicate transects were completed in 2 dives within ~500–1000 m of each other. To estimate the average length of an LS, GPS readings were taken to measure a subset of 16 LS surveys at Glorieuses Island. The mean length of an LS was 147.4 m (SD 54.6). Thus, fish densities and biomass per LS were calculated based on a sampled reef area of ~3000 m^2.

Data analyses

Biomass (kilograms per hectare) was estimated from fish size census estimates based on published length–weight relationships (Froese & Pauly, 2023; Kulbicki et al., 2005), and medians and means were calculated (Appendix S3). Biomass was used as the standard metric because it is generally more sensitive to fish population change (Graham et al., 2017). Density values (number of individuals per hectare) were also calculated for the zero-inflated negative binomial (ZINB) modeling.

Biomass of the 10 taxonomic groups was compared across the 7 regions and 4 protection levels with a Kruskal–Wallis test because data did not conform to parametric assumptions. Regions that showed no variance in biomass (i.e., zeros) were excluded from the test. This was followed by a post hoc Mann–Whitney test to identify significant differences.

A ZINB model was fitted to assess the influence of protection on the density of each of the taxonomic groups. We selected a ZINB based on the likelihood ratio test that showed better model performance than a zero-inflated Poisson model (Lewsey & Thomson, 2004). The intercept was omitted from the ZINB model to allow assessment of the influence of each level of protection on fish density. Moran's I test was used to check the effect of spatial autocorrelation in each taxonomic group, and where an effect was detected, the glm model was fitted using spatial correlation structures, with Akaike information criterion (AIC) selection methods applied to select the best model. Spatial

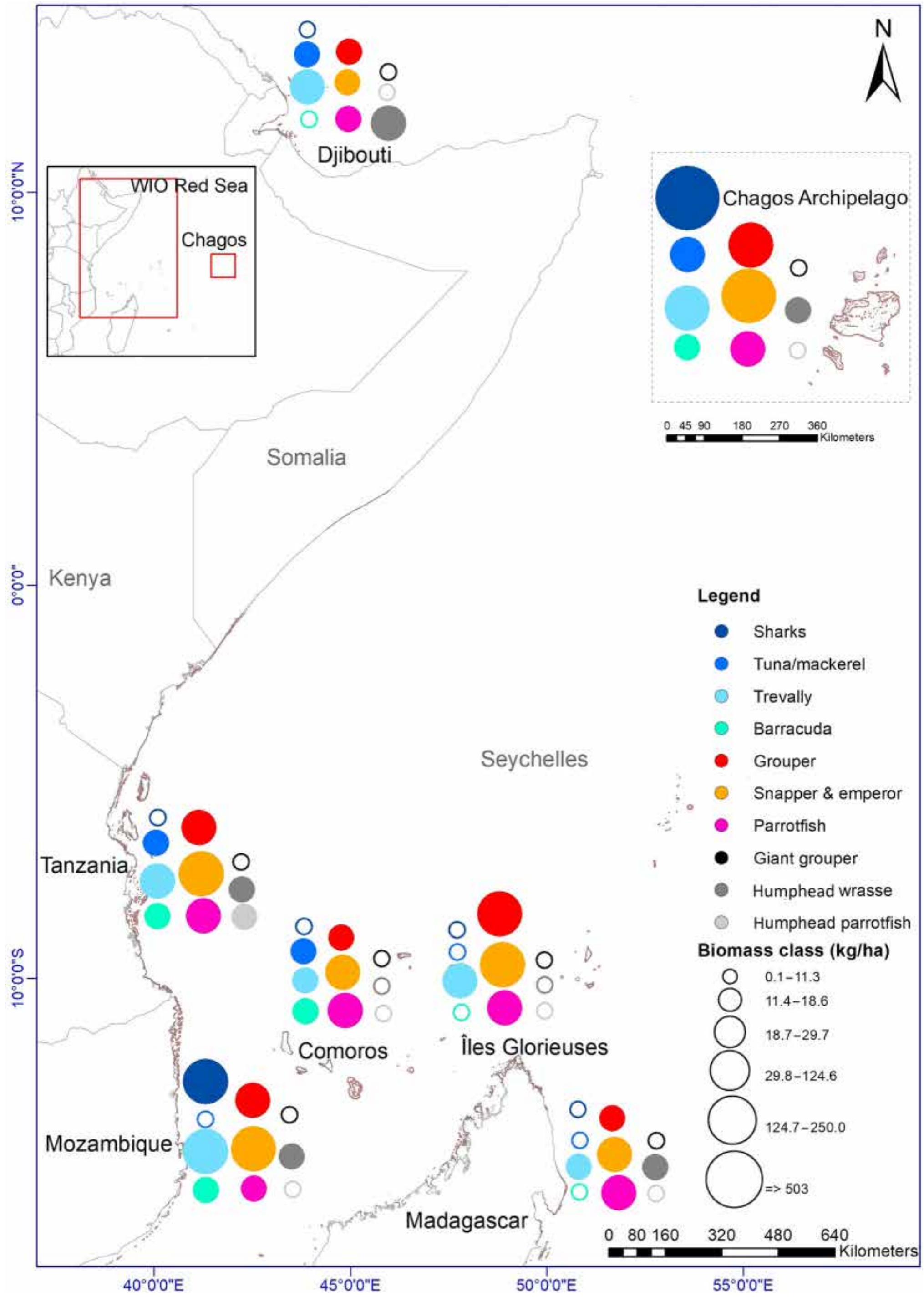

FIGURE 1 Mean biomass for 10 taxonomic groups of large-bodied reef fishes across 7 regions in the western and central Indian Ocean and Gulf of Aden (smallest open circles, zero individuals observed).

autocorrelation was detected in the Epinephelidae and Scarinae; therefore, the model was corrected using rational quadratic and Gaussian spatial correlation structures, respectively. To reduce the influence of uneven sampling effort, we conducted all our analyses at a country level. We also ran the ZINB model with the offset function within the model formula for selected taxa and found no major differences in the results.

RESULTS

Population biomass between geographic locations

Carcharhinidae were absent in 5 of the 7 regions, occurring only in Mozambique and the Chagos Archipelago (Figure 1; Table 2).

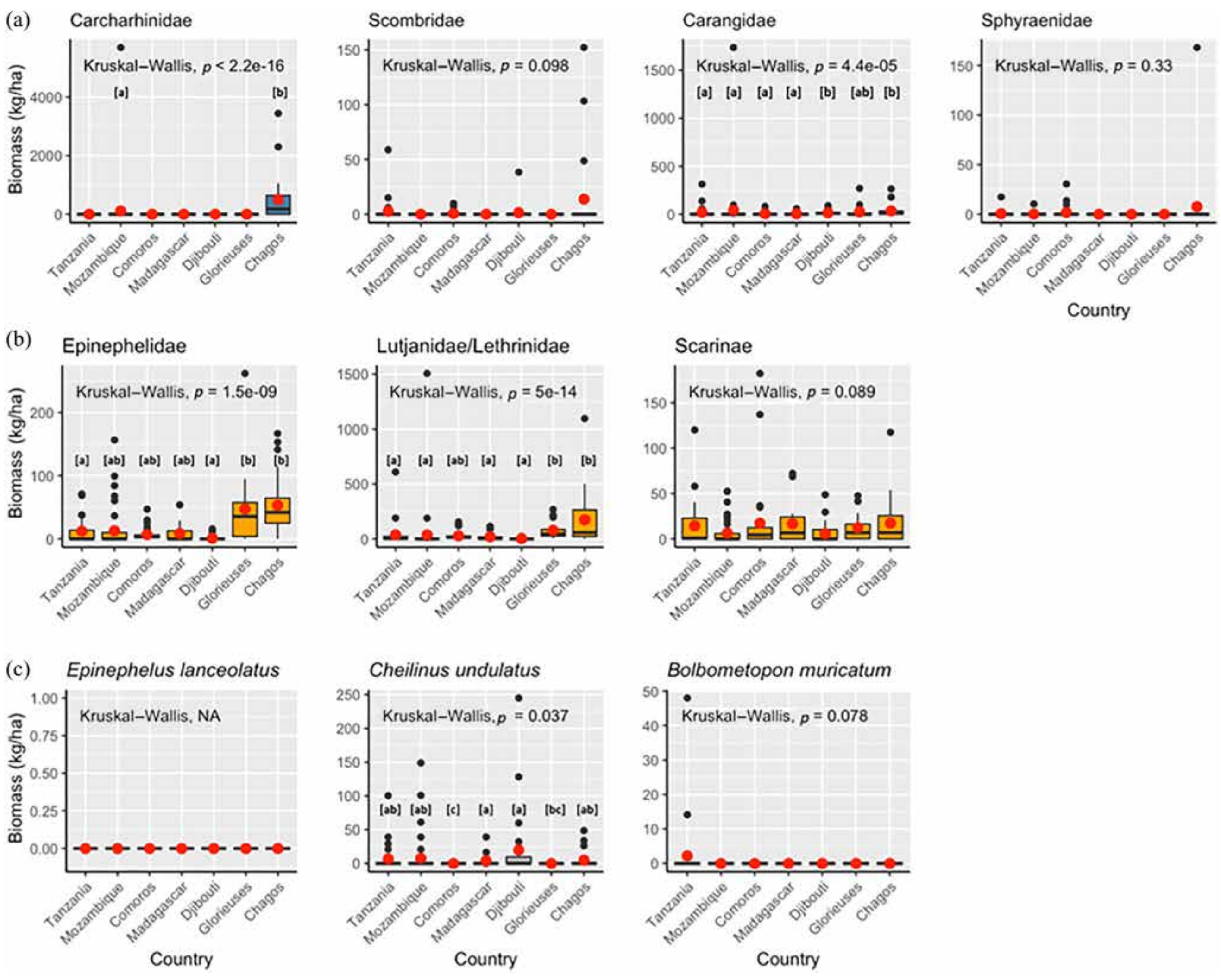

FIGURE 2 Median (interquartile range) and mean (red point) biomass for (a) pelagic taxa, (b) demersal taxa, and (c) large-bodied single species across the 7 regions in the western and central Indian Ocean and Gulf of Aden based on Kruskal–Wallace tests (biomass values in Table 2) (letters, Mann–Whitney pairwise comparisons; NA, not available).

Regional absences also occurred in 2 other pelagic taxa, Scombridae and Sphyraenidae, which were missing in Madagascar, Djibouti, and Iles Glorieuses. Giant grouper was absent in all regions, Humphead wrasse was absent in Comoros and Glorieuses, and Green Humphead parrotfish was only observed in Tanzania (Figure 1).

Significant differences between geographic locations in pelagic taxa were found only in Carcharhinidae and Carangidae (Figure 2a); median biomass of Carcharhinidae was significantly higher in Chagos than in Mozambique ($H = 19.64$, $p < 0.001$) (Figure 2a). Carangidae had significantly higher median biomass in Djibouti (2.6 kg/ha) and Chagos (4.0 kg/ha) compared with other locations ($H = 21.75$, $p < 0.001$), except Iles Glorieuses (Figure 2a; Table 2). For Scombridae, zero observations were recorded in Mozambique, Madagascar, and Iles Glorieuses; biomass was low elsewhere and highest in Chagos, where *Euthynnus affinis* (Kawakawa tuna), *Gymnosarda unicolor* (Dogtooth tuna), and other unidentified species were present. Other large-bodied scombrids included *Grammatorcynus bilineatus* (double-lined mackerel), which was observed rarely in Tanzania. In Comoros, only the small scombrid *Rastrelliger kanagurta* (Indian mackerel) was observed.

Outliers illustrate the high spatial variation in these data largely driven by pelagic species. For example, in Mozambique, trevally were substantially more abundant in Nacala and sharks were only seen at one reef location, Vamizi (Figure 2). In the Chagos Archipelago, outliers represented more abundant scombrids and barracuda on the Chagos Bank. These outliers did not prevent the detection of significant differences between geographic locations or protection effects but did show variability, which should be considered in local- or national-level population management.

All 3 groups of demersal large-bodied taxa showed significant regional differences. Higher median biomass of Epinephelidae ($H = 52.50$, $p < 0.001$) was recorded in Chagos (12.6 kg/ha) and Iles Glorieuses (10.7 kg/ha) compared with other countries, and

TABLE 1 Species recorded using the timed long swim survey method in 7 regions spanning the western and central Indian Ocean and the Gulf of Aden (2009–2018).

Functional group	Family or subfamily	Species	Common English name	Maximum total length (cm)[a]	Trophic level[a]	IUCN RL status[b]
Reef associated predators (highly mobile and wide ranging)	Carcharhinidae	*Carcharhinus amblyrhynchos*	Grey Reef Shark	255	4.1	EN 2020
		Carcharhinus melanopterus	Blacktip Reef Shark	200	3.9	VU 2020
		Carcharhinus *albimarginatus*	Silvertip Shark	300	4.2	VU 2015
		Carcharhinus spp.				
		Triaenodon obesus	Whitetip Reef Shark	213	4.2	VU 2020
	Scombridae	*Euthynnus affinis*	Kawakawa/ little tuna	107	4.5	LC 2011
		Grammatorcynus bilineatus	Double-lined Mackerel	105	4.2	LC 2011
		Gymnosarda unicolor	Dogtooth Tuna	272	4.5	LC 2011
		Rastrelliger kanagurta	Indian mackerel	42	3.2	DD 2011
		Scomberomorus commerson	Narrow barred King Mackerel	250	4.5	NT 2011
		Sarda orientalis	Striped bonito	108	4.2	LC 2009
		Scombrid spp.				
	Carangidae	*Carangoides bajad*	Orangespotted Trevally	55	4.0	LC 2016
		Carangoides ferdau	Blue Trevally	70	4.3	LC 2016
		Carangoides fulvoguttatus	Yellowspotted Trevally	133	4.4	LC 2016
		Carangoides gymnostethus	Bludger	90	4.1	LC2016
		Caranx ignobilis	Giant Trevally	170	4.2	LC 2016
		Caranx heberi	Blacktip Trevally	88	3.7	LC 2016
		Caranx melampygus	Bluefin Trevally	127	4.5	LC 2016
		Caranx sexfasciatus	Bigeye Trevally	120	4.5	LC 2019
		Decapterus sp. (cf *russelli*)[c]	looks like Indian scad	45	3.7	N/A
		Gnathanodon speciosus	Golden Trevally	120	3.8	LC 2016
		Elagatis bipinnulata	Rainbow Runner	180	4.3	LC 2016
		Scomberoides commersonnianus	Talang queenfish	120	4.4	LC 2016
		Scomberoides lysan	Doublespotted Queenfish	110	4.0	LC 2016
		Scomberoides tol	Needlescaled queenfish	60	4.1	LC 2016
		Selar crumenophthalmus	Bigeye Scad	70	3.8	LC 2015
		Trachinotus blochii	Snubnose pompano	110	3.7	LC 2016
		Carangids				
	Sphyraenidae	*Sphyraena acutipinnis*	Sharpfin Barracuda	80	4.5	Not evaluated
		Sphyraena barracuda	Great Barracuda	200	4.5	LC 2015
Large-bodied rare and threatened Labridae	Labridae[d] (Scarinae)	*Cheilinus undulatus*	Humphead Wrasse	270	4.0	EN 2004
		Bolbometopon muricatum	Green Humphead Parrotfish	130	2.7	VU 2012
Demersal piscivores	Epinephelidae	*Aethaloperca rogaa*	Redmouth Grouper	60	4.2	LC 2018

(Continues)

TABLE 1 (Continued)

Functional group	Family or subfamily	Species	Common English name	Maximum total length (cm)[a]	Trophic level[a]	IUCN RL status[b]
		Anyperodon leucogrammicus	Slender Grouper	65	3.9	LC 2018
		Cephalopholis argus	Peacock Grouper	60	4.5	LC 2018
		Dermatolepis striolata	Smooth Grouper	85	4.0	LC 2018
		Epinephelus caeruleopunctatus	Whitespotted Grouper	76	3.7	LC 2018
		Epinephelus coioides	Orange-spotted Grouper	120	4.0	LC 2018
		Epinephelus flavocaeruleus	Blue and Yellow Grouper	90	4.2	LC 2018
		Epinephelus fuscoguttatus	Brown-marbled Grouper	120	4.1	VU 2018
		Epinephelus malabaricus	Malabar grouper	234	4.2	LC 2018
		Epinephelus polyphekadion	Camouflage Grouper	75	4.0	VU 2018
		Epinephelus tukula	Potato Grouper	200	4.2	LC 2018
		Epinephelus multinotatus	Whiteblotched Grouper	100	3.9	LC 2018
		Plectropomus areolatus	Squaretail Coral Grouper	80	4.5	VU 2018
		Plectropomus laevis	Blacksaddled Coral Grouper	125	4.1	LC 2018
		Plectropomus punctatus	Marbled Coral Grouper	96	4.5	LC 2018
		Variola albimarginata	White-edged Lyre Tail	65	4.5	LC 2018
		Variola louti	Yellow-edged Lyretail	83	4.3	LC 2018
Demersal omnivores/some piscivores	Lutjanidae	*Aphareus furca*	Small-toothed Jobfish	70	4.1	LC 2016
		Aprion virescens	Green Jobfish	112	4.3	LC 2016
		Lutjanus argentimaculatus	Mangrove Red Snapper	150	3.6	LC 2016
		Lutjanus bohar	Two-spot Red Snapper	90	4.3	LC 2016
		Lutjanus monostigma	One-spot Snapper	60	4.3	LC 2016
		Lutjanus rivulatus	Blubberlip Snapper	80	4.1	LC 2016
		Macolor macularis	Midnight Snapper	60	4.0	LC 2016
		Macolor niger	Black and White Snapper	75	4.0	LC 2016
	Lethrinidae	*Gymnocranius grandoculis*	Blue-lined Large-eye Bream	80	3.8	LC 2016
		Lethrinus erythracanthus	Orange-spotted Emperor	70	3.4	LC 2016
		Lethrinus mahsena	Sky emperor	65	3.4	EN 2019
		Lethrinus microdon	Smalltooth Emperor	80	3.8	LC 2016
		Lethrinus nebulosus	Spangled emperor	87	3.8	LC 2016
		Lethrinus obsoletus	Orange-striped Emperor	60	3.9	LC 2016
		Lethrinus olivaceus	Longface emperor	100	4.0	LC 2016
		Lethrinus xanthochilus	Yellowlip Emperor	70	3.8	LC 2016
		Monotaxis grandoculis	Humpnose Big-eye Bream	60	3.4	LC 2016

(Continues)

TABLE 1 (Continued)

Functional group	Family or subfamily	Species	Common English name	Maximum total length (cm)[a]	Trophic level[a]	IUCN RL status[b]
Demersal herbivores (excavators and scrapers)	Scarinae[b]	*Cetoscarus ocellatus*	Bicolor Parrotfish	80	2.0	LC 2016
		Chlorurus strongylocephalus	Indian Ocean Steephead Parrotfish	70	2.0	LC 2012
		Hipposcarus harid	Candelamoa Parrotfish	75	2.0	LC 2012
		Scarus falcipinnis	Sicklefin Parrotfish	60	2.0	LC 2012
		Scarus ghobban	Blue-barred Parrotfish	75	2.0	LC 2012
		Scarus prasiognathos	Singapore parrotfish	70	2.0	LC 2012
		Scarus rubroviolaceus	Ember Parrotfish	70	2.0	LC 2012

[a] Maximum total length and trophic levels from FishBase.

[b] International Union for Conservation of Nature Red List (IUCN RL) source (www.iucnredlist.org).

[c] Species of *Decapterus* not identified. *Decapterus russelli* (Indian Scad) maximum total length and trophic group values used as proxy.

[d] In the Labridae family, 3 taxonomic groups were separated for analyses: *Cheilinus undulatus*; *Bolbometopon muricatum* (because of their huge size and rarity); and the remaining 7 large-bodied Scarinae subfamily species.

these biomass values were significantly higher than in Tanzania and Djibouti (Figure 2b; Table 2). Higher median biomass of Lutjanidae and Lethrinidae combined was recorded in Chagos (17.3 kg/ha) and Iles Glorieuses (13.9 kg/ha), and these were significantly higher than in all other locations, except Comoros ($H = 68.96, p < 0.001$). For Scarinae, no significant differences in median biomass were detected ($H = 9.77, p > 0.05$). Medians ranged from 0 (Mozambique and Djibouti) to 2.1 kg/ha (Iles Glorieuses).

No statistical analyses were possible for Giant grouper due to a lack of observations. Green Humphead parrotfish was only sighted in Tanzania, and there were no significant differences ($H = 0.36$, $p > 0.05$) in the median biomass across all sites (Figure 2c). For Humphead wrasse, significant differences were detected across sites; median biomass in Tanzania, Mozambique, Madagascar, Djibouti, and Chagos was significantly higher than in Comoros ($H = 4.38, p < 0.05$) (Figure 2c). Relatively high biomass was recorded in Djibouti, but there were zero observations in Iles Glorieuses and Comoros (Table 2). However, significant differences were not detected between Iles Glorieuses and Chagos or between Tanzania and Mozambique, suggesting these median values were not significantly higher than zero (Figure 2a; Table 2).

Effects of protection

Protection effects were detected in the median fish biomass of 2 pelagic families (Carcharhinidae and Carangidae) (Figure 3a) and 3 demersal taxonomic groups (Epinephelidae, Lutjanidae and Lethrinidae combined, and Scarinae) (Figure 3b). No significant protection effects were detected for Sphyraenidae and Scombridae (Figure 3a) or for Humphead wrasse and Green Humphead parrotfish (Figure 3c), largely due to many zero observations of these taxa. For the 5 taxonomic groups that showed protection effects, differences were not always aligned with significantly higher median biomass with greater protection except for Carcharhinidae (Figure 3). For Carangidae, biomass was greater in high, medium, and none protection areas compared with areas with low levels of protection (Mann–Whitney $p < 0.05$; Figure 3a; Appendix S3). The biomass of Epinephelidae was higher in high-protection sites than in other levels of protection, and medium protection showed significantly higher biomass levels than in sites with low and no protection (Figure 3b). For the Lutjanidae and Lethrinidae combined, significant differences in median biomass with protection level were detected, but results were not straightforward. High-protection sites had significantly higher biomass than medium, low, and none sites, whereas medium-protection sites were only greater than no-protection sites (Figure 3b). For the Scarinae, sites with high, medium, and low protection had statistically similar median biomass, although they were all significantly higher than the no-protection sites (Figure 3b).

Several significant predictions of protection effects across the taxonomic groups were found through the ZINB modeling (Table 3), although few were consistent with an increase in density as protection level increased. For example, higher densities were predicted in medium-protection sites (11.99 individuals/ha) relative to high-protection sites (5.63 individuals/ha) for Carcharhinidae. However, the odds of observing excess zero counts of sharks were significantly higher in medium levels of protection. For Scombridae, all protection levels significantly influenced predicted densities (Table 3): high-protection sites (14 fish/ha) had the most effect, medium-protection sites (6 fish/ha) had the least effect, and low-protection sites (10–11 fish/ha) had a moderate effect. The odds of observing excess zero counts were significant at all protection levels (highest for medium-protection sites). For Carangidae, there was no clear effect of increasing protection level on population densities (Table 3). All protection levels significantly influenced predicted densities. Sites with no protection had the most influence (52 individuals/ha). Estimates for low, medium, and high protection, although significantly >0, were similar. Carangidae were not affected by protection, or the medium- or high-protection sites were not suitable for Carangidae. High densities (180 fish/ha) of Sphyraenidae were predicted in high-protection

TABLE 2 Median and mean biomass (kilograms per hectare) for 10 taxonomic groups across countries in the western and central Indian Ocean and Gulf of Aden.

Taxa	Tanzania (*n* = 28)	Mozambique (*n* = 49)	Comoros (*n* = 29)	Madagascar (*n* = 16)	Djibouti (*n* = 26)	Iles Glorieuses (*n* = 16)	Chagos (*n* = 22)
Carcharhinidae							
Median (interquartile range [IQR])	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	178.1 (0.0–641.4)
Mean (SD)	0.0 (0.0)	116.1 (813.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	503.0 (849.3)
Scombridae							
Median (IQR)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)
Mean (SD)	2.9 (11.4)	0.0 (0.0)	0.7 (2.3)	0.0 (0.0)	1.5 (7.5)	0.0 (0.0)	13.8 (39.0)
Carangidae							
Median (IQR)	0.0 (0.0–4.8)	0.0 (0.0–0.0)	0.0 (0.0–0.4)	0.0 (0.0–0.0)	8.6 (2.9–17.9)	0.0 (0.0–10.1)	13.3 (0.0–34.8)
Mean (SD)	21.3 (64.3)	41.6 (248.0)	6.2 (17.2)	5.0 (15.1)	15.3 (20.8)	25.8 (69.8)	35.8 (65.7)
Sphyraenidae							
Median (IQR)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)
Mean (SD)	0.6 (3.3)	0.2 (1.5)	1.9 (6.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	7.6 (35.9)
Epinephelidae							
Median (IQR)	0.0 (0.0–13.7)	0.0 (0.0–10.1)	3.3 (1.9–6.3)	0.0 (0.0–13.0)	0.0 (0.0–0.0)	35.5 (4.1–57.5)	42.0 (25.0–64.5)
Mean (SD)	12.3 (20.0)	12.9 (30.4)	6.9 (10.6)	8.6 (15.3)	1.0 (3.8)	47.1 (65.4)	53.0 (49.1)
Lutjanidae/Lethrinidae							
Median (IQR)	4.5 (0.0–23.3)	0.0 (0.0–4.4)	14.3 (6.4–27.4)	34 (0.0–18.7)	0.0 (0.0–0.0)	46.3 (27.4–87.0)	57.8 (21.8–264.0)
Mean (SD)	38.6 (117.5)	38.0 (215.9)	28.2 (40.1)	20.2 (35.1)	2.8 (6.4)	77.9 (79.4)	173.8 (259.5)
Scarinae							
Median (IQR)	0.9 (0.0–22.9)	0.0 (0.0–5.9)	4.5 (0.0–12.4)	6.6 (0.0–24.1)	0.0 (0.0–10.3)	6.8 (0.3–16.4)	6.9 (0.0–25.7)
Mean (SD)	14.5 (26.2)	6.6 (13.1)	17.4 (41.0)	16.6 (23.4)	5.9 (11.6)	12.4 (15.4)	17.3 (27.2)
Epinephelus lanceolatus							
Median (IQR)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)
Mean (SD)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Cheilinus undulatus							
Median (IQR)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	00 (0.0–0.1)	0.0 (0.0–9.6)	0.0 (0.0–0.0)	0.0 (0.0–0.0)
Mean (SD)	6.8 (20.8)	7.6 (27.1)	0.0 (0.0)	4.0 (10.4)	20.0 (53.6)	0.0 (0.0)	5.0 (13.2)
Bolbometopon muricatum							
Median (IQR)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)
Mean (SD)	2.2 (9.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)

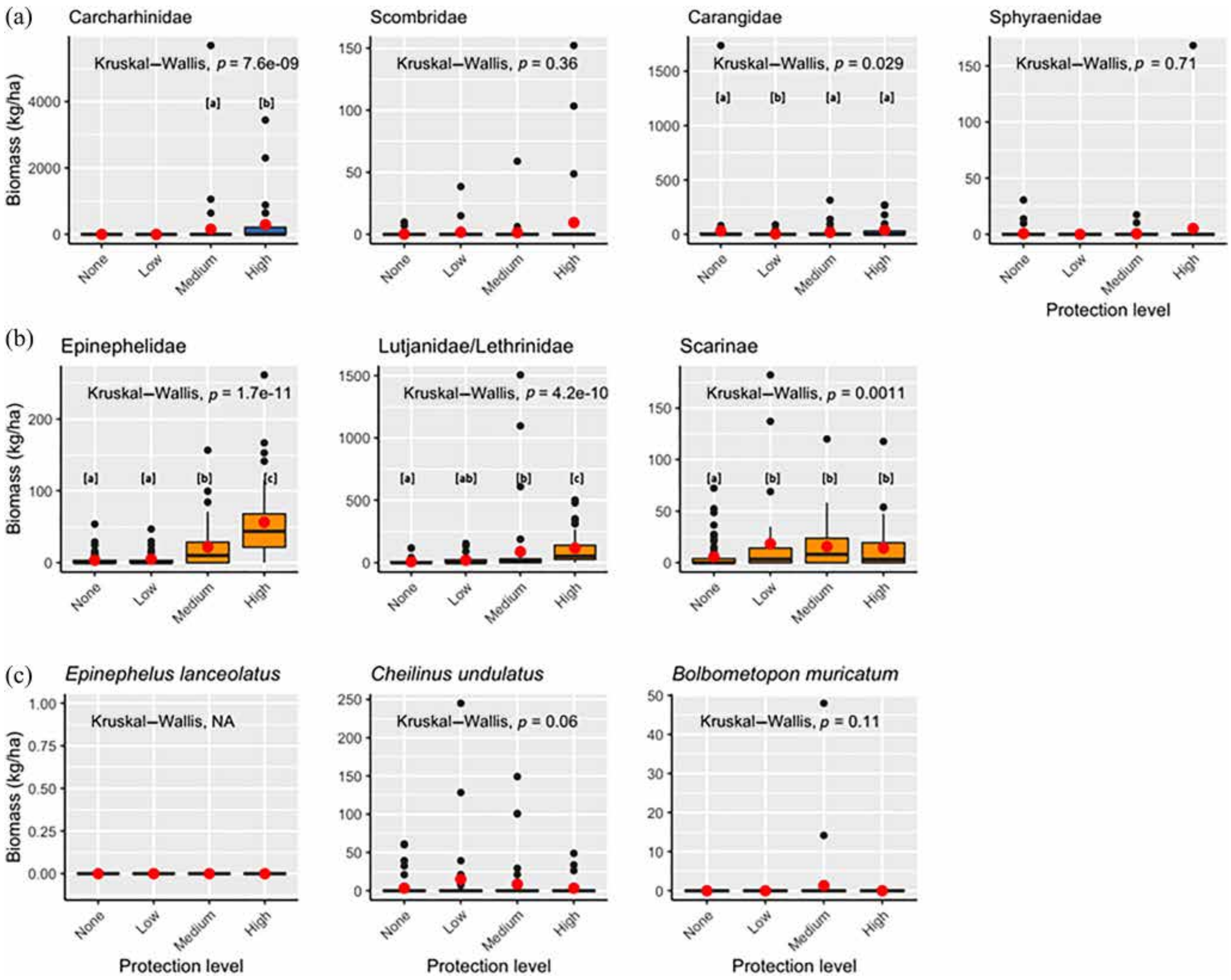

FIGURE 3 Median biomass for (a) pelagic taxa, (b) demersal taxa, and (c) large-bodied single species in the western and central Indian Ocean and Gulf of Aden across 4 protection levels based on Kruskal–Wallace tests. Abbreviations as for Figure 2.

sites relative to medium- and no-protection sites, which had 20–60 times lower predicted densities. The highest odds of observing excess zero counts were for sites with no protection; together, these were evidence for a protection effect in Sphyraenidae.

All protection levels significantly influenced predicted densities of Epinephelidae (Table 3). Predicted densities were slightly lower for sites with no or low protection (5.4–6.6 individuals/ha) than for high- and medium-protection sites (8.5–9.2 individuals/ha). The odds of observing excess zero counts of Epinephelidae decreased significantly only in high-protection sites (by 0.19). For the Lutjanidae and Lethrinidae combined, all protection levels significantly influenced predicted densities (Table 3). The highest densities were predicted in sites with medium (56 individuals/ha) and high (34 individuals/ha) protection. The odds of observing excess zero counts of Lutjanidae and Lethrinidae were not significant. For large-bodied Scarinae, all protection levels significantly influenced predicted densities, but the effect was inconsistent among no-protection (9 individuals/ha), low-protection (20 individuals/ha), medium-protection (12 individuals/ha), and high-protection (8 individuals/ha) sites. Protection level did not affect the odds of observing excess zeros.

For Humphead wrasse, all protection levels significantly influenced predicted densities, but the highest predicted density was in low-protection sites. Significant odds of observing excess zero counts were seen in all protection levels except low protection, and the highest odds of observing excess zero counts were predicted in high-protection sites.

DISCUSSION

Zero observations

Local extirpation of large-bodied reef-associated fishes, including sharks, Giant grouper, Green Humphead parrotfish, and Humphead wrasse, on many WIO coral reefs is suggested by

TABLE 3 Results of a zero-inflated negative binomial (ZINB) model predicting influence of protection on the density of 4 pelagic fish taxa (Carcharhinidae, Scombridae, Carangidae, and Sphyraenidae), 3 demersal taxa (Epinephelidae, Lutjanidae/Lethrinidae, and Scarinae), and one large-bodied species (*Cheilinus undulatus*).

Model[a]	**Protection (predictor)**	**Estimate**	**CI**	***p***	**Estimate**	**CI**	***p***	**Estimate**	**CI**	***p***
		Carcharhinidae			**Scombridae**			**Carangidae**		
Count	None	–	–	–	10.84	4.87–24.09	<0.001	52.67	22.43–123.71	<0.001
	Low	–	–	–	10.33	3.86–27.61	<0.001	10.13	1.91–53.80	0.007
	Medium	11.99	6.93–20.74	<0.001	5.69	1.25–26.04	0.025	12.32	3.99–37.98	<0.001
	High	5.63	3.98–7.96	<0.001	14.88	6.86–32.30	<0.001	12.28	4.43–34.06	<0.001
Zero-inflated	None	–	–	–	18.04	5.63–57.80	<0.001	0.48	0.09–2.58	0.396
	Low	–	–	–	6.87	1.55–30.37	0.011	0.80	0.09–6.84	0.839
	Medium	11.65	3.58–37.89	<0.001	35.07	4.76–258.23	<0.001	0.70	0.12–4.03	0.686
	High	2.22	1.08–4.54	0.029	10.91	3.34–35.61	<0.001	0.23	0.01–8.10	0.417
		Sphyraenidae			Epinephelidae			Lutjanidae/Lethrinidae		
Count	None	9.00	4.68–17.30	<0.001	5.41	4.07–7.18	<0.001	9.18	5.85–14.40	<0.001
	Low	–	–	–	6.60	3.45–12.60	<0.001	13.83	6.40–29.90	<0.001
	Medium	2.82	1.17–6.82	0.021	9.23	7.33–11.62	<0.001	56.41	35.10–90.67	<0.001
	High	180.00	155.53–208.31	<0.001	8.50	6.78–10.64	<0.001	33.78	22.11–51.62	<0.001
Zero-inflated	None	56.99	7.89–411.58	<0.001	1.43	0.83–2.46	0.194	0.56	0.26–1.18	0.127
	Low	–	–	–	2.91	0.93–9.11	0.067	0.39	0.10–1.61	0.194
	Medium	16.87	4.00–71.10	<0.001	0.34	0.16–0.72	0.005	0.38	0.17–0.86	0.020
	High	35.00	4.80–255.47	<0.001	0.19	0.07–0.47	<0.001	0.01	0.00–777.96	0.428
		Scarinae			*Cheilinus undulatus*					
Count	None	9.15	6.13–13.66	<0.001	4.09	2.08–8.06	<0.001			
	Low	20.14	11.42–35.52	<0.001	6.03	3.62–10.05	<0.001			
	Medium	12.23	8.63–17.33	<0.001	5.05	2.49–10.24	<0.001			
	High	8.60	5.75–12.86	<0.001	4.63	1.83–11.69	0.001			
Zero-inflated	None	1.46	0.83–2.56	0.192	7.79	3.26–18.61	<0.001			
	Low	0.56	0.19–1.62	0.281	0.69	0.24–2.03	0.504			
	Medium	0.29	0.12–0.69	0.005	6.11	2.34–15.96	<0.001			
	High	0.52	0.23–1.14	0.101	10.11	3.04–33.62	<0.001			

Note: The estimate represents the expected change in the outcome variable (density) associated with a change in the predictor variable (protection). Unavailable estimates (–) indicate zeros were observed and therefore the modeled estimates are not reliable.

[a] For the count model, the estimate is density; for the zero-inflated model, the estimate is the rate ratio (log odds).

our results. We found reef sharks at only one reef in northern Mozambique. In contrast, reef sharks were regularly observed in the Chagos Archipelago. However, with a mean biomass of only 503 kg/ha (SD 849), compared with 3147–6663 kg/ha at 2 other Iles Eparses islands (Chabanet et al., 2016), even Chagos shark populations appeared depleted. The 3 large-bodied species vulnerable to extinction (IUCN, 2023)—Green Humphead parrotfish (VU), Humphead wrasse (EN), and Giant grouper (DD)—were rarely observed or not observed at all throughout the 7 countries. Ours is the first study to demonstrate that the population abundance of large-bodied reef fishes from 8 functionally important families appears to be extremely low across the WIO region.

The pelagic tunas and barracudas also appeared to be depleted; there were multiple zero observations at sites in Madagascar, Iles Glorieuses, Mozambique (tuna), and Djibouti (barracuda) and low biomass elsewhere except within Chagos. The scombrid tuna and tuna-like species contribute to some of the most valuable commercial fisheries in the Indo-Pacific (Dahlet et al., 2019; Gillett & Cartwright, 2010), but they are threatened by intense fishing pressure and climate change (Bell et al., 2016; Kumar et al., 2012). Although many of these species spend a large portion of their time foraging away from coral reefs, the low numbers we recorded support concerns that scombrids are depleted in the WIO (Tidd et al., 2023).

Barracuda are circumglobal, large piscivorous fishes that move from nearshore mangroves and seagrass beds to coral reefs for their adult phase (de Sylva, 1963). Two barracuda species were recorded in the present study: *Sphyraena barracuda* (Great Barracuda) in WIO locations, whereas *Sphyraena acutipinnis* (Sharpfin) was the only barracuda sighted in the Chagos Archipelago. Great Barracuda biomass values ranged from 0.2 to 1.9 kg/ha in eastern Africa, suggesting their populations may be depleted. However, knowledge of the ecology of Giant Barracuda is sparse, limited to Florida and the Bahamas. Although adult Giant Barracuda commonly occur in <10 m near coral reefs (O'Toole et al., 2011), they also move distances of hundreds of kilometers over the continental shelf and open water to >175-m depth (Hansen, 2015). The zero observations in the WIO may therefore represent false zeros (Blasco-Moreno et al., 2019) because our rapid timed surveys did not adequately sample these species.

Trevally (jacks) are naturally abundant predators, often occurring in schools on or near coral reefs (Anderson, 2005), and associate positively with high and low coral complexity and strong currents (Sartori et al., 2021). Exceptionally high biomass values (up to 626 kg/ha) of trevally were found in 250-m^2 transect area surveys at Iles Glorieuses (Chabanet et al., 2016), whereas biomass was 26 kg/ha in Iles Glorieuses and 36 kg/ha in Chagos in our ~3000-m^2 surveys (both data sets from 2014). In Madagascar, Comoros, and Djibouti, trevally biomass was exceptionally low. Population abundance values are limited for trevally in the Indo-Pacific, making our results difficult to interpret. The large discrepancy in biomass values at Iles Glorieuses could have been due to the different UVC methods or aggregation behavior in Carangidae (Daly et al., 2018). Nevertheless, the low biomass in eastern Africa of these predatory species is of concern for coral reef ecosystem functioning and local fisheries.

Threatened species

Awareness of endangered species and the IUCN Red List is still relatively poor in many WIO countries, and this is linked to limited data. For example, previous IUCN assessments of the Green Humphead parrotfish, Humphead wrasse, and Giant grouper contained little or no population data from the WIO (Chan et al., 2012; Fennessy et al., 2018; Russell, 2004). We found Giant grouper was not sighted throughout the study sites, despite reports of their occurrence across a range of locations (Fricke et al., 2022), including in Chagos in 1999 (Winterbottom & Anderson, 1999). However, the species is poorly studied and its early life history is not well understood. Other ad hoc underwater observations in the region by one of us (M.S.) are from Zanzibar (3 adults) on inner reefs in northern Kenya (one juvenile) and at Iles Glorieuses (one adult). Giant grouper is also reported from Juan de Nova in the Iles Eparses (Chabanet et al., 2016). The lack of observations of Giant grouper suggests severe depletion, but with no baselines and limited ecological understanding, the status of this species in the WIO remains unknown.

The Green Humphead parrotfish was observed only in Tanzania at one site. This species is not known from oceanic locations (Chabanet et al., 2016; Hamilton et al., 2008; Winterbottom & Anderson, 1997, 1999) and therefore might not be expected in Comoros or Iles Glorieuses. However, a recent observation of 15 individuals in Grande Comore (M.S., November 2023) refutes this assumption. Early records show the Humphead parrotfish was widely distributed in the Red Sea and Gulf of Aden (Ormond & Edwards, 1987). No observations in Djibouti support previous reports that this species is highly depleted in the Gulf of Aden (Hassan et al., 2002). In summary, zero observations of Green Humphead parrotfish in all but one site suggest severe depletion in its population in the WIO.

The Humphead wrasse occurs across Indo-Pacific coral reefs (Donaldson & Sadovy, 2001; Sadovy et al., 2003) and in the WIO as far east as Reunion and Mauritius (Fricke et al., 2009; P.C. personal observation). The species prefers deep reef drop-offs and is reported close to seagrass beds (Daly et al., 2020); therefore, it would be expected on many of the sites we surveyed. The species was not observed in Iles Glorieuses, a fully protected uninhabited French military zone. This contrasts with the relatively high biomass of Humphead wrasse in other islands in the Mozambique Channel (Chabanet et al., 2016). Elsewhere, the biomass of Humphead wrasse was low and variable, with the highest abundance observed in Djibouti. It is known to have high site fidelity, which makes it vulnerable to local fishing pressure but also amenable to protection through MPAs (Daly et al., 2020). Except for Daly et al.'s (2020) study in Seychelles, spatial and ecological knowledge is sparse, with only 2 studies from New Caledonia and Palmyra Atoll (Chateau & Wantiez, 2007; Weng et al., 2015). Research is needed urgently on this endangered species (Fricke et al., 2009) globally and in the WIO to improve existing conservation approaches.

Our data can improve IUCN Red List global assessments, raise awareness of the threats vulnerable reef fish species face in the WIO region, and improve funding (Betts et al., 2020). The status of the WIO populations of the 3 large-bodied threatened species will be provided to regional and national red lists under the IUCN National Red List project, where a different threat status may be decided. This would help nations measure and report their progress toward international multilateral agreements and raise awareness locally. However, in the WIO region, only South Africa has completed a national red list, likely because of a lack of capacity and resources in marine biodiversity research (Wafar et al., 2011).

Effectiveness of protected areas for large-bodied reef fishes

Although protection level significantly influenced population biomass and predicted density of these large-bodied fishes, the predictions were not consistent with higher population abundance associated with increasing levels of protection. The Chagos Archipelago and Iles Glorieuses can provide high protection from fishing primarily because there are no resident fishing communities and fishers coming from outside these territories are excluded (Hays et al., 2020). In addition, with great size and age (Appendix S1), Chagos Marine Park would be expected to contain the greatest population densities and biomass of large-bodied fishes (Ziegler et al., 2024). Although some illegal fishing occurs (Collins et al., 2021), these remote MPAs did contain the highest population biomass of sharks (Carcharhinidae) and large-bodied groupers (Epinephelidae) compared with all other protection levels. However, there was little evidence of positive protection effects for tuna, barracuda, trevally, and parrotfishes, though barracuda and tuna were predicted to have the highest population densities in high-protection sites. Little conservation impact on Indian Ocean tuna populations from the Chagos MPA has been reported previously (Curnick et al., 2020).

Protection effects were not detected throughout the study region for the large-bodied Humphead wrasse; predicted densities were similar for all protection levels. No conclusions could be made on the effectiveness of protection for Giant grouper and Green Humphead parrotfish because either population densities were zero throughout or individuals were observed only in medium protection sites. Because high-protection sites in this study were isolated oceanic reefs where Green Humphead parrotfish are not expected (Hamilton et al., 2008), these areas cannot be considered refuges for this species. In contrast, the lack of sightings of Giant grouper in the Chagos Archipelago suggests that a previous fishery on groupers that closed in ~2010 may have had long-term impacts on this species (Samoilys et al., 2018). The lack of knowledge of the population status of this species is illustrated by its DD listing on the IUCN Red List (Fennessy et al., 2018) and highlights a research gap.

Two taxonomic groups important in WIO artisanal fisheries revealed a particularly poor response to protection—the trevally and the 7 large-bodied parrotfish species. The highest population densities of trevally were predicted in sites with no protection status, and biomass varied 20 times in remote highly protected sites in the Mozambique Channel (this study; Chabanet et al., 2016). Further ecological research is needed to better understand the dynamics of this large family (Skinner et al., 2020). Little evidence of positive protection effects on large-bodied parrotfishes is surprising; the highest population densities were predicted in low-protection sites. Possibly, this reflects that other processes besides protection drive parrotfish populations, such as climate-change-induced changes in habitat and productivity and species-specific responses to coral mortality (McClanahan et al., 2019; Robinson et al., 2019; Samoilys et al., 2018; Williams et al. 2015). In contrast, medium- and low-protection sites, typical of MPAs in the WIO (Osuka et al., 2021), were effective for 2 of the 3 demersal large-bodied taxonomic groups—the grouper, and snapper and emperor combined. This may be related to the long period that some of the medium-protection MPAs have been established (Ziegler et al., 2024), such as those in Tanzania. This has positive implications for coastal livelihoods because these taxonomic groups are important in WIO artisanal fisheries (Rehren et al., 2022).

Usefulness of rapid timed swim UVC method

The characteristics of sites with the highest levels of protection in this study, in the Chagos Archipelago and Iles Glorieuses, were not replicated on the eastern African coast in terms of being remote and uninhabited but also in terms of their geomorphology and oceanic characteristics, which can influence taxa presence and abundance. However, inclusion of these locations represents the best available method to examine differences in the abundance of large-bodied and high-trophic-level fish across large gradients of fishing pressure within the WIO. Generally, we based our interpretations on the assumption that zero observations of a taxonomic group are true zeros and not false zeros caused by sampling errors. This assumption is based on Blasco-Moreno et al.'s (2019) definitions of *structural zeros* (related to ecological or evolutionary restrictions of the hypothesis being examined) and *sampling zeros* (If sampling is inadequate, the zero is false.). Where a species' range is conclusively known to exclude certain locations, such as oceanic reefs, then zero observations at these sites would represent structural zeros, such as Green Humphead parrotfish (*B. muricatum*) not occurring in the Chagos Archipelago. In contrast, the several zero observations of Giant barracuda may be false zeros due to inadequate sampling based on their movements and behavior. The zero observations throughout all sites of the widely distributed Giant grouper likely represent true zeros, though movement and behavior of this species are poorly known.

Remote camera methods, particularly baited remote underwater videos, are increasingly deployed to estimate populations of large roving reef predators and fish assemblages (Harvey et al., 2021; Osuka et al., 2022; Simpfendorfer et al., 2023; Skinner et al., 2020; Stefanoudis et al., 2023). However, they are not readily accessible in many WIO countries, and the capacity to analyze such video data is still low. The timed swim we used was designed to be a rapid add-on to regular GCRMN fish transect surveys that many nations deploy regularly in the WIO. It built on historic UVC attempts to estimate the abundance of large mobile and diver-shy fish species (Kimmel, 1985; Thresher & Gunn, 1986). Our results showed that the rapid timed scuba swim could detect significant differences between geographic locations and protection levels in large-bodied reef-associated fishes, thereby providing valuable conservation information for these lesser-known species.

Implications for ecosystem functioning and fisheries management

Many large-bodied fishes on reefs perform a critical role in the functioning of coral reef ecosystems. Depletions in populations of large-bodied and high-trophic-level demersal reef fishes affect reef ecosystems directly and indirectly (Frisch et al., 2014; Heithaus et al., 2008), whereas high grouper biomass has been linked to more complex coral reef systems (Karkarey et al., 2014; Sartori et al., 2021). Our data suggest that many large-bodied predatory fishes are at or close to functional extinction (MacNeil et al., 2020) in the WIO and that populations of several taxa are depleted even in remote, highly protected locations of the Chagos Archipelago and Iles Glorieuses. When fishing removes these large-bodied species, the fish community changes with cascading effects. For example, depletion in populations of Black tip (*Carcharhinus melanopterus*) and Gray reef sharks (*Carcharhinus amblyrhynchos*) has been clearly linked to changes in prey communities (Hammerschlag et al., 2018). However, these relationships are complex; for example, scale dependency (Heenan et al., 2020), inverted trophic pyramids (Sandin & Zgliczynski, 2015), and low-trophic-level fishes can enhance fish biomass under heavy fishing (Graham et al., 2017). Productivity and energy flow on coral reefs are also influenced by large-bodied fishes that feed in pelagic or deep waters beyond the reef, such as the highly mobile scombrids, barracuda, trevally, and sharks. Such allochthonous pelagic subsidies (Morais & Bellwood, 2019) enhance fish biomass production on a coral reef, with obvious deleterious consequences if these fishes are removed.

The effectiveness of a protected area improves substantially if it is surrounded by strong fisheries management (Goetze et al., 2024; Roos et al., 2020). The gillnet is widely used in the WIO but is one of the most damaging fishing gears because it is unselective, capturing a wide range of taxa including large-bodied species of snapper, emperor, grouper, parrotfish, and Humphead wrasse (Samoilys et al., 2017; Samoilys, Osuka, et al., 2019). Small-mesh gillnets capture high proportions of juveniles, whereas large mesh sizes capture adults, including sharks and rays (Osuka et al., 2021). Prohibiting gill nets in buffer zones around protected areas or at least within locally managed protected areas (Kawaka et al., 2017) is recommended to enhance ecosystem function and conservation benefits (MacNeil et al., 2020, Goetze et al., 2024). Such prohibition of gillnets does, however, pose substantial socioeconomic challenges. A successful ban would require minimizing trade-offs between ecological goals and the economic well-being of fishers, ideally through working with fishers in gear modification trials and enforcement (Osuka et al., 2021) while facilitating livelihood diversification (Roscher et al., 2022).

We found that the best-protected MPAs in the WIO, those with medium levels of protection, were not effective for several large-bodied coral reef fishes, including sharks and 3 globally threatened species. Only the highly protected reefs of Iles Glorieuses and Chagos in the central Indian Ocean were effective in protecting these species. Medium-level protection included nationally gazetted or privately established MPAs in Tanzania (some over 20 years old) and Mozambique and some reefs in Chagos (Diego Garcia) and Iles Glorieuses (Jeyser), where recreational fishing occurs. The medium-protection MPAs in eastern Africa were, however, effective for the demersal large-bodied groupers, snappers, and emperors. Eastern Africa is one of 5 regions with the lowest numbers of reef sharks in the world (MacNeil et al., 2020). Our results support these findings and suggest that sharks will disappear from reefs in the WIO if their management continues to be neglected. Our results also highlight the refuge that the Chagos Archipelago is providing to reef sharks in the WIO, despite the poaching (Collins et al., 2021). Based on the zero observations in this study of key reef fish species, including globally threatened large-bodied species (Green Humphead parrotfish, Humphead wrasse, and Giant grouper), we recommend urgent action to initiate protection for these 3 species in the WIO and to expand standard coral reef monitoring to include the timed LS for large-bodied reef fishes. We recommend additional conservation actions include targeted fisheries restrictions, for example, on gill nets, and species-specific protection of critical habitats to improve the effectiveness of protected areas.

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