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Depth and habitat are important drivers of abundance for predatory reef fish off Pemba Island, Tanzania

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Abstract

Coral reefs across the world face significant threats from fishing and climate change, which tends to be most acute in shallower waters. This is the case off Pemba Island, Tanzania, yet the effects of these anthropogenic stressors on the distribution and abundance of economically and ecologically important predatory reef fish, including how they vary with depth and habitat type, is poorly understood. Thus, we deployed 79 baited remote underwater video stations (BRUVs) in variable water depths and habitats off Pemba Island, and modelled the effects of depth and habitat on abundance of predatory reef fish. Predatory reef fish types/taxa were significantly predicted by depth and habitat types. Habitats in relatively deeper waters and dominated by hard and soft corals hosted high species richness and abundance of predatory reef fish types/taxa compared to mixed sandy and rubble habitats. The findings add to the growing evidence that deep waters around coral reefs are important habitats for predatory reef fish. Thus, careful management, through effective area and species protection measures, are needed to prevent further depletion of predatory reef-associated populations and conservation of this biologically important area.

Keywords: Coral reefs, depth refugia, habitat effects, predation, movement behaviour, fisheries, conservation

Introduction

Coral reef predatory fishes - fish that feed on other fish or marine animals - have profound economic and ecological importance (Moberg and Folke, 1999; Hammerschlag *et al.*, 2019). They are an important source of animal protein and contribute significantly to the livelihoods of more than 20 million people living in close proximity to the eastern African coast (Bell *et al.*, 2016). Their large body size makes them desirable and a relatively easy target, but the late maturation and longevity of many species makes them more susceptible to overfishing (de Mitcheson *et al.*, 2020). Fishing pressure on large reef predators has increased significantly in recent decades, causing major declines in many areas around the world (Worm *et al.*, 2013). Overfishing of predatory fish populations can have severe ecological impacts as it often destabilizes food webs leading to community-wide impacts (Bascompte et al., 2005; Worm *et al.*, 2013; Hussey *et al.*, 2014; Sandin and Zgliczynski, 2015). Reef predators structure reef fish communities by directly exerting top-down control of prey organisms (Stewart and Jones, 2001; Baum and Worm, 2009), and indirectly by influencing the behavior of prey assemblages while searching for food (Hixon, 2015; Rasher et al., 2017) or when resting and mating as part of their life history (Green *et al.*, 2015). The role of predatory fishes is therefore multi-faceted, extending from the oceans to the coastal communities.

Predatory fish show preferences for particular habitat types such as forereef ledges (Papastamatiou *et al.*, 2009), outer atolls and shelf areas (Cappo et al., 2007; Skinner *et al.*, 2020) that are associated with abrupt changes in depth. Such habitats are characterised by increased depth that can provide refuge to a wide variety of reef predator populations (Tyler *et al.*, 2009; Stefanoudis *et al.*, 2019). These outer deeper reef habitats or contiguous to deep are nutrient rich hence attract a high abundance of schooling planktivorous species, which are an important food item for the highly mobile predators (Wyatt *et al.*, 2013). Thus, abundance, biomass and diversity of predators often increases from shallower lagoon reefs to deeper seaward reefs (Jennings et al., 1996; Pinheiro *et al.*, 2016). Shallower areas are more vulnerable to climate-induced coral bleaching (Graham et al., 2013; Obura et al., 2017), which can lead to coral mortality and loss of structural complexity. This in turn can cause declines in the prey that predatory reef fish generally consume (Hempson et al., 2017). Recovery of such reefs after bleaching is generally greatest where reefs are structurally complex and in deeper waters (Graham et al., 2015). However, the cover of live coral also declines below a certain depth, due to light limitation (Kahng et al., 2019; Osuka et al, 2021a). Interactions between different predator types (e.g., schooling transient and resident predators) with habitat types and their associated depths remains unclear (Hixon, 2015). Fishing pressure is usually highest in shallow coral reef areas and can amplify the depth-predator pattern (Tyler *et al.*, 2009). Increasing water depth is anticipated to have positive and negative relationships with abundance of fish predators and fishing pressure, respectively (Tyler *et al.*, 2009; Pinheiro *et al.*, 2016; Stefanoudis *et al.*, 2019). Therefore, the depth distribution of predatory reef fish will be governed by the combined influences of habitat structure, food availability and fishing disturbance, and how they interact with one another.

One area that is thought to support high numbers of predatory coral reef fish, but that is also under pressure from fishing, is the Pemba channel off the coast of Tanzania. The western margins of Pemba Island neighbors a deep channel that averages 300 m and reaches a maximum of 800 m, making the Island a true oceanic Island (Semba et al., 2019). The shallow (<20 m) marine areas of Pemba Island have highly variable coral reef conditions, with some in healthy states with a high cover of hard coral, while others are in degraded states with low hard coral cover (Grimsditch et al., 2009). Reefs with low coral cover have been linked to destructive fishing activities particularly dynamite fishing (Grimsditch *et al.*, 2009; Wells *et al.*, 2010; Slade and Kalangahe, 2015). The mesophotic reef areas (30-150 m) are characterised by ledges, and oceanic steep outer reef slopes forming “staircase” walls in some locations (Osuka *et al.*, 2021a). These seafloor features, together with a deep channel and the remoteness of the island, makes Pemba Island a potential hotspot for large reef predators. Yet, little is understood of the influence of depth and habitat on fish predators in this area.

The Pemba Island fishery is mainly artisanal involving the use of traditional gears (e.g. gillnets, hook and line) and introduced gears (e.g. small purse seines) to target coral associated fish (Rehren et al., 2020). Evidence of overfishing has been reported at several sites. Indeed, a study conducted a decade ago in waters <21 m recorded no sharks, implying high rates of overfishing (Grimsditch *et al.*, 2009). Similarly, other large predatory taxa like groupers and snappers were either rare or of small size. In recent times, surveys on apex predators in Tanzanian waters (western margins of Pemba Channel) suggest that shark populations are “functionally extinct” (MacNeil *et al.*, 2020). Further, biomass projections of commercial species including large reef-associated predators in the Tanzanian Exclusive Economic Zone predict declines of up to 56-69% under increased fishing scenarios by the end of the 21st Century (Wilson et al., 2021). The decline in large reef-associated predator stocks is considered a key driver motivating fishers’ migration to other distant fishing grounds as far as Mozambique and Kenya, where depletion of fish stocks has been reported in the host fishing grounds (Wanyonyi *et al.*, 2016).

Sampling of coral reef fish communities in areas that are inaccessible or challenging for SCUBA divers was traditionally done with traps or nets (Collin, 1990; Bacheler et al., 2017). However, an increasingly popular method is the use of baited remote underwater videos (BRUVs). BRUVs are considered a non-invasive and non-destructive technique, which has been applied to assess occurrences of larger and more mobile species (Harvey *et al.*, 2012; White *et al.*, 2013). The method has been widely applied over extensive geographic areas, depth ranges and habitats (Harvey *et al.*, 2013; MacNeil *et al.*, 2020). Surveys with BRUVs ensure fish are not disturbed by divers, species are likely attracted from larger areas by the bait, and a permanent record is produced. Use of BRUVS enhances species ID and allows more detailed analysis of the surrounding habitats and more importantly can be deployed much deeper than SCUBA (Harvey *et al.*, 2012).

Coral reef communities show clear spatial patterns that vary across a range of fine-scale local habitat conditions (Karisa et al., 2020). The outer reefs of Pemba Island have been little surveyed to date, likely due to logistical challenges associated with sampling deeper reefs with standard SCUBA underwater visual censuses. Indeed, previous ecological fish surveys conducted in Pemba Island were restricted to depths <21m and conducted either on SCUBA (e.g., Daniels et al., 2003; Grimsditch et al., 2009) or snorkel (e.g., Jones et al., 2019). The results from these studies lacked consensus on the diversity of reef predators. Therefore, we considered that BRUVs would be ideal for providing a more complete picture of the predatory reef fish community in this area.

This study aimed to examine key environmental characteristics that may be driving the abundance, distribution and diversity of predatory reef fish populations around Pemba Island. We hypothesized that predatory reef fish would be more confined to deeper than shallower reefs and would show significant relationships with healthy habitats dominated by hard corals. Further, habitat type (e.g., live coral vs rubble) were expected to be stronger predictors of the occurrence, abundance and diversity of resident predatory species (i.e., those showing strong association with the reef structure), rather than transient species (i.e., schooling and epipelagic species).

Materials and methods

Study site

The survey was conducted on the outer reefs of the western margins of Pemba Island (Figure 1). Reefs selected for sampling corresponded in part with previous surveys conducted in the

Greater Pemba Channel within the Pemba Community Conservation Area (PECCA) using SCUBA (Grimsditch *et al.*, 2009; Gudka et al., *in prep*) and autonomous underwater vehicles - AUV (Osuka *et al.*, 2021a). Sites were chosen to be representative of different reef habitats and on the basis of depth (5-47 m) using a real-time depth echo sounder (Figure 1). Stations were largely fore reefs on the western margins of Pemba Island spanning from reefs in the north to the south (Figure 1). The BRUV stations occurring in continuous reef and separated to the next set of stations by a reef pass were pooled together to form a 'sector'. This resulted in three sectors conveniently named as north, central and south. The north and central sectors were separated by a deep channel called the Fundo Gap (Figure 1). Similarly, the central and south sectors were separated by a channel north of Misali Island (Figure 1). The survey was conducted in November 2019 over a five-day period during daytime hours.

Each sampling involved deployment of a mono-BRUV unit consisting of a video GoPro Hero4 camera Silver fixed on a stainless-steel frame, which was attached to a 1.65 m conduit pipe in the field of view of the camera (Appendix 1). A meshed bait bag was mounted on the pipe and filled with bait of ca. 1 kg composed of oily fish from the families Scombridae and Carangidae. The bait was cut into small pieces, which was filled into the bait bags. The BRUV unit was tied with a rope to the top of the frame to facilitate deployment and a buoy on the other end to enable detection and retrieval.

Each BRUV system was assembled and deployed following the Standard Operating Procedure described in Langlois et al. (2020). The first BRUV unit was deployed close to preset GPS coordinates while subsequent deployments were done approximately 500 m away but along the reef. This distance was selected to minimize the chances of the same fish individuals being documented on neighboring BRUV deployments. If there was insufficient reef in an area to allow this spacing, re-sampling was done at an interval of ~ 250 m but on a different day. The deployment points were geo-referenced using a handheld Global Positioning System (GPS). The time of deployment, depth, visibility, cloud cover, tidal state, currents and GPS readings were recorded during the deployment. Each BRUV unit was retrieved after at least 1-hour of recording.

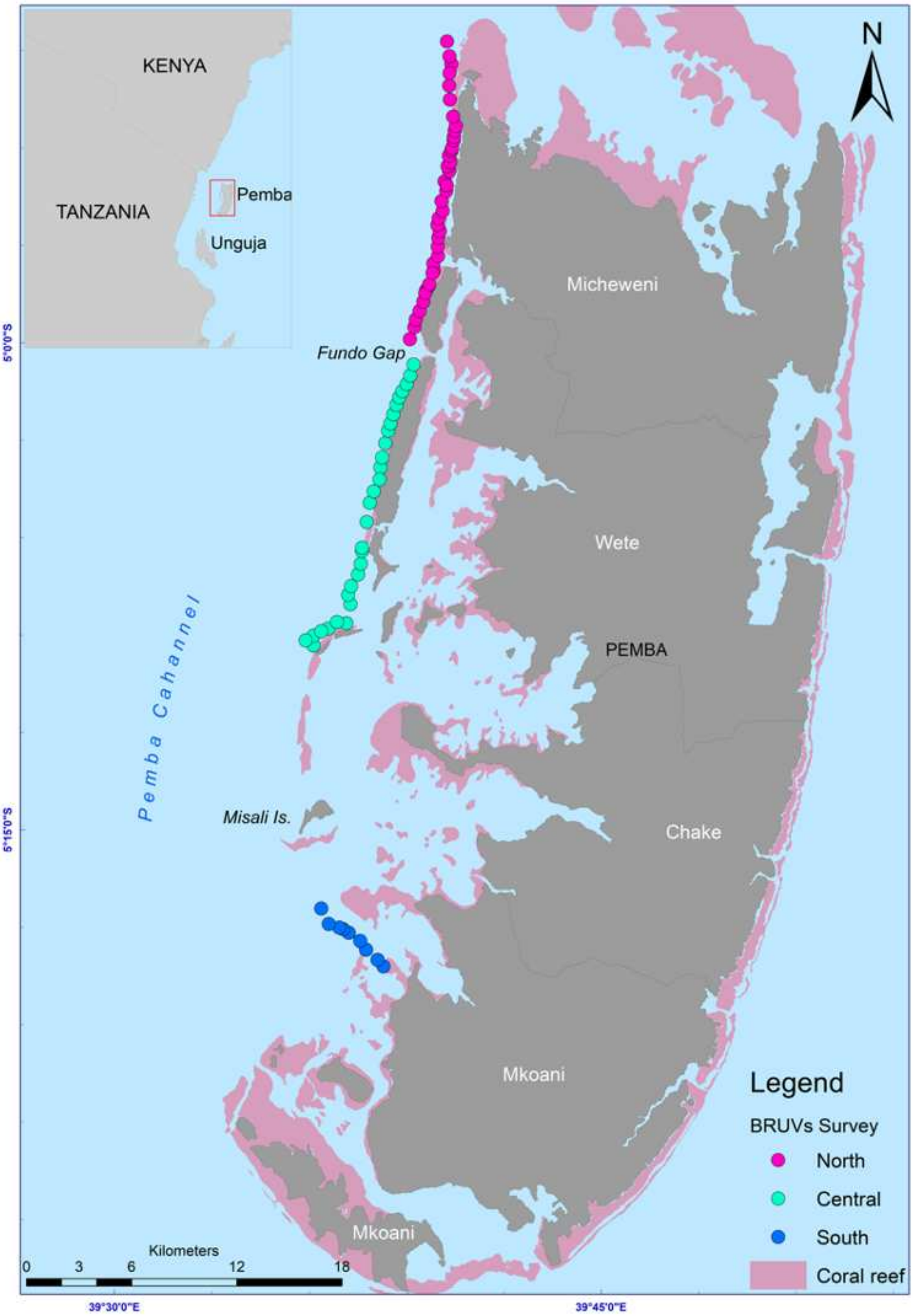

Figure 1: Map showing location of 79 baited remote underwater video (BRUV) stations in Pemba Island deployed in three sectors north, central and south.

Video footage processing

After the BRUV unit was retrieved, visibility, field of view, profile and percentage cover of habitat/substrate types (hard coral, soft coral, sea fans, halimeda, sponges, fleshy and turf algae, rubble and sand) was visually estimated for each video recording. Fish species identification from the video footage focused solely on predatory fish from 14 families at normal play speed. These were: Aulostomidae (trumpetfish), Carangidae (jacks), Carcharhinidae (sharks), Congridae (conger eels), Dasyatidae (whiptail stingrays), Haemulidae (sweetlips), Fistulariidae (cornetfish), Lethrinidae (emperors), Lutjanidae (snappers), Muraenidae (moray eels), Myliobatidae (eagle rays), Scombridae (mackerel), Epinephelidae (groupers), and Sphyraerinidae (barracuda) (Appendix 2). Wherever video footage of individuals was unclear the genus or family was used. Two researchers (KO, PM) reviewed species identification to ensure accuracy. Species identification was done using Lieske and Myers, (1994) and Taquet and Diringer, (2012) and confirmed using Eschmeyer's Catalog of Fishes (Fricke et al., 2021). Species observed were classified according to their association with the reef as either resident or transient (Hixon, 2015; Froese and Pauly, 2020). Resident predators were species showing strong association with the reef structure or seafloor such as groupers, snappers, emperors, sweetlips and eels. Transient predators were fast swimming, schooling and epipelagic species, such as sharks, barracuda, jacks and mackerel (Appendix 2). The conservation status of each species was derived from the International Union for Conservation of Nature (IUCN) Red List website (IUCN, 2021).

Data analysis

The maximum number of individuals (MaxN) of each species of predatory reef fish observed at one time from each video with a recording time of 1-hour was quantified. These data were used to derive a summary of the number of individuals and species per reef sector, and a rarefaction curve based on the cumulative number of BRUV deployments (Hammer et al., 2001).

Nonmetric multidimensional scaling (nMDS) based on Bray–Curtis similarity (Clarke and Warwick 2001), was performed on square root transformed MaxN data (Supplementary material Figure S1) to graphically assess patterns in abundance of reef predators across the three geographic sectors. A one-way SIMPER analysis was used to identify species that contributed the most towards dissimilarity of the sectors.

Principal components analysis (PCA) was applied to benthic variables to determine key variables contributing greatest to the variation. The loading of the first component was used to differentiate BRUVs stations into two major habitat types: hard coral and soft coral *versus* sand and rubble. An ordinary least squares regression of the first component loadings and depth was thereafter conducted to determine the relationship of habitat variables with depth.

Three predictor variables of fish abundance: sector, habitat and depths were modeled (Table 1) using zero-inflated Poisson (ZIP) model. Generalised linear model (GLM) and zero-inflated Poisson (ZIP) model outputs were first compared using Vuong Non-Nested Hypothesis Test-Statistic (Vuong, 1989; Long and Long, 1997). The test showed ZIP was better than the standard Poisson model. Therefore, ZIP was fitted to MaxN data on pooled predators, resident predators, transient predators, species richness, fish family and species. The ZIP model had two parts: a Poisson regression model to model fish count (MaxN) using predictor variables of Depth and Habitat; and the logit model for predicting the probability of excess zeros in random variables of Sector. The logit model provided the basis for uncovering the excessive absence of reef predators in a sector, an indication of overfishing. To help with the interpretation of the results we assessed the interaction effects between depth and habitat type using GLM.

Table 1. Predictors used in the analysis of predatory fish taxa

Predictor	Abbreviation	Data type	Description
Habitat	Hab	Categorical	Two major habitat-types identified from PCA i.e. Sand and Rubble (SA_RU) and Hard coral and Soft coral (HC_SC).
Sector	Sec	Categorical	Three sectors separated by reef passes i.e. North, Central and South
Depth	Dep	Continuous	Station depth in metres

Results

Predatory reef fish abundance and taxonomic richness

A total of 5,767 individuals from 71 species and 14 families were recorded, with 83% of the species occurring in depths > 20 m (Appendix 2). Overall, a majority (89%) of the species sampled were in the Least Concern category under the IUCN Red List of species. Only two species (< 3% of the total) the sky emperor *Lethrinus mahsena* and honeycomb stingray *Himantura uarnak*, were classified as Endangered. Vulnerable species accounted for 4% and included the silvertip shark *Carcharhinus albimarginatus,* spotted eagle ray *Aetobatus ocellatus,* brown-marbled grouper *Epinephelus fuscoguttatus*, while only one Near Threatened species, the narrow-barred Spanish mackerel *Scomberomorus commerson* was observed. Two species assessed as Data Deficient were also recorded – Indian mackerel *Rastrelliger kanagurta* and Kuhl's maskray *Neotrygon kuhlii.*

The species rarefaction curve of the cumulative number of BRUV deployments showed that the curve was flattening suggesting that the predatory reef fish community had been relatively well sampled overall (Figure 2). However, the southern sector was least sampled yielding fewer species compared to the northern and central sectors. The total number of species encountered in the northern and central sectors were 54 and 42 species, respectively, compared to six in the southern sector.

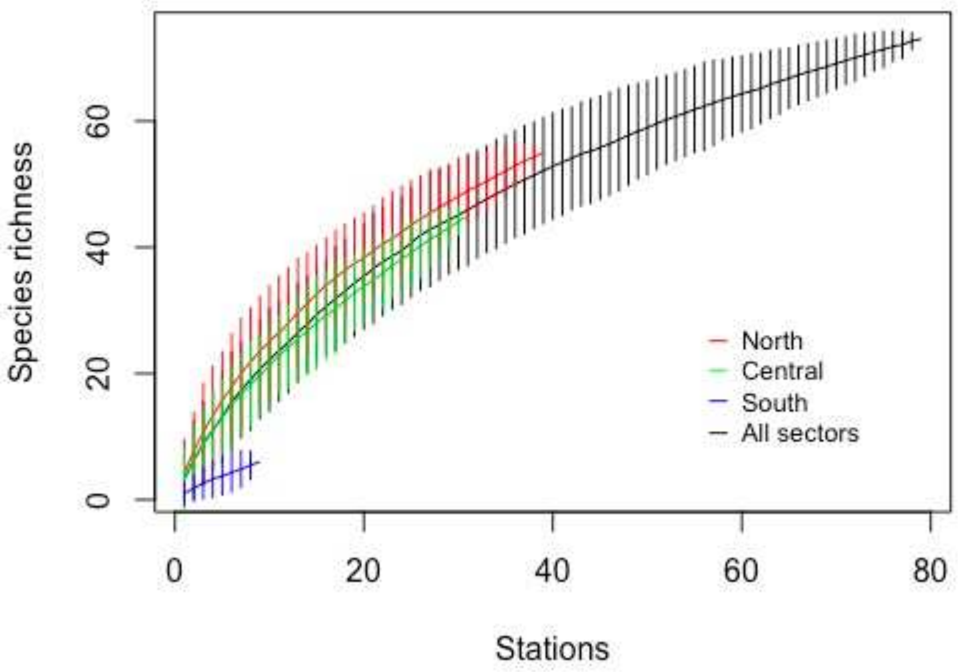

Figure 2: Species rarefaction curve with their 95% confidence interval separated by sectors: north - red, central - green, south - blue and all sectors - black.

The mean fish abundance (MaxN) showed no significant differences across the sectors (ANOVA, F = 0.494; p = 0.612), although relatively higher values were found in the northern (8.87 ± 1.49 (se)) and central (9.90 ± 2.98 (se)) sectors compared to the southern sector (5.11 ± 3.30 (se)). Proportion of zero counts for species encountered during the survey across three sectors showed predators were more encountered in the north than the central and the south

(Figure 3). Resident predators were more encountered in the north and central sectors while transient predators occurred more in the north sector (Figure 3).

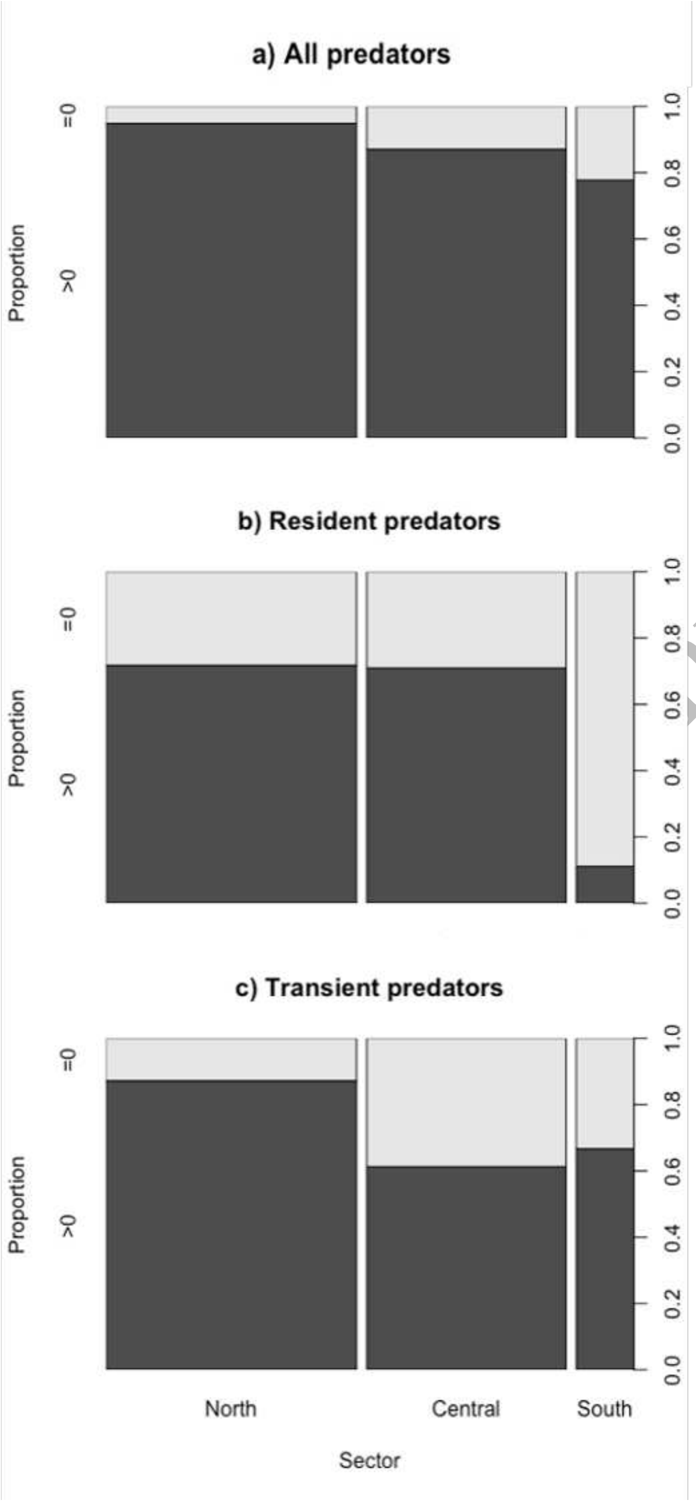

Figure 3: Proportion of zero counts (light shadings) across three sectors for all predators (a), resident predators (b), and transient predators (c). The widths of the bars show the number of BRUVS per sector North n = 39, Central n = 31 and South n = 9.

Predator community structure

SIMPER analysis revealed that dissimilarity in predatory reef fish between the sectors was generally high (> 90%). The greatest dissimilarity was between North and South (Average dissimilarity = 96.2%) driven by snubnose pompano *Trachinotus blochii,* small-toothed jobfish *Aphareus furca,* green jobfish *Aprion virescens* and Chinese trumpetfish *Aulostomous chinensis* (Table 2).

Table 2: Results of one-way SIMPER analyses of species contributing more than 5% of the dissimilarity in abundance (%) in the three sectors of Pemba Island – North, Central and South. Species are classified according to their association with the reef as either resident (R) or transient (T).

Species	Average abundance		Average dissimilarity	Contribution (%)
Average dissimilarity = 93.2	North	Central		
Aprion virescens (T)	1.3	0.1	8.6	9.3
Aulostomous chinensis (T)	0.6	0.5	6.7	7.2
Lethrinus olivaceus (R)	0.3	0.8	6.3	6.8
Aphareus furca (T)	0.8	0.4	5.9	6.4
Cephalopholis argus (R)	0.2	0.7	5.0	5.4
Average dissimilarity = 94.5	South	Central		
Aphareus furca (T)	1.1	0.4	14.5	15.3
Trachinotus blochii (T)	3.3	0.0	13.3	14.1
Aulostomous chinensis (T)	0.1	0.5	6.4	6.8
Cephalopholis argus (R)	0.0	0.7	6.2	6.6
Lethrinus olivaceus (R)	0.0	0.8	5.8	6.1
Average dissimilarity = 96.2	North	South		
Trachinotus blochii (T)	0.0	3.3	12.5	13.0
Aphareus furca (T)	0.8	1.1	12.3	12.8
Aprion virescens (T)	1.3	0.0	10.4	10.8
Aulostomous chinensis (T)	0.6	0.1	7.4	7.7

Description of benthic structure

On the face value, the cover of benthic variables showed minimal differences between the north and central sectors, but together they differed from the southern sector that had high cover of sand (52%) and fleshy algae (20%) (Supplementary material Figure S2). Hard and soft coral cover averaged around 19% and 9% respectively in the north and central sectors. Overall, sand was dominant in all sectors, although the percent cover was 21% and 30% in central and northern sectors respectively. The cover of rubble was 15%, 10% and 4% in north, central and south sectors respectively.

The first component (PC1) of the PCA explained 51.53% of variation in habitat composition (Figure 4), showing positive correlation with the cover of sand ($r = 0.82$) and rubble ($r = 0.13$), and negative correlations with the cover of hard corals ($r = -0.48$) and soft corals ($r = -0.27$). The second PCA explained an additional 19.12% and was positively correlated to sand (0.41) and hard coral (0.39) and negatively correlated to rubble (-0.81). Linear regression of PC1 loadings and depth showed sites with high cover of sand and rubble to be in deeper areas compared to those with high cover of hard corals and soft corals depth ($R2 = 0.13$; $p<0.001$; Figure 5)

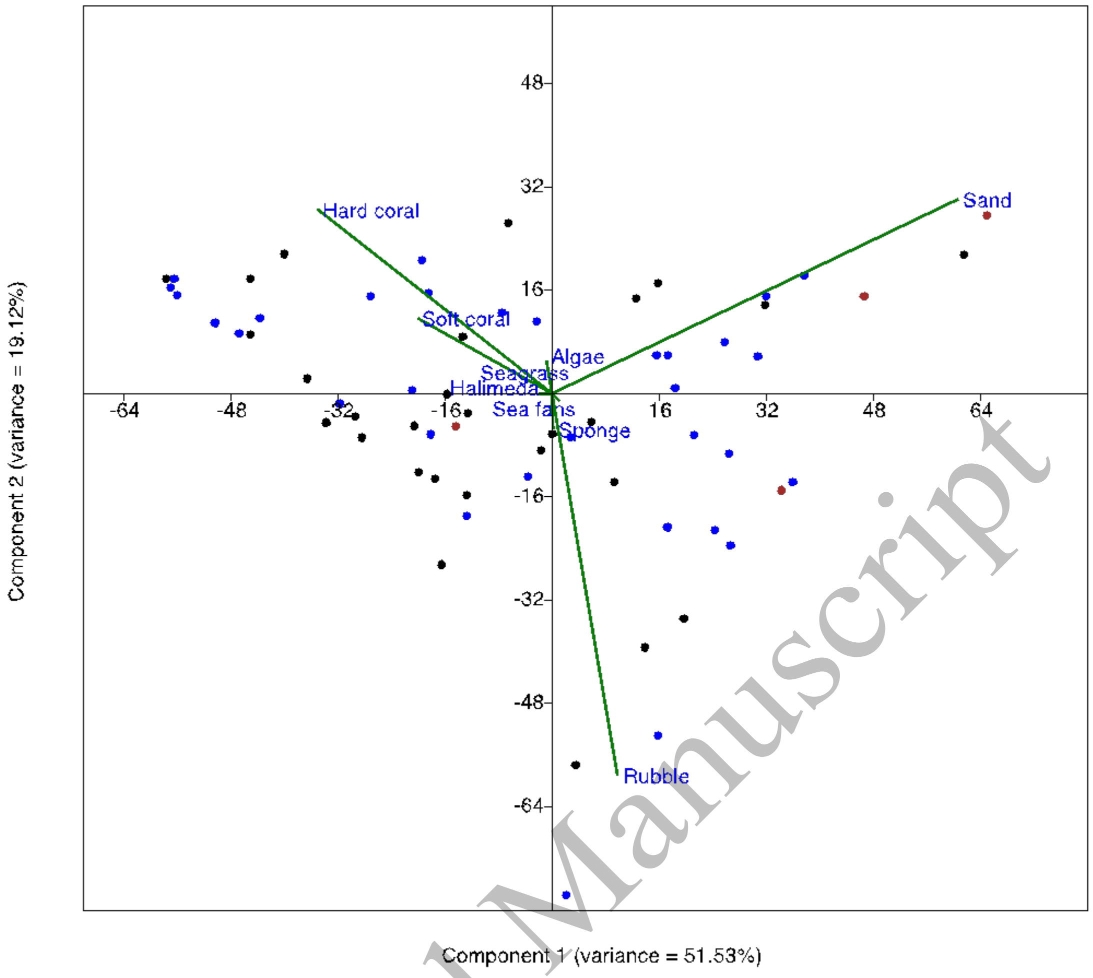

Figure 4: Principal component analysis plot showing the loadings of stations on the first and second principal components and bi-plots of the benthic variables. North, central and south sectors represented by blue, black and red dots.

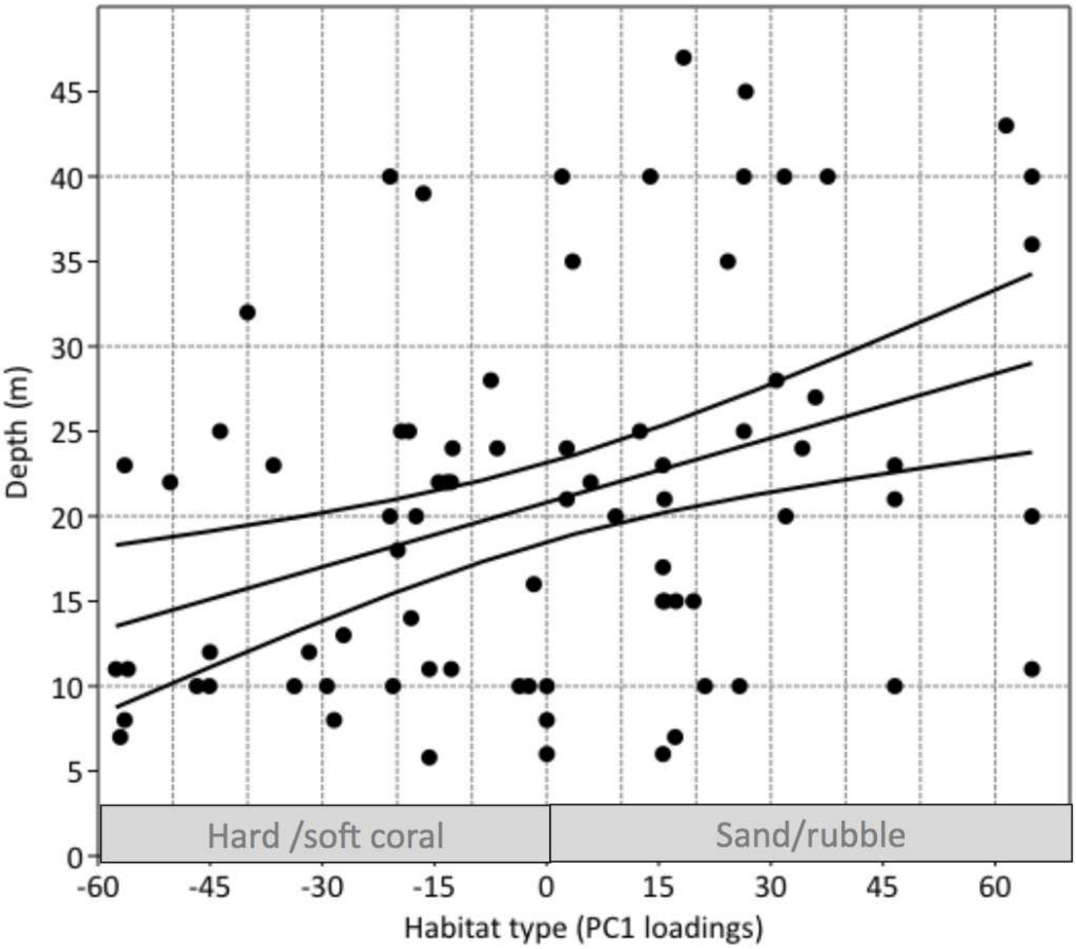

Figure 5: Relationship between first principal component (PC1) habitat loadings and depth. Sites with negative loadings were correlated with high cover of hard and soft coral while those with positive loadings were correlated with sand and rubble cover.

Influence of depth and habitat types

Species richness and the abundance of all predators (cumulative MaxN) and resident predators were significantly ($p<0.05$) influenced by depth and habitat type, with higher counts in deeper than in shallower areas as well as in coral habitats than in sandy and rubble habitats (Supplementary material Table S1). The zero-inflation model showed resident predators had significantly excess zeros in the south in comparison to the central sector, while transient predators had significantly excess zeros in the central in comparison to the north sector (Table 3a-b). GLM results showed significant interaction between habitat type and depth for all predators, resident and transient predators (Figure 6). In sandy and rubble habitats, every

10m increase in depth was associated with an average increase in abundance of 0.3, 0.3 and 0.2 individuals for all predators, resident and transient predators respectively.

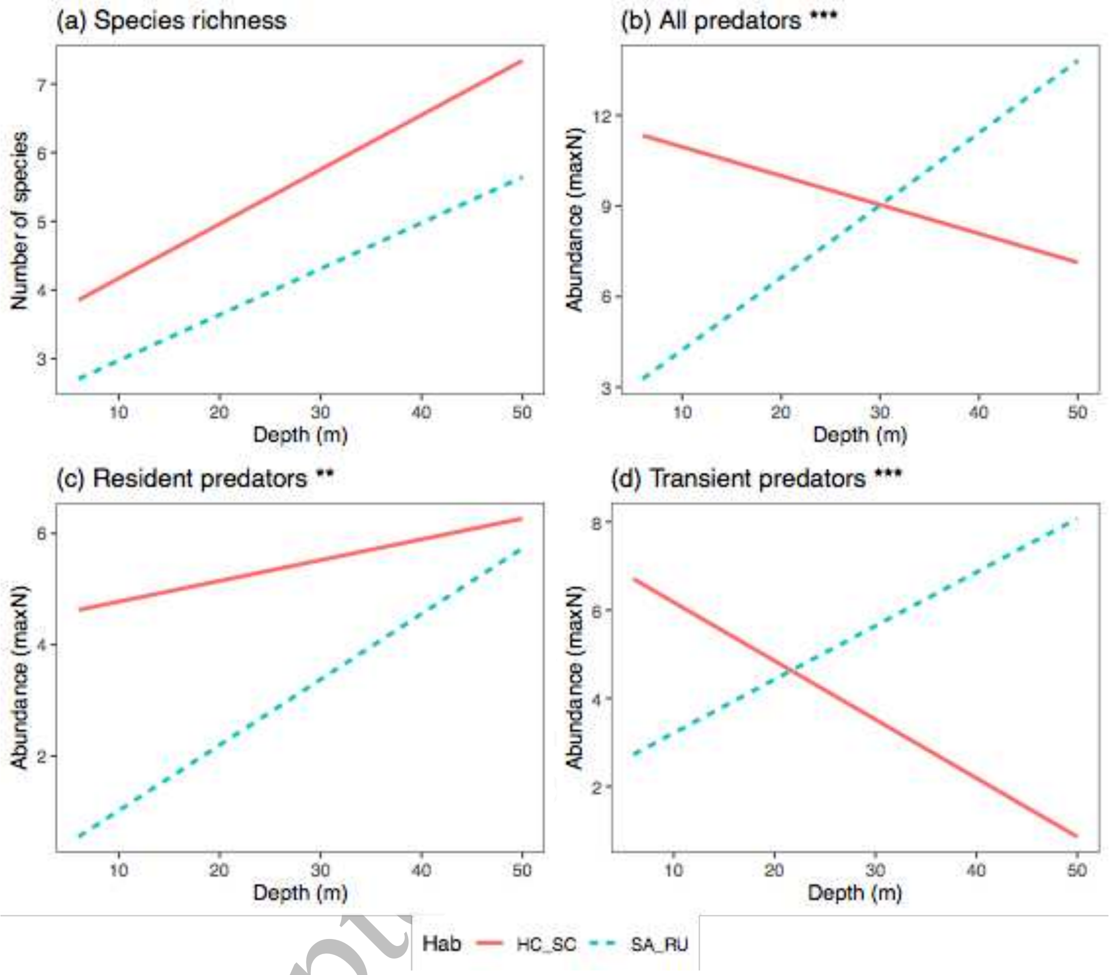

Figure 6: Simple-slope plots of the interaction between depth and habitat type (Hab) in predicting four aggregate abundance metrics. Habitat is represented by Hard coral and Soft coral (HC_SC) and Sand and Rubble (SA_RU). All trend lines indicate significant relationships and asterisks indicate significant interaction with '***' = <0.001, '**' = <0.01, '* = <0.05.

Table 3: Estimated coefficients of zero-inflation model (ZIP) and their standard errors (S.E.) for resident and transient predators and three species. Significant codes: '***' = <0.001, '**' = <0.01, '* = <0.05. Sec = sector. Reference group for Sec was the Central sector.

	Estimate	Coefficients	S.E
a) Resident predators	Intercept*	-0.92	0.40
	Sec_North	-0.07	0.55
	Sec_South**	2.98	2.63
b) Transient predators	Intercept	-0.46	0.37
	Sec_North*	-1.47	0.61
	Sec_South	-0.24	0.80
c) Species			
Lethrinus harak	Intercept**	2.80	1.05
	Sec_North**	-3.19	1.22
	Sec_South	15.17	5797.15
L. rubrioperculatus	Intercept*	1.47	0.80
	Sec_North*	-0.43	0.95
	Sec_South	15.89	2183.26
Aprion virescens	Intercept***	2.07	0.62
	Sec_North**	-2.08	0.73
	Sec_South	16.33	3994.54

The predictor variables showed significant influence on four families (Figure 7; Supplementary material Table S2). The abundance of Haemulidae and Lethrinidae showed significant positive relationships with increasing depth, while only Aulostomidae displayed significant negative relationships. Other families particularly Carcharhinidae, Dasyatidae, Fistulariidae, Muraenidae, Myliobatidae, Epinephalidae and Sphyraerinidae exhibited non-significant relationships. Abundance of Lutjanidae was greater in hard and soft coral habitats compared to sandy and rubble habitats. A contrast observation was found for Carangidae showing higher abundance in sandy and rubble than hard and soft coral habitats.

The GLM with interaction effects showed significant interaction between habitat type and depth for Lethrinidae, Lutjanidae, Haemulidae, Fistulariidae and Scombridae (Figure 7). Every

10m increase in depth within hard coral and soft coral habitats was associated with an average increase in abundance of 0.6, 0.1 and 0.1 individuals for Lethrinidae, Haemulidae and Fistulariidae respectively. In sandy and rubble habitats, every increase in depth was associated with an average increase in abundance of 0.7 and 0.4 individuals for every 10 m for Lutjanidae and Scombridae respectively.

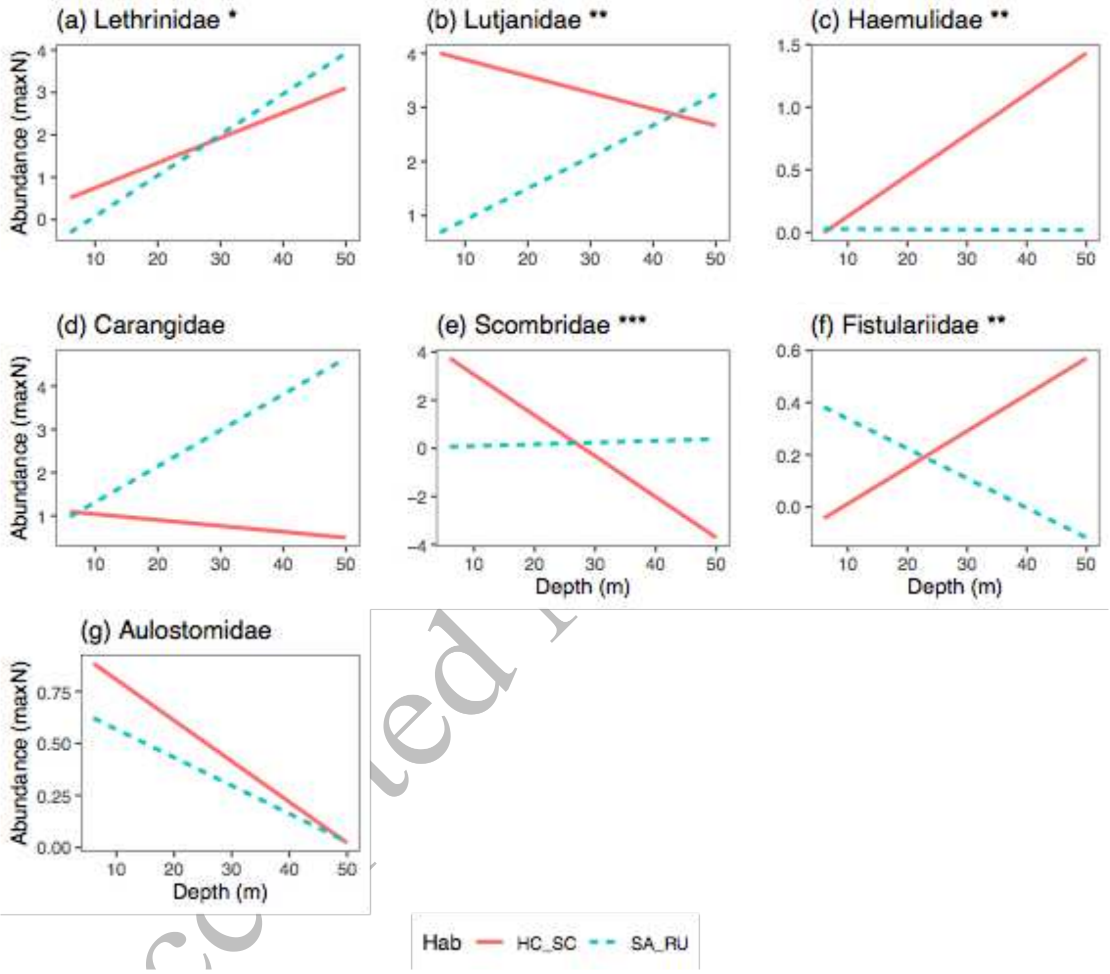

Figure 7: Simple-slope plots of the interaction between depth and habitat type (Hab) in predicting abundance of three resident predator fish families (a-c) and four transient predator fish families (d-g). Habitat is represented by hard coral and soft coral (HC_SC) and sand and rubble (SA_RU). All trend lines indicate significant relationships and asterisks indicate significant interaction with '***' = <0.001, '**' = <0.01, '* = <0.05.

The abundance of *Trachinotus blochii* and spotcheek emperor *Lethrinus rubrioperculatus* increased with increased depth, while for *Aulostomous chinensis,* bluefin trevally *Caranx melampygus* and Indian mackerel *Rastrelliger kanagurta* it decreased with depth (Figure 8;

Supplementary material Table S3). The abundance of thumbprint emperor *Lethrinus harak* and *Aprion virescens* was higher in hard and soft coral habitats compared to sandy and rubble habitats. This was different for *Aphareus furca* and *Rastrelliger kanagurta,* which had greater abundance in sandy and rubble habitats than hard and soft coral habitats. The zero inflated models showed that excess zeros occurred in central in comparison to the northern sectors for three species: *Lethrinus harak, Lethrinus rubrioperculatus* and *Aprion virescens* (Table 3c). GLM results showed significant interaction between habitat type and depth for *Lethrinus olivaceus* (Figure 8), with every 10 m increase in depth within hard coral and soft coral habitats being associated with an average increase in abundance of 1.3 individuals.

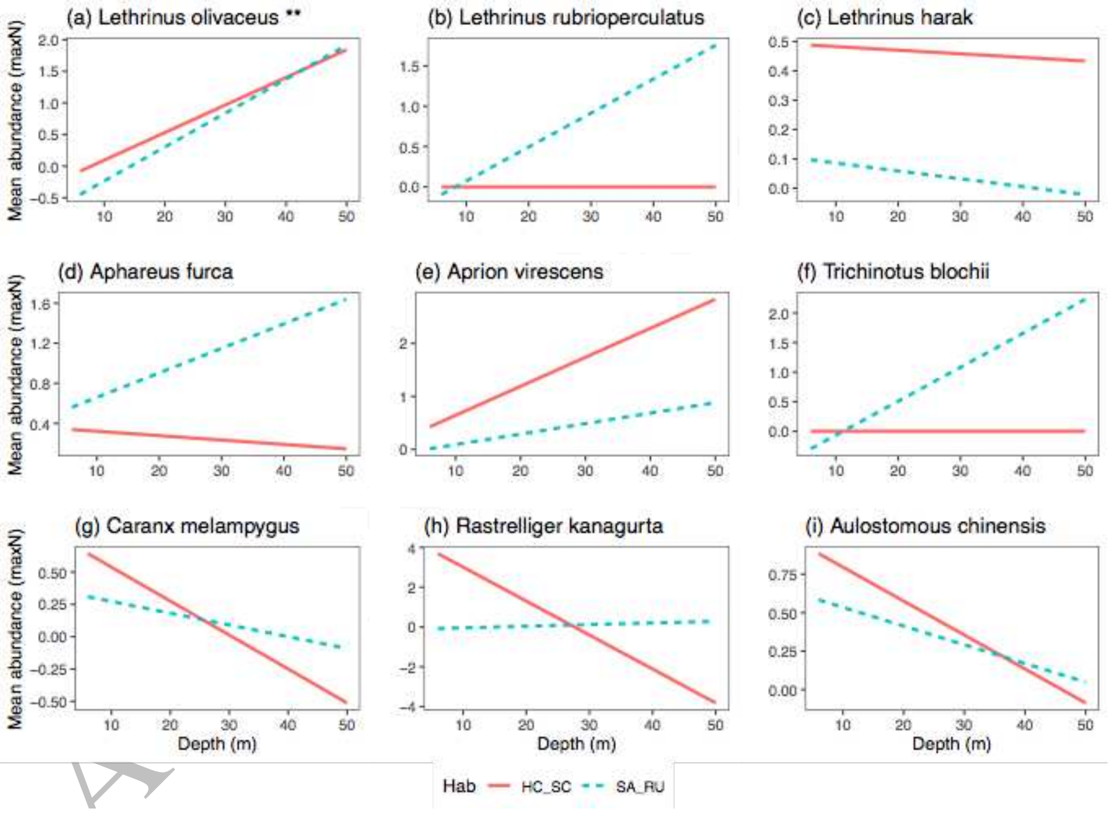

Figure 8: Simple-slope plots of the interaction between depth and habitat type (Hab) in predicting fish abundance of three resident predator species (a-c) and six transient predator species. Habitat is represented by hard coral and soft coral (HC_SC) and sand and rubble (SA_RU). All trend lines indicate significant relationships and asterisks indicate significant interaction with '***' = <0.001, '**' = <0.01, '* = <0.05.

Discussion

General observations and novelty of the study

Predatory reef fish have excessively been targeted around the world and latest studies show that many of these species are increasingly becoming absent in regions such as the western Indian Ocean (WIO) (de Mitcheson *et al.*, 2020; MacNeil *et al.*, 2020). The present study, one of the first reef surveys to sample the west coast of Pemba Island, showed 83% of the 71 predator species encountered were present in depths greater than 20 m. This provides strong evidence of the importance of deeper waters for predatory reef fish. Habitat types were also found to influence abundance of predatory fish types in varying ways. Thus, habitat and depth have a profound influence on predator abundance, although these factors often interact (Pinheiro *et al.*, 2016; Skinner *et al.*, 2020). In our study, the abundance of all reef-associated predators in the shallow areas was high in the hard and soft coral habitats, but in relatively deeper areas of up to 47m, high levels of abundance were seen in the sandy and rubble habitats. While the interaction between depth and habitat may indicate fishing effects on predatory reef fishes (Tyler, et al., 2009), a more plausible ecological cause of the observed pattern is changing habitat use of fishes with depth, for example due to ontogenetic shifts (Green *et al.*, 2015; Nash *et al.*, 2015). This imply that shallow coral reefs areas in relatively healthy state play an important role in hosting predatory fishes. However, ontogenetic shifts coupled with the high fishing pressure that is prevalent in shallow areas such as around Pemba Island (Grimsditch et al., 2009) appears to be leading to a shift in the distribution of predatory fishes into the deep areas where sandy habitats dominate. This study therefore provides both a valuable baseline for the study area, and findings that are likely to be of wider interest to coastal communities and managers in coral reef areas around the world.

Transient and resident predators -habitat and depth associations

The abundance of predatory reef types with different movement behaviours (transient *versus* resident) was influenced by habitat types and depth in a non-random manner (Hixon, 2015; Filous *et al.*, 2017; Paxton *et al.*, 2020). Resident predators presented strong positive relationships with hard and soft coral habitat and increasing depth. This habitat association was expected since resident predators show high degrees of site fidelity and are usually confined to 'home' reefs’, which offer both shelter and food resources (Stewart and Jones, 2001; Dance et al., 2011). Contrastingly, transient predators are highly mobile epipelagic species that generally show the weakest relationships with coral habitat types, except when the abundance of target prey species is above certain thresholds or the habitat is structurally complex with an extensive vertical relief (Paxton *et al.*, 2020). Interestingly, the depth effect was observed in all habitat types for resident predators but only in sandy and rubble habitats for transient predators. This suggests preferences of particular habitat and depth by different types of predatory fish, which could in turn be targeted by local fisheries (Tyler, et al., 2009; Bongaerts et al., 2010). Certainly, predatory reef fish are attracted to areas of high prey fish density that tend to occur in areas of live coral and high structural complexity (Stewart and Jones 2001; Chong-Seng et al., 2012). Therefore, the influence of habitat and depth on the abundance of reef fish was clearer in resident predators but more complex for transient predators.

Incorporation of depth and habitat information into management strategies for resident and transient predatory fish is likely to benefit the fisheries of Pemba Island. This will certainly require information comparing the effects of depth and habitat in fished areas versus un-fished areas. Indeed, such information is critical in selecting management measures geared towards promoting the attainment and maintenance of thresholds of prey and predatory fish densities (McClanahan et al., 2011; Hill et al., 2020). To ensure the sustainability of predatory reef fish in areas like Pemba Island, where human population is growing (NBS 2018) and fishing effort is increasing (Jacquet and Zeller, 2007; Rehren et al., 2020), it will be important to manage both the fisheries and protect the habitats that their prey fish rely upon.

Species driving the pattern

We found three to six key species within the resident and transient predator types were the most responsible for the patterns in the habitat and depth relationships. Within the resident predators, significant interaction between habitat and depth was only apparent in longface emperor, *Lethrinus olivaceus,* highlighting increased abundance in deeper areas but more so for those individuals occurring in sandy and rubble habitats. A positive depth effect was evident in spotcheek emperor, *Lethrinus rubrioperculatus,* while coral habitat effects were detected in thumbprint emperor, *Lethrinus harak*. In general, emperors are linked to sandy habitats where they feed by hunting less mobile prey (Kulbicki et al., 2005). Spotcheek emperors prefer outer reef slopes in waters greater than 10 m (Sommer et al., 1996; Fricke et al., 2011) thus it was not surprising that their abundance increased with increasing depth. Similar studies in the Maldives have shown coral habitats to host more thumbprint emperors (Skinner *et al.*, 2020). The species move either in small schools or solitary and can traverse different habitats including shallow sandy and hard coral habitats (Carpenter and Allen, 1989). We therefore postulate that emperor species respond to habitat and depth effects in varying ways.

We observed habitat and depth effects with no interaction effects within the transient predators. Green jobfish, *Aprion virescens,* showed significant association with hard coral and soft coral in contrast to small-toothed jobfish *Aphareus furca*, which were more affiliated to sandy and rubble habitats. The opposing patterns in these closely related species is likely related to their biology and movement patterns. The adults of green job fish inhabit seaward reefs, while those of small-toothed jobfish prefer inshore coral and sandy habitats (Anderson and Allen, 2001). Positive depth effects were evident in snubnose pompano, *Trachinotus blochii,* while negative relationships with depth were found for Chinese trumpetfish, *Aulostomous chinensis,* and schooling species of bluefin trevally, *Caranx melampygus,* and Indian mackerel, *Rastrelliger kanagurta*. These associations are coherent with ontogenetic shifts and feeding behaviour that involve various depths and habitat types (Green *et al.*, 2015; Nash *et al.*, 2015). For example, the juveniles of snubnose pompano occur in shallow sandy habitats and later move to adjacent relatively deeper coral reef habitats as they grow (Fischer et al., 1990). This suggests the individuals surveyed in sandy habitats were all sub-adults. Chinese trumpetfish utilise multiple habitat types such as seagrass lagoons, coral and rocky reefs in the shallow areas and caves reaching 200 m in the deep areas (Bowen *et al.*, 2001; McGratten and Pollom, 2015). The species is not fished which makes it ubiquitous in shallow water depths. Bluefin trevally and Indian mackerel are mobile predators and often hunt in shallow waters (Sancho, 2000), where their food items are generally most abundant, and they may exhibit high residency in such depths (Filous *et al.*, 2017). Taken together, these findings indicate that schooling transient predator species are least dependent on healthy coral habitat types and therefore, less likely to be affected by changes in habitat conditions.

Family patterns

Resident fish families like Haemulidae and Lethrinidae increased in abundance with increasing depth, particularly in hard and soft coral habitats. This finding may be explained by the idea that during the day, coral heads on the reef offer shelter to nocturnal species. For example, at night haemulids forage on diets composed of small fish, invertebrates and dead animals in seagrass beds but during the day shift to coral associated habitats to escape predation from meso-predators (Burkepile and Hay, 2008). A contrasting result was found for Lutjanidae. While Lutjanidae also rest during the day in reef ledges and feed during the night (Nagelkerken et al., 2000), it is possible that the pattern observed was due to the bait plume from our BRUVs (Harvey et al., 2012; Espinoza et al., 2014) attracting them during the day (Bacheler et al., 2021) and especially in the open sandy and rubble habitats.

A non-significant influence of habitat type and depth was found on resident predators of the subfamily Epinephelinae. This could reflect high abundance or diversity within this group, which can influence the ability to detect relationships (Gerrodette, 1987). Nonetheless, the non-significant results are in contrast to a previous study in the Maldives that showed deep outer reefs had greater abundance of Epinephelinae than shallow lagoonal reefs (Skinner *et al.*, 2020). However, the depth preferences of different species within the Epinephelinae (Froese and Pauly, 2020), could be masking the relationships with depth.

Among the transient predators, there was evidence of habitat effects for the family Carangidae and interaction effects for Scombridae and Fistularidae. Fish belonging to the families Carangidae and Scombridae generally move in schools, often at speed, and therefore can quickly respond to temporal and spatial fluctuations in prey fish density (Stewart and Jones, 2001). As for Fistularidae, members of this family are generalist, usually very broad ranging inhabiting shallow reef habitats to sandy habitats in depths reaching up to 100 m (Watson and Sandknop, 1996).

The north, central and south differences

Coral reefs in the western Indian Ocean have shown declines in coral cover due to climate change causing coral bleaching and subsequent coral mortality, and are predicted to decrease further (Obura *et al.*, 2017; McClanahan *et al.*, 2020). Critically, healthy coral habitats are essential for different groups of predatory fish. Therefore, future habitat loss through destructive fishing activities like dynamite fishing, which has previously been reported in Pemba Island (Slade and Kalangahe, 2015), will adversely affect the abundance of predatory species. Dynamite fishing and bleaching damage create accumulation of rubble, which could hamper recruitment and re-growth of coral. The cover of rubble can be used to disentangle these effects, particularly if one driver like dynamite fishing is localised and the other like bleaching is widespread. In our study the cover of rubble was relatively high in the north (15%) and central (10%) sectors compared to the south (4%). However, the low cover in the south is potentially due to artefacts of sampling, which was hindered by logistical constraints of rough sea conditions. Alternatively, the differences between the north and south sectors could be due to effects of historical dynamite fishing (Slade and Kalangahe, 2015).

Excessive absence of predators is an indication of widespread overfishing (Myers and Worms, 2003). The relatively high proportion of zero counts in the southern and central reef sectors of Pemba Island may therefore indicate overfishing, particularly for emperor reef species: *Lethrinus harak,* and *L. rubrioperculatus.* Previous studies in the southern sector (i.e., Misali Island) point to relatively healthy habitats and fish diversity but a disproportionately decreased abundance and diversity of large reef-associated predators (Grimsditch et al., 2009; Jones et al., 2019; Osuka *et al.*, 2021a). Indeed, in 2017, estimates of species richness drawn from six families: Carangidae, Epinephelinae, Lethrinidae, Lutjanidae, Carcharhinidae and Sphyraenidae at Misali stood at 15 species, down from 46 species in 2004 (Daniels et al., 2004; Jones et al., 2019). In combination these studies suggest overfishing may have worsened in recent decades.

The central sector was the only sector where Vulnerable (silvertip shark, *Carcharhinus albimarginatus,* brown-marbled grouper, *Epinephelus fuscoguttatus)* IUCN Red Listed species were recorded. Also recorded in the central and southern sectors was the Vulnerable spotted eagle ray *Aetobatus ocellatus*. The appearance of these species in the central sector could be an indication of relatively high habitat quality (Harborne et al., 2011), which is critical in maintaining the remaining populations of threatened species (Root 1998; Friedlander et al., 2007). While there were no clear differences in live hard coral cover, a proxy of habitat quality, between central and northern sectors, it is important to highlight the presence of a continuous forereef area in the central sector, making the area ideal for reef predators like sharks and groupers (Papastamatiou et al., 2018; Skinner et al., 2020). Further, the sector's isolation from the main island through an extensive inner reef likely results in lower fishing pressure and implies that future species and area protection measures would certainly be beneficial.

Using BRUVs to survey predatory coral reef fish

This study joins a growing number illustrating the utility of BRUVs for gaining unique insights into coral reef fish communities across a range of depths and environments. However, it is appropriate to recognize limitations of the method. Our study deployed mono-BRUVs and thus it was not possible to estimate fish size and subsequently fish biomass (Bernard et al., 2014; Langlois et al., 2020). Fish size is an important indicator used to determine reef productivity (Shin et al., 2005; Osuka et al., 2021b). Thus, application of mono-BRUVS has the tendency of missing the opportunity to derive reef-associated variables like biomass and productivity, which would be possible when stereo-BRUVS are applied (Langlois et al., 2020). That said, mono-BRUVS compared to stereo-BRUVS are: easy to assemble as they do not require calibration of the stereo-video streams that enable accurate measurement of length and range (Boutros et al., 2015), relatively cheaper in cost due to use of one camera per BRUV unit and not necessarily requiring specialised software to annotate and measure fish from stereo-video (Gomes-Pereira et al., 2016). An important, but unanswered, question is how biomass of reef-associated predators would change across the sectors. Despite the limitation of mono-BRUVS, we are confident that the central sector had a higher biomass than the other sectors. This is due to the presence of large-sized reef predators including sharks, rays, groupers and trevally in that area. The rarefaction curves showed that our BRUVs surveys were reasonably adequate to estimate the species richness of predatory reef fish of the outer reefs of Pemba Island. However, the asymptote of the curve had not yet been fully reached suggesting that the observed species richness was somewhat underestimated. As such, it is possible that our sampling might have missed observing some of the rarer, cryptic and more wary reef predators (Asher et al., 2017; Skinner et al., 2020).

The addition of Misali Island (see Figure 1) as a study site would be informative, as this area is known to support high coral cover (Grimsditch et al., 2009) and a potential hotspot for mesophotic coral ecosystem composed of corals, algae, invertebrate and fish (Osuka et al., 2021a). Thus, in future it would be useful to extend the reef studies using BRUVs by examining predators at Misali Island. But perhaps research using stereo-BRUVs (Langlois et al., 2020) complemented by transect based approaches such as mini-ROV (remote operated vehicle) would provide further insight into spatial and depth related variations in predatory reef fish biomass. Of particular relevance would be the mid-water stereo BRUVs (Santana-Garcon et al., 2014), which may be appropriate for the outer reefs with ledges and walls that make it difficult for BRUV units to settle. Future work especially in the outer reefs of Pemba Island would also benefit from application of complementary coral reef survey methods able to survey shallow and mesophotic depths (e.g., AUVs, Osuka et al., 2021a). AUVs have the ability to follow a pre-determined track, map deep areas down to 500 m and beyond, and collect high-resolution data including photos and videos of both the water column and benthic community. Such an effort would provide a much comprehensive insight into the drivers of the diversity, distribution, density and biomass of higher trophic level predatory reef fish in the area.

Predatory reef fish populations are facing immense pressures worldwide, leading to alarming losses in abundance and diversity. The present study has shed light on the abundance and distribution of predatory reef fish populations off the under-researched oceanic island of Pemba Island. Clearly, different types of predators are discordantly predicted by depth and habitat type with three to six key species within the resident and transient predator categories being responsible for the patterns we observed. Habitats dominated by hard and soft corals, and in relatively deeper waters, hosted high species richness and abundance of reef-associated predators. Our findings add to the growing evidence that deep waters around coral reefs provide important habitats for fish predators and corals. Thus, careful management, through effective area and species protection measures, are needed to prevent further impending reductions in their populations.

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Appendix 1: Image of a BRUV unit being deployed off the coast of Pemba Island.

Appendix 2: Species list and their behaviour, IUCN Red List Categories and minimum and maximum depths sampled. EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient.

Family	**Species**	**Predator type**	**Reference (in FishBase)**	**IUCN Red List Category**	**Min depth (m)**	**Max depth (m)**
Carcharhinidae	*Carcharhinus albimarginatus (Rüppell, 1837)*	Transient	Compagno, 1984	VU	39.0	39.0
Carcharhinidae	*Carcharhinus sp*	Transient	Compagno, 1984	VU	10.0	40.0
Dasyatidae	*Neotrygon kuhlii (Muller & Henle 1841)*	Resident	Michael, 1993	DD	23.0	23.0
Dasyatidae	*Himantura uarnak (Gmelin 1789)*	Resident	Compagno et al., 1989	EN	40.0	40.0
Myliobatidae	*Aetobatus ocellatus (Kuhl 1823)*	Transient	Kapoor et al., 2002	VU	20.0	22.0
Muraenidae	*Gymnothorax buroensis (Bleeker 1857)*	Resident	Lieske and Myers, 1994	LC	22.0	28.0
Muraenidae	*Gymnothorax eurostus (Abbott 1860)*	Resident	Mundy, 2005	LC	23.0	23.0
Muraenidae	*Gymnothorax favagineus Bloch & Schneider 1801*	Resident	Lieske and Myers, 1994	LC	16.0	40.0
Muraenidae	*Gymnothorax fimbriatus (Bennett 1832)*	Resident	Kuiter, 1998	LC	35.0	35.0
Muraenidae	*Gymnothorax flavimarginatus (Rüppell 1830)*	Resident	Mundy, 2005	LC	10.0	15.0
Muraenidae	*Gymnothorax javanicus (Bleeker 1859)*	Resident	Mundy, 2005	LC	10.0	45.0
Muraenidae	*Gymnothorax meleagris (Shaw 1795)*	Resident	Mundy, 2005	LC	10.0	23.0
Muraenidae	*Gymnothorax nudivomer (Günther 1867)*	Resident	Mundy, 2005	LC	40.0	40.0
Muraenidae	*Gymnothorax undulatus (Lacepède 1803)*	Resident	Mundy, 2005	LC	25.0	25.0
Muraenidae	*Gymnothorax griseus (Lacepède 1803)*	Resident	Sommer et al., 1996	LC	10.0	21.0
Congridae	*Heteroconger hassi (Klausewitz & Eibl-Eibesfeldt 1959)*	Resident	Bacchet et al., 2006	LC	20.0	32.0
Aulostomidae	*Aulostomus chinensis (Linnaeus, 1766)*	Transient	Mundy, 2005	LC	5.8	35.0
Echeneidae	*Echeneis naucrates Linnaeus 1758*	Transient	Smith, 1997	LC	11.0	20.0

Fistulariidae	*Fistularia commersonii Ruppell 1838*	Transient	Mundy, 2005	LC	7.0	28.0
Epinephelinae	*Aethaloperca rogaa (Fabricius 1775)*	Resident	Kuiter and Tonozuka 2001	LC	7.0	32.0
Epinephelinae	*Cephalopholis argus Schneider 1801*	Resident	Mundy, 2005	LC	5.8	32.0
Epinephelinae	*Cephalopholis cyanostigma (Valenciennes 1828)*	Resident	Lieske and Myers, 1994	LC	20.0	20.0
Epinephelinae	*Cephalopholis boenak (Bloch 1790)*	Resident	Kuiter and Tonozuka 2001	LC	10.0	40.0
Epinephelinae	*Epinephelus caeruleopunctatus (Bloch 1790)*	Resident	Craig et al., 2011	LC	23.0	23.0
Epinephelinae	*Epinephelus fuscoguttatus (Forsskal 1775)*	Resident	Lieske and Myers, 1994	VU	32.0	32.0
Epinephelinae	*Epinephelus sp.*	Resident	Lieske and Myers, 1994	LC	25.0	39.0
Epinephelinae	*Epinephelus tukula Morgans 1959*	Resident	Kuiter and Tonozuka 2001	LC	47.0	47.0
Epinephelinae	*Plectropomus laevis (Lacepede 1801)*	Resident	Kailola et al., 1993	LC	23.0	23.0
Epinephelinae	*Variola albimarginata Baissac 1953*	Resident	Lieske and Myers, 1994	LC	10.0	45.0
Epinephelinae	*Variola louti (Fabricius 1775)*	Resident	Lieske and Myers, 1994	LC	15.0	28.0
Carangidae	*Carangoides dinema Bleeker, 1851*	Transient	Allen and Erdmann 2012	LC	25.0	25.0
Carangidae	*Carangoides ferdau (Forsskål, 1775)*	Transient	Sommer et al., 1996	LC	12.0	40.0
Carangidae	*Carangoides fulvoguttatus (Forsskål, 1775)*	Transient	Sommer et al., 1996	LC	40.0	40.0
Carangidae	*Carangoides gymnostethus (Cuvier, 1833)*	Transient	Lieske and Myers, 1994	LC	28.0	28.0
Carangidae	*Carangoides orthogrammus (Jordan & Gilbert, 1882)*	Transient	Mundy, 2005	LC	10.0	40.0
Carangidae	*Carangoides sp.*	Transient	Mundy, 2005	LC	21.0	45.0
Carangidae	*Caranx ignobilis (Forsskål, 1775)*	Transient	Mundy, 2005	LC	10.0	15.0
Carangidae	*Caranx melampygus Cuvier, 1833*	Transient	Mundy, 2005	LC	10.0	22.0
Carangidae	*Caranx sexfasciatus Quoy & Gaimard, 1825*	Transient	Mundy, 2005	LC	5.8	40.0
Carangidae	*Caranx sp*	Transient	Mundy, 2005	LC	17.0	22.0
Carangidae	*Caranx tille Cuvier, 1833*	Transient	Paxton et al, 1989	LC	8.0	35.0

Carangidae	*Trachinotus blochii (Lacepède, 1801)*	Transient	Fischer et al., 1990	LC	11.0	40.0
Lutjanidae	*Macolor niger (Forsskal 1775)*	Resident	Lieske and Myers, 1994	LC	10.0	27.0
Lutjanidae	*Aphareus furca (Lacepède 1801)*	Transient	Mundy, 2005	LC	6.0	43.0
Lutjanidae	*Aprion virescens Valenciennes 1830*	Transient	Mundy, 2005	LC	7.0	47.0
Lutjanidae	*Lutjanus bohar (Fabricius 1775)*	Transient	Sommer et al., 1996	LC	10.0	40.0
Lutjanidae	*Lutjanus gibbus (Forsskal 1775)*	Resident	Kuiter and Tonozuka 2001	LC	23.0	25.0
Lutjanidae	*Lutjanus kasmira (Fabricius 1775)*	Resident	Mundy, 2005	LC	10.0	16.0
Lutjanidae	*Lutjanus monostigma (Cuvier 1828)*	Resident	Allen, 1985	LC	16.0	16.0
Lutjanidae	*Lutjanus quinquelineatus (Bloch 1790)*	Resident	Allen, 1985	LC	16.0	16.0
Lutjanidae	*Lutjanus rivulatus (Cuvier 1828)*	Resident	Sommer et al., 1996	LC	10.0	10.0
Lutjanidae	*Lutjanus russellii (Bleeker 1849)*	Resident	Sommer et al., 1996	LC	40.0	40.0
Lutjanidae	*Lutjanus vitta (Quoy & Gaimard 1824)*	Resident	Allen, 1985	LC	40.0	40.0
Haemulidae	*Plectorhinchus gaterinus Fabricius 1775*	Resident	Bianchi, 1985	LC	22.0	25.0
Haemulidae	*Plectorhinchus vittatus (Linnaeus 1758)*	Resident	Sommer et al., 1996	LC	23.0	23.0
Lethrinidae	*Lethrinus erythropterus Valenciennes 1830*	Resident	Carpenter and Allen, 1989	LC	40.0	40.0
Lethrinidae	*Lethrinus harak (Fabricius 1775)*	Resident	Carpenter and Allen, 1989	LC	7.0	28.0
Lethrinidae	*Lethrinus mahsena (Fabricius 1775)*	Resident	Sommer et al., 1996	EN	25.0	25.0
Lethrinidae	*Lethrinus microdon Valenciennes 1830*	Resident	Sommer et al., 1996	LC	14.0	14.0
Lethrinidae	*Lethrinus nebulosus (Forsskal 1775)*	Resident	Carpenter and Allen, 1989	LC	28.0	28.0
Lethrinidae	*Lethrinus obsoletus (Forsskal 1775)*	Resident	Carpenter and Allen, 1989	LC	7.0	7.0
Lethrinidae	*Lethrinus olivaceus Valenciennes 1830*	Resident	Sommer et al., 1996	LC	10.0	45.0
Lethrinidae	*Lethrinus rubrioperculatus Sato 1978*	Resident	Sommer et al., 1996	LC	7.0	45.0
Lethrinidae	*Lethrinus sp*	Resident	Sommer et al., 1996	LC	25.0	25.0

Lethrinidae	*Lethrinus xanthochilus Klunzinger 1870*	Resident	Carpenter and Allen, 1989	LC	22.0	35.0
Lethrinidae	*Monotaxis grandoculis (Forsskal 1775)*	Resident	Carpenter and Allen, 1989	LC	11.0	40.0
Sphyraenidae	*Sphyraena barracuda (Edwards 1771)*	Transient	De Sylva, 1990	LC	40.0	40.0
Sphyraenidae	*Sphyraena forsteri Cuvier 1829*	Transient	Senou, 2001	LC	15.0	15.0
Scombridae	*Gymnosarda unicolor (Rüppell 1836)*	Transient	Collette and Nauen, 1983	LC	15.0	25.0
Scombridae	*Rastrelliger kanagurta (Cuvier 1816)*	Transient	Collette and Nauen, 1983	DD	10.0	40.0
Scombridae	*Scomberomorus commerson (Lacepède 1800)*	Transient	Collette and Nauen, 1983	NT	12.0	12.0

References

Allen, G.R., 1985. FAO Species Catalogue. Vol. 6. Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date. FAO Fish. Synop. 125(6):208 p. Rome: FAO.

Allen, G.R. and M.V. Erdmann, 2012. Reef fishes of the East Indies. Perth, Australia: Universitiy of Hawai'i Press, Volumes I-III. Tropical Reef Research.

Anderson, W.D. Jr. and Allen, G.R., 2001. Lutjanidae. Jobfishes. In: Carpenter K.E. and Niem V. (eds.) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Vol. 5. Bony fishes part 3 (Menidae to Pomacentridae)*. FAO, Rome. p. 2840-2918.

Asher, J., Williams, I.D. and Harvey, E.S., 2017. An assessment of mobile predator populations along shallow and mesophotic depth gradients in the Hawaiian Archipelago. *Scientific reports*, *7*(1), pp.1-18.

Bacchet, P., T. Zysman and Y. Lefèvre, 2006. Guide des poissons de Tahiti et ses îles. Tahiti (Polynésie Francaise): Editions Au Vent des Îles. 608 p.

Bacheler, N.M., Geraldi, N.R., Burton, M.L., Muñoz, R.C. and Kellison, G.T., 2017. Comparing relative abundance, lengths, and habitat of temperate reef fishes using simultaneous underwater visual census, video, and trap sampling. *Marine Ecology Progress Series*, *574*, 141-155.

Bacheler, N.M., Runde, B.J., Shertzer, K.W., Buckel, J.A. and Rudershausen, P.J., 2021. Fine scale behavior of red snapper (*Lutjanus campechanus*) around bait: approach distances, bait plume dynamics, and effective fishing area. *Canadian Journal of Fisheries and Aquatic Sciences*, (ja).

Baum, J. K. and Worm, B., 2009. Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, *78*(4), pp. 699–714.

Bascompte, J., Melián, C.J. and Sala, E., 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences*, 102(15), pp. 5443–5447.

Bell, J., Cheung, W., De Silva, S., Gasalla, M., Frusher, S., Hobday, A., Lam, V., Lehodey, P., Pecl, G., Samoilys, M. and Senina, I., 2016. Impacts and effects of ocean warming on the contributions of fisheries and aquaculture to food security. In: Laffoley D, Baxter JM (eds), *Explaining ocean warming: causes, scale, effects and consequences*. Gland, Switzerland: International Union for the Conservation of Nature.

Bernard, A.T., Götz, A., Parker, D., Heyns, E.R., Halse, S.J., Riddin, N.A., Smith, M.K., Paterson, A.W., Winker, H., Fullwood, L. and Langlois, T.J., 2014. New possibilities for research on reef fish across the continental shelf of South Africa. *South African Journal of Science*, *110*(9-10), pp.01-05.

Beukers-Stewart, B.D., Beukers-Stewart, J.S. and Jones, G.P., 2011. Behavioural and developmental responses of predatory coral reef fish to variation in the abundance of prey. *Coral Reefs* 30:855–864.

Bianchi, G., 1985. FAO species identification sheets for fishery purposes. Field guide to the commercial marine and brackish-water species of Tanzania. Prepared and published with the support of TCP/URT/4406 and FAO (FIRM) Regular Programme. FAO, Rome. 199 p.

Bongaerts, P., Ridgway, T., Sampayo, E.M. and Hoegh-Guldberg, O., 2010. Assessing the ‘deep reef refugia’ hypothesis: focus on Caribbean reefs. *Coral Reefs* 29, 309–327.

Bowen, B.W., Bass, A.L., Rocha, L.A., Grant, W.S. and Robertson, D.R., 2001. Phylogeography of the trumpetfishes (Aulostomus): ring species complex on a global scale. *Evolution*, *55*(5), pp.1029-1039.

Burkepile, D.E. and Hay, M.E., 2008. Coral Reefs. Encyclopedia of Ecology Pages 784-796

Cappo, M., De'ath, G. and Speare, P., 2007. Inter-reef vertebrate communities of the Great Barrier Reef Marine Park determined by baited remote underwater video stations. *Marine Ecology Progress Series*, 350, pp. 209–221.

Boutros, N., Shortis, M.R. and Harvey, E.S. 2015. A comparison of calibration methods and system configurations of underwater stereo-video systems for applications in marine ecology. *Limnology and Oceanography: Methods*, 13, 224–236.

Carpenter, K.E. and Allen., G.R. 1989. *FAO Species Catalogue. Vol. 9. Emperor fishes and large-eye breams of the world (family Lethrinidae). An annotated and illustrated catalogue of lethrinid species known to date*. FAO Fish. Synop. 125(9):118 p. Rome: FAO.

Chong-Seng, K. M., Mannering, T. D., Pratchett, M. S., Bellwood, D. R. and Graham, N.A., 2012. The influence of coral reef benthic condition on associated fish assemblages. *PLoS One*, *7*(8), e42167.

Clarke, K.R. and Warwick, R.M., 2001. Change in marine communities: an approach to statistical analysis and interpretation (2nd edn). Plymouth, UK: PRIMER-E.

Collette, B.B. and C.E. Nauen, 1983. FAO Species Catalogue. Vol. 2. Scombrids of the world. An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. Rome: FAO. FAO Fish. Synop. 125(2):137 p.

Collins, M.R., 1990. A comparison of three fish trap designs. *Fish Res 9*:325–332

Compagno, L.J.V., 1984. FAO Species Catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2 - Carcharhiniformes. FAO Fish. Synop. 125(4/2):251-655. Rome: FAO

Compagno, L.J.V., D.A. Ebert and M.J. Smale, 1989. Guide to the sharks and rays of southern Africa. New Holland (Publ.) Ltd., London. 158 p.

Craig, M., YJ.S. de Mitcheson and P.C. Heemstra, 2011. Groupers of the world: a field and market guide. North America: CRC Press/Taylor and Francis Group. 356 p.

Dance, M.A., Patterson III, W.F. and Addis, D.T., 2011. Fish community and trophic structure at artificial reef sites in the northeastern Gulf of Mexico. *Bulletin of Marine Science*, 87(3), pp. 301–324.

Daniels C., Fanning E. and Redding D., 2003. Marine resource management for Misali Island: preliminary analysis by Frontier-Tanzania. *West Indian Ocean J Mar Sci.* 2:85–93.

de Mitcheson, Y.J.S., Linardich, C., Barreiros, J.P., Ralph, G.M., Aguilar-Perera, A., Afonso, P., Erisman, B.E., Pollard, D.A., Fennessy, S.T., Bertoncini, A.A. and Nair, R.J., 2020. Valuable but vulnerable: Over-fishing and under-management continue to threaten groupers so what now?. *Marine Policy*, *116*, p.103909.

De Sylva, D.P., 1990. Sphyraenidae. p. 860-864. In J.C. Quero, J.C. Hureau, C. Karrer, A. Post and L. Saldanha (eds.) Check-list of the fishes of the eastern tropical Atlantic (CLOFETA). JNICT, Lisbon; SEI, Paris; and UNESCO, Paris. Vol. 2

Espinoza, M., Cappo, M., Heupel, M.R., Tobin, A.J. and Simpfendorfer, C.A., 2014. Quantifying shark distribution patterns and species-habitat associations: implications of marine park zoning. *PloS one*, *9*(9), p.e106885.

Filous, A., Friedlander, A., Wolfe, B., Stamoulis, K., Scherrer, S., Wong, A., Stone, K. and Sparks, R., 2017. Movement patterns of reef predators in a small isolated marine protected area with implications for resource management. *Marine Biology*, *164*(1), pp.1-16.

Fischer, W., Sousa, I., Silva, C., de Freitas, A., Poutiers, J.M., Schneider, W., Borges, T.C., Feral, J.P. and Massinga, A., 1990. Field guide to commercial marine and brackishwater species of Mozambique. 230.

Fricke, R., Eschmeyer, W. N. and van der Laan R., (eds) 2021. Eschmeyer's Catlog of Fishes: Genera, Species, References. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp

Fricke, R., Kulbicki, M. and Wantiez, L., 2011. Checklist of the fishes of New Caledonia, and their distribution in the Southwest Pacific Ocean (Pisces). *Stuttgarter Beiträge zur Naturkunde A, Neue Serie*, *4*, pp.341-463.

Friedlander, A.M., Brown, E. and Monaco, M.E., 2007. Defining reef fish habitat utilization patterns in Hawaii: comparisons between marine protected areas and areas open to fishing. *Marine Ecology Progress Series*, *351*, pp.221-233.

Frisch, A.J., Ireland, M. and Baker, R., 2014. Trophic ecology of large predatory reef fishes: energy pathways, trophic level, and implications for fisheries in a changing climate. *Marine Biology*, *161*(1), pp.61-73.

Froese, R. and Pauly, D., 2020. FishBase. World Wide Web electronic publication. www.fishbase.org, (06/2020)

Gerrodette, T.I.M., 1987. A power analysis for detecting trends. *Ecology*. Wiley Online Library, 68(5), pp. 1364–1372.

Gomes-Pereira, J.N., Auger, V., Beisiegel, K., Benjamin, R., Bergmann, M., Bowden, D., Buhl-Mortensen, P., De Leo, F.C., Dionísio, G., Durden, J.M. and Edwards, L., 2016. Current and future trends in marine image annotation software. *Progress in Oceanography*, *149*, pp.106-120.

Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A., Gleason, M.G., Mumby, P.J. and White, A.T., 2015. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews*, *90*(4), pp.1215-1247.

Graham, N.A., Jennings, S., MacNeil, M.A., Mouillot, D. and Wilson, S.K., 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, *518*(7537), pp.94-97.

Grimsditch, G.D., Tamelander, J., Mwaura, J., Zavagli, M., Takata, Y. and Gomez, T. 2009. *Coral reef resilience assessment of the Pemba channel conservation area, Tanzania*. Gland, Switzerland: IUCN. 40pp.

Hammer, Ø., Harper, D.A. and Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia electronica*, *4*(1), p.9.

Hammerschlag, N., Schmitz, O.J., Flecker, A.S., Lafferty, K.D., Sih, A., Atwood, T.B., Gallagher, A.J., Irschick, D.J., Skubel, R. and Cooke, S.J., 2019. Ecosystem function and services of aquatic predators in the Anthropocene. *Trends in ecology & evolution*, *34*(4), pp.369-383.

Harborne, A. R., Mumby, P. J., Kennedy, E. V. and Ferrari, R., 2011. Biotic and multi-scale abiotic controls of habitat quality: their effect on coral-reef fishes. *Marine Ecology Progress Series*, *437*, 201-214.

Harvey, E., McLean, D., Frusher, S., Haywood, M., Newman, S.J. and Williams, A., 2013. The use of BRUVs as a tool for assessing marine fisheries and ecosystems: a review of the hurdles and potential. *University of Western Australia*, (2010/002).

Harvey, E.S., Newman, S.J., McLean, D.L., Cappo, M., Meeuwig, J.J. and Skepper, C.L., 2012. Comparison of the relative efficiencies of stereo-BRUVs and traps for sampling tropical continental shelf demersal fishes. *Fisheries Research*, *125*, pp.108-120.

Hempson, T.N., Graham, N.A., MacNeil, M.A., Williamson, D.H., Jones, G.P. and Almany, G.R., 2017. Coral reef mesopredators switch prey, shortening food chains, in response to habitat degradation. *Ecology and Evolution*, *7*(8), pp.2626-2635.

Hill, S.L., Hinke, J., Bertrand, S., Fritz, L., Furness, R.W., Ianelli, J.N., Murphy, M., Oliveros-Ramos, R., Pichegru, L., Sharp, R. and Stillman, R.A., 2020. Reference points for predators will progress ecosystem-based management of fisheries. *Fish and Fisheries*, *21*(2), pp.368-378.

Hixon, M.A., 2015. Predation: piscivory and the ecology of coral-reef fishes. In: Mora C. (Ed.) *Ecology of fishes on coral reefs*. Cambridge University Press Cambridge, UK, pp. 41–53.

Hussey, N.E., MacNeil, M.A., McMeans, B.C., Olin, J.A., Dudley, S.F., Cliff, G., Wintner, S.P., Fennessy, S.T. and Fisk, A.T., 2014. Rescaling the trophic structure of marine food webs. *Ecology letters*, *17*(2), pp.239-250.

IUCN (2021). The IUCN Red List of Threatened Species. Version 2021-1. https://www.iucnredlist.org

Jacquet, J. L. and Zeller, D. 2007. Putting the 'United' in the United Republic of Tanzania: Reconstructing marine fisheries catches'. Putting the 'United' in the United Republic of Tanzania: Reconstructing marine fisheries catches. In: Zeller D. and Pauly D., (Ed) *Reconstruction of marine fisheries catches for key countries and regions (1950-2005) Fisheries Centre Research Reports 15(2) Fisheries Centre*, University of British Columbia.

Jennings, S., Boullé, D.P. and Polunin, N.V.C., 1996. Habitat correlates of the distribution and biomass of Seychelles' reef fishes. *Environmental Biology of fishes*. Springer, 46(1), pp. 15–25.

Jones, S.T., Levine, A. and Jiddawi, N.S., 2019. Effective co-management and long-term reef fish recovery from severe coral bleaching: Insights from Misali Island, PECCA, Tanzania. *Ocean & Coastal Management*, *178*, 104843.

Kahng, S.E., Akkaynak, D., Shlesinger, T., Hochberg, E.J., Wiedenmann, J., Tamir, R. and Tchernov, D., 2019. Light, temperature, photosynthesis, heterotrophy, and the lower depth limits of mesophotic coral ecosystems. *In*: Loya, Y., Puglise, K.A. and Bridge, T.C.L. (Eds.), *Mesophotic Coral Ecosystems*. Springer, Cham, pp. 801–828.

Kailola, P.J., M.J. Williams, P.C. Stewart, R.E. Reichelt, A. McNee and C. Grieve, 1993. Australian fisheries resources. Bureau of Resource Sciences, Canberra, Australia. 422 p.

Kapoor, D., R. Dayal and A.G. Ponniah, 2002. Fish biodiversity of India. National Bureau of Fish Genetic Resources Lucknow, India.775 p

Karisa, J. F., Obura, D. O. and Chen, C.A., 2020. Spatial heterogeneity of coral reef benthic communities in Kenya. *PloS one*. 15(8), p. e0237397.

Kuiter, R.H., 1998. Photo guide to fishes of the Maldives. Atoll Editions, Victoria, Australia. 257 p.

Kuiter, R.H. and T. Tonozuka, 2001. Pictorial guide to Indonesian reef fishes. Part 1. Eels-Snappers, Muraenidae - Lutjanidae. Zoonetics, Australia. 1-302.

Kulbicki, M., Bozec, Y.M., Labrosse, P., Letourneur, Y., Mou-Tham, G. and Wantiez, L., 2005. Diet composition of carnivorous fishes from coral reef lagoons of New Caledonia. *Aquatic Living Resources*, *18*(3), pp.231-250.

Langlois, T., Goetze, J., Bond, T., Monk, J., Abesamis, R.A., Asher, J., Barrett, N., Bernard, A.T., Bouchet, P.J., Birt, M.J., Cappo, M. et al., 2020. A field and video annotation guide for baited remote underwater stereo-video surveys of demersal fish assemblages. *Methods in Ecology and Evolution*, *11*(11), pp.1401-1409.

Lieske, E. and Myers, R., 1994. *Collins Pocket Guide. Coral reef fishes. Indo-Pacific & Caribbean including the Red Sea*. Harper Collins Publishers, 400 p.

Long, J.S. and Long, J.S., 1997. *Regression models for categorical and limited dependent variables*. Sage.

MacNeil, M.A., Chapman, D.D., Heupel, M., Simpfendorfer, C.A., Heithaus, M., Meekan, M., Harvey, E., Goetze, J., Kiszka, J., Bond, M.E. and Currey-Randall, L.M., 2020. Global status and conservation potential of reef sharks. *Nature*, *583*(7818), pp.801-806.

McClanahan, T.R., Graham, N.A., MacNeil, M.A., Muthiga, N.A., Cinner, J.E., Bruggemann, J.H. and 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), pp.17230-17233.

McClanahan, T.R., Maina, J.M., Darling, E.S., Guillaume, M.M., Muthiga, N.A., D'agata, S., Leblond, J., Arthur, R., Jupiter, S.D., Wilson, S.K. and Mangubhai, S., 2020. Large geographic variability in the resistance of corals to thermal stress. *Global Ecology and Biogeography*, *29*(12), pp.2229-2247.

McGratten, K. and Pollom, R., 2015. *Aulostomus chinensis*. The IUCN Red List of Threatened Species 2015: e. T65134886A82934000.

Michael, S.W., 1993. Reef sharks and rays of the world. A guide to their identification, behavior, and ecology. Sea Challengers, Monterey, California. 107 p

Moberg, F. and Folke, C., 1999. Ecological goods and services of coral reef ecosystems. *Ecological economics*. Elsevier, 29(2), pp. 215–233.

Mundy, B.C., 2005. Checklist of the fishes of the Hawaiian Archipelago. Bishop Mus. Bull. Zool. (6):1-704.

Myers, R.A. and Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature*, *423*(6937), pp.280-283.

Nagelkerken, I., Van der Velde, G., Gorissen, M. W., Meijer, G. J., Van't Hof, T. and Den Hartog, C., 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine, coastal and shelf science*, *51*(1), 31-44.

Nash, K.L., Welsh, J.Q., Graham, N.A. and Bellwood, D.R., 2015. Home-range allometry in coral reef fishes: comparison to other vertebrates, methodological issues and management implications. *Oecologia*, *177*(1), pp.73-83.

Nagelkerken, I., Dorenbosch, M., Verberk, W.C.E.P., De La Morinière, E.C. and Van Der Velde, G., 2000. Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Marine Ecology Progress Series*, *194*, pp.55-64.

NBS. 2018. Tanzania in Figures 2017 National Bureau of Statistics, Dar es Salaam, Tanzania. p. 1–105.

Obura, D., Gudka, M., Rabi, F.A., Gian, S.B., Bijoux, J., Freed, S., Maharavo, J., Mwaura, J., Porter, S., Sola, E. and Wickel, J., 2017. *Coral reef status report for the Western Indian Ocean (2017).* Nairobi Convention, Global Coral Reef Monitoring Network (GCRMN)/International Coral Reef Initiative (ICRI).

Osuka, K.E., McClean, C., Stewart, B.D., Bett, B.J., Le Bas, T., Howe, J., Abernerthy, C., Yahya, S., Obura, D. and Samoilys, M., 2021a. Characteristics of shallow and mesophotic environments of the Pemba Channel, Tanzania: Implications for management and conservation. *Ocean & Coastal Management*, *200*, p.105463.

Osuka, K.E., Stewart, B.D., Samoilys, M.A., Roche, R.C., Turner, J., McClean, C., 2021b. Protection outcomes for fish trophic groups across a range of management regimes. *Marine Pollution Bulletin*, 173, p.113010.

Papastamatiou, Y.P., Lowe, C.G., Caselle, J.E. and Friedlander, A.M., 2009. Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. *Ecology*, *90*(4), pp.996-1008.

Papastamatiou, Y.P., Bodey, T.W., Friedlander, A.M., Lowe, C.G., Bradley, D., Weng, K., Priestley, V. and Caselle, J.E., 2018. Spatial separation without territoriality in shark communities. *Oikos*, *127*(6), pp.767-779.

Paxton, J.R., D.F. Hoese, G.R. Allen and J.E. Hanley, 1989. Pisces. Petromyzontidae to Carangidae. Zoological Catalogue of Australia, Vol. 7. Australian Government Publishing Service, Canberra, 665 p.

Paxton, A.B., Newton, E.A., Adler, A.M., Van Hoeck, R.V., Iversen Jr, E.S., Taylor, J.C., Peterson, C.H. and Silliman, B.R., 2020. Artificial habitats host elevated densities of large reef-associated predators. *PloS one*, *15*(9), p.e0237374.

Pinheiro, H.T., Goodbody-Gringley, G., Jessup, M.E., Shepherd, B., Chequer, A.D. and Rocha, L.A., 2016. Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in two Caribbean locations. *Coral Reefs*, *35*(1), pp.139-151.

Rasher, D.B., Hoey, A.S. and Hay, M.E., 2017. Cascading predator effects in a Fijian coral reef ecosystem. *Scientific Reports*, 7(1), pp. 1–10.

Rehren, J., Samoilys, M., Reuter, H., Jiddawi, N. and Wolff, M., 2020. Integrating Resource Perception, Ecological Surveys, and Fisheries Statistics: A Review of the Fisheries in Zanzibar. *Reviews in Fisheries Science & Aquaculture*, pp.1-18.

Root, K. V., 1998. Evaluating the effects of habitat quality, connectivity, and catastrophes on a threatened species. *Ecological Applications*, *8*(3), 854-865.

Sancho, G., 2000. Predatory behaviors of *Caranx melampygus* (Carangidae) feeding on spawning reef fishes: a novel ambushing strategy. *Bulletin of Marine Science*. University of Miami-Rosenstiel School of Marine and Atmospheric Science, 66(2), pp. 487–496.

Sandin, S. A. and Zgliczynski, B., 2015. Inverted trophic pyramids. *In:* Mora, C. (ed.) *Ecology of Fishes on Coral Reefs*. Cambridge: Cambridge University Press, pp. 247–251.

Santana-Garcon, J., Newman, S.J. and Harvey, E.S., 2014. Development and validation of a mid-water baited stereo-video technique for investigating pelagic fish assemblages. *Journal of Experimental Marine Biology and Ecology*, *452*, pp.82-90.

Semba, M., Lumpkin, R., Kimirei, I., Shaghude, Y. and Nyandwi, N., 2019. Seasonal and spatial variation of surface current in the Pemba Channel, Tanzania. *PloS one*, *14*(1), p.e0210303.

Senou, H., 2001. Sphyraenidae. Barracudas. p. 3685-3697. In K.E. Carpenter and V. Niem (eds.) FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Vol. 6. Bony fishes part 4 (Labridae to Latimeriidae), estuarine crocodiles. FAO, Rome.

Shin, Y.J., Rochet, M.J., Jennings, S., Field, J.G. and Gislason, H., 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* 62 (3), 384–396

Skinner, C., Mill, A.C., Newman, S.P., Alsagoff, S.N. and Polunin, N.V., 2020. The importance of oceanic atoll lagoons for coral reef predators. *Marine Biology*, *167*(2), pp.1-16.

Slade, L.M. and Kalangahe, B., 2015. Dynamite fishing in Tanzania. *Marine pollution bulletin*, *101*(2), pp.491-496.

Smith, C.L., 1997. National Audubon Society field guide to tropical marine fishes of the Caribbean, the Gulf of Mexico, Florida, the Bahamas, and Bermuda. Alfred A. Knopf, Inc., New York. 720 p

Sommer, C., Schneider, W. and Poutiers, J. M. 1996. *FAO species identification field guide for fishery purposes: The living marine resources of Somalia.*

Stefanoudis, P.V., Gress, E., Pitt, J.M., Smith, S.R., Kincaid, T., Rivers, M., Andradi-Brown, D.A., Rowlands, G., Woodall, L.C. and Rogers, A.D., 2019. Depth-dependent structuring of reef fish assemblages from the shallows to the rariphotic zone. *Frontiers in Marine Science*, *6*, p.307.

Stewart, B.D. and Jones, G.P., 2001. Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality. *Marine Biology*, 138(2), pp. 383–397.

Taquet, M. and Diringer, A., 2012. Fishes of the Indian Ocean and the Red Sea. Éditions Quæ RD 1078026 Versailles Cedex, France 707p.

Tyler, E.H., Speight, M.R., Henderson, P. and Manica, A., 2009. Evidence for a depth refuge effect in artisanal coral reef fisheries. *Biological Conservation*, *142*(3), pp.652-667.

Vuong, Q.H., 1989. Likelihood ratio tests for model selection and non-nested hypotheses. *Econometrica: Journal of the Econometric Society*. JSTOR, pp. 307–333.

Wanyonyi, I.N., Wamukota, A., Tuda, P., Mwakha, V.A and Nguti, L.M., 2016. Migrant fishers of Pemba: Drivers, impacts and mediating factors. *Marine Policy*, *71*, pp.242-255.

Watson, W. and Sandknop, E.M., 1996. Fistulariidae: cornetfishes. p. 718-723. In Moser, H.G. (ed.) *The early stages of fishes in the California Current Region*. California Cooperative Oceanic Fisheries Investigations (CalCOFI) Atlas No. 33. Allen Press, Inc., Lawrence, Kansas. 1505 p.

Wells, S., Samoilys, M., Makoloweka, S. and Kalombo, H., 2010. Lessons learnt from a collaborative management programme in coastal Tanzania. *Ocean & Coastal Management*, *53*(4), pp.161-168.
White, J., Simpfendorfer, C.A., Tobin, A.J. and Heupel, M.R., 2013. Application of baited remote underwater video surveys to quantify spatial distribution of elasmobranchs at an ecosystem scale. *Journal of Experimental Marine Biology and Ecology*, *448*, pp.281-288.
Wilson, R.J., Sailley, S.F., Jacobs, Z.L., Kamau, J., Mgeleka, S., Okemwa, G.M., Omukoto, J.O., Osuka, K.E., Samoilys, M., Sauer, W., Silas, M.O., Sululu, J.S. and Roberts, M.J., 2021. Large projected reductions in marine fish biomass for Kenya and Tanzania in the absence of climate mitigation. *Ocean & Coastal Management*, *215*, p.105921.
Worm, B., Davis, B., Kettemer, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R., Kessel, S.T. and Gruber, S.H., 2013. Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy*, *40*, pp.194-204.
Wyatt, A.S., Lowe, R.J., Humphries, S. and Waite, A.M., 2013. Particulate nutrient fluxes over a fringing coral reef: Source-sink dynamics inferred from carbon to nitrogen ratios and stable isotopes. *Limnology and Oceanography*, *58*(1), pp.409-427.