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Authors	Murie, Calum J. G.;Lebrato, Mario;Gavard, Livia;Oliver, Simon P.
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OPEN Fish and coral communities shape elasmobranch reef use in southern Mozambique

Calum J.G. Murie^{1,2}✉, Mario Lebrato³, Livia Gavard² & Simon P. Oliver^{1,4}

Few studies have explored whether a reef's bioecological structure affects the presence of elasmobranchs. To examine if the structure of a reef's fish and coral community influences the likelihood of observing certain elasmobranch species, we deployed a remote underwater video station (RUVS) on four reefs in southern Mozambique. A single RUVS was deployed monthly on each reef for 12 months, resulting in 48 deployments and 140 h of video recordings. Images were extracted from the video recordings to estimate the relative abundance of teleost fish and following each camera deployment a 30 m² belt transect was completed to measure the percentage cover of corals. Coral and fish abundances were then separated into common functional metrics describing each community. NMDS and PERMANOVA were used to estimate if the calculated metrics and observations of elasmobranchs by RUVS varied between the four reefs. Metrics were then analysed for their influence on the composition of each reef's elasmobranch community within the NMDS ordination space. The relative abundance of coral species was primarily found to be linked with the depth of the reef surveyed. Relative abundances of coral measured on the shallow reef site were distinct from the other examined reefs in ordination space, with less coral cover and a lower overall abundance of teleost and elasmobranch fish. The richness and abundance of teleost fish species, particularly piscivorous fish, was highest on the northern reef where the elasmobranch community was dominated by several species of reef shark. The southern reef also had a distinct richness and abundance of teleost fish species, with a heightened abundance of herbivorous and cleaner fish, and the observed elasmobranch community was mostly comprised of *Mobula* rays and guitarfish. Our findings suggest that fish and coral communities can significantly differ between reefs with similar abiotic conditions in a relatively small region, and that this can lead to spatially heterogeneous patterns of reef use by elasmobranchs. This may suggest that including the protection of reefs with different biological characteristics within local conservation strategies may promote rare and vulnerable regional elasmobranch species ranging from stingrays, guitarfishes, reef sharks, and pelagic rays.

Keywords Marine biology, Elasmobranch, Behaviour, Environment, Habitat use, Marine ecology, Reef, Environmental change

Coral reefs are one of the ocean's most productive ecosystems, providing a habitat for more than 25% of the ocean's marine life^{1,2}. Coastal reef ecosystems contain a variety of coral, fish, and invertebrate species that form the reef community and food web^{1,2}. Coastal reefs also function as an important habitat for a variety of rare and vulnerable elasmobranch species^{3,4}. Heightened numbers of reef sharks, pelagic sharks, stingrays, and guitarfish are key indicators of reef health due to their predatory diet and high requirement for food⁴⁻⁶. Reefs in the coastal environment face a multitude of pressures, including climate change, coastal runoff and pollution, over-fishing, habitat destruction, invasive species, and sedimentation deposits from coastal developments^{2,4,7-9}. These pressures constrain the biodiversity, ecological function, and productivity of coastal reefs around the world, but it is currently unclear how this affects many vulnerable reef-associated elasmobranch species^{2,8,10,11}.

Reductions in the health of a reef's coral community can catalyse long-term losses in its productivity^{2,8}, causing reductions in the abundance of reef-associated species including elasmobranchs^{12,13}. Since corals are essential habitat-forming organisms, their relative abundance and diversity are robust indicators of the basal health of a reef's ecosystem^{2,10,14,15}. A reef's fish community is a robust measure of its productivity^{10,14,15}.

¹Department of Biological Sciences, University of Chester, Chester, UK. ²Underwater Africa, Inhambane, Mozambique. ³Bazaruto Centre for Scientific Studies (BCSS), Bazaruto Archipelago, Inhambane, Mozambique. ⁴The Thresher Shark Research and Conservation Project, Cebu, The Philippines. ✉email: calum@underwater-africa.com

Measuring functional groups in a reef's fish community (e.g., herbivorous species, corallivorous species, piscivorous species) can provide insights into its health and ecological state^{1,10,14}. Fish that occupy the highest trophic levels on reefs rely on the longest energy pathways in the reef food web and are the most acutely affected by pressures on a reef ecosystem^{2,16–18}. Since many elasmobranch species are reef predators, they occupy high trophic levels within reef food webs^{2,13,19,20}. Several species of shark and stingray function as apex predators within the reef food web and require healthy fish communities to predate^{2,13,19}. Few studies have explored how a reef's bioecological structure affects the abundance of elasmobranchs.

Overexploited reef fish communities have been linked to reductions in foraging opportunities for elasmobranchs in several locations^{10,15,16}. In the northern Great Barrier Reef, increasing the abundance and diversity of reef fish by protecting reefs catalysed a 75% increase in elasmobranch abundance suggesting that the health of their populations is intrinsically linked^{13,18,20}. Many studies predict that under future conditions the health of reef ecosystems will be significantly degraded, leading to dramatic changes to the bioecological structure of reefs^{4,7–9}. It is currently unclear how vulnerable reef-associated elasmobranchs will be affected by such future conditions since little research has investigated links between elasmobranch populations and fish and coral communities on reefs^{2,5,6,8,10}. Identifying the bioecological characteristics of reefs that currently attract elasmobranchs to certain reef sites may inform the best practices for managing their populations^{19,21,22}.

In this study we investigate the bioecological characteristics of coral reefs in southern Mozambique (Western Indian Ocean – WIO – region) with the goal of assessing if they affect the habitat use of regional elasmobranch species. We address the hypotheses that (1) the structure of fish and coral communities on the sampled reefs only vary with changes in depth; and (2) the relative abundance of functional groups within the fish and coral communities influences the structure of reef-associated elasmobranch communities. Our results are discussed in the context of reef biodiversity and elasmobranch ecology.

Methods

This work complied with the University of Chester's research ethics framework and was granted ethical approval by the University of Chester's research ethics committee who approved all experimental protocols (1669/20/CM/BS). Informed consent was obtained from all participants in this study. Fieldwork was undertaken in collaboration with the Bazaruto Centre for Scientific Studies (BCSS) (No: 101218511) and was undertaken by permit (the Department of Conservation 04/GDG/ANAC/MTA/2020). All the methods complied with the relevant guidelines and regulations.

Sampling

Fish and coral species were documented at four reefs off the coast of Praia do Tofo (23° 51.205' S; 35° 32.882' E) in the Inhambane province of southern Mozambique^{23–25}. Data was collected by completing belt transects and by deploying a single Remote Underwater Video Station (RUVS) (Fig. 1).

A Go-Pro Hero 5⁺ camera, housed in a Marlin Marine[®] custom-built camera housing was connected to a voltage-regulating charging unit fed by two 12v, 9ah, batteries. The camera was set to automatically start recording one hour after being deployed (to counter possible bias stemming from the presence of SCUBA divers) for a total time of 7 h in 4000-pixel (4 K) quality²⁶. SCUBA divers deployed the RUVS system at a fixed point (central cleaning station on each reef's crest) with the camera facing into the current²⁷. The system was deployed on concurrent days, once a month, on each of the four reefs from April 2020 to April 2021 around 09:00 (Fig. 1.)^{26,28}. Seven hours of video observations were recorded on each of the four reefs each month (28 h total). Across the study's one year period, (April – April), a total of 336 h of video observations were recorded.

Following each RUVS deployment, a 1 × 1 m quadrat was continuously deployed along a 30 m path ($n = 30$ quadrats), resulting in a 30 m² belt transect²⁹. Still images were captured of each quadrat with a Canon[®] 5D Mk3 fitted with a 50 mm Canon[®] lens, housed in a Marlin Marine[®] underwater housing²⁹. The camera was positioned at a set distance (1 m) above the quadrat so that the quadrat filled the entire camera frame³⁰. Still images were downloaded and analysed in the Coral Point Count with Excel Extensions³⁰ software package (CPCE), which allowed us to designate coral types and estimate their percentage cover (%)³⁰. Each coral was identified to the genus level³⁰. We calculated each coral genera's percentage cover within each still image^{29,30} and repeated the approach to calculate the percentage cover of dead coral, live coral, hard coral, and soft coral in each photograph since these groups are robust indicators of the health of the coral community^{23,29}. Percentage cover data for each of the quadrat photos was then summed to produce relative abundance data per remote camera system deployment^{29,30}.

To investigate the diversity and richness of each reef's fish community, video recordings were stopped, and a still image was captured every 30 min of the seven-hour ($n = 14$) camera system recordings^{31–33}. Each reef was surveyed by the camera system for a total of 336 h (seven hours over 12 deployments) resulting in 168 images captured for each reef^{27,34}. The still images were then analysed independently by two researchers^{27,32,33}. Each researcher identified the fish in the still image, making use of the video recordings associated with each photograph's timestamp^{27,31,32}. The researchers established the number of fish species present per site (species richness: Supplementary Table 1) and the number of individuals per species (relative abundance) per deployment^{27,32}. The relative abundance and richness data was then binned into functional groups of fish species (herbivorous, piscivorous, corallivorous, cleaners) that are important indicators of reef ecosystem function^{27,32,35}.

Video footage captured by remote camera was downloaded and analysed in VLC Media Player (Video LAN) in 32 frames s⁻¹ resolution²⁸. Recordings of elasmobranch species were spliced from the footage^{18,26,31}, and reviewed frame by frame until a species identification was independently confirmed by two researchers^{18,31}. Due to their distance from the remote camera, it was not possible to sex or scale the elasmobranchs^{18,26,28,31}. If a second sighting of the same species occurred within five minutes of the initial sighting it was assumed that the same individual had returned to the camera's field of view so was not included in that species' count^{18,26,28}.

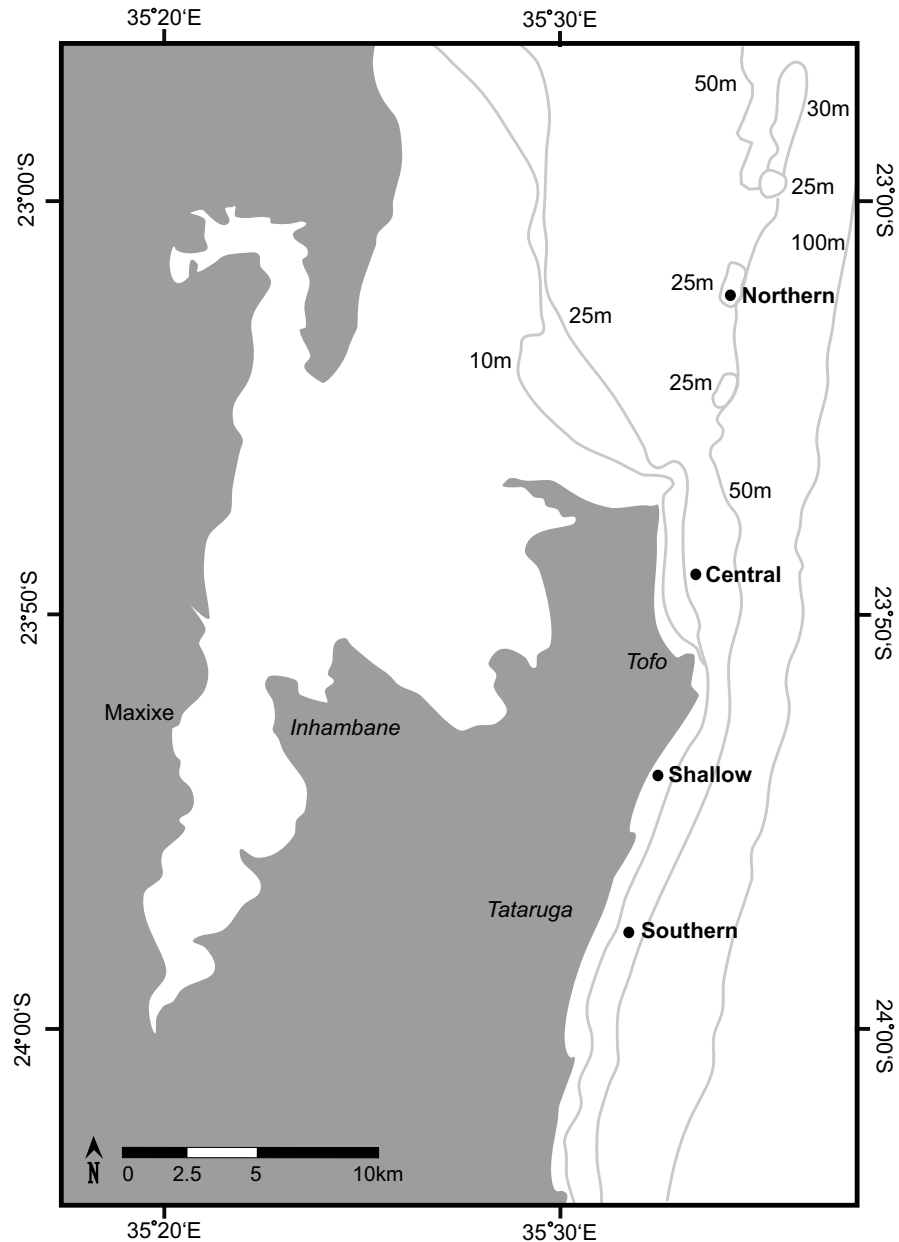


Fig. 1. The locations of the four reefs (solid circles) where a remote camera system was deployed to survey for elasmobranchs and collect data on the fish and coral communities offshore of Praia do Tofo in southern Inhambane, Mozambique. The land is outlined in a solid dark grey colour, and the ocean is in white. The light grey lines show the bathymetric contours in the studied region. The figure was created by the authors in R Statistics version 3.6.1.

Statistical analyses

All statistical analyses were undertaken in the vegan package³⁶ of R Statistics version 3.6.1³⁷.

Species accumulation curves comparing the diversity of the coral, fish, and elasmobranch communities across the video observations were created using the “specaccum” function and a sample-based rarefaction method (developed independently through numerous iterations)^{36,38,39}. Since all the curves became asymptotic as consecutive samples were added (which suggested that species richness was unlikely to increase) it was assumed that the coral, fish, and elasmobranch communities had been sufficiently sampled^{36,38,39}.

To estimate if metrics describing the coral and fish communities (the relative abundance of live coral, dead coral, soft coral, hard coral, herbivorous fish, coralivorous fish, cleaner fish, and piscivorous fish, richness of fish, and coral) varied between the four monitored reefs, a series of one-way repeated measures analyses of variance

models were developed using a conservative p value of 0.01^{40,41}. Each metric was included as the response variable for each model^{41,42}. The reef location formed the explanatory variable and Poisson error distributions were applied^{40,41}.

A second series of one-way repeated measures analyses of variance models were developed to examine if the numbers of each elasmobranch species varied between the four monitored reefs^{40,41}. The number of observations of each of the species (*Triacodon obesus*, *Carcharhinus amblyrhynchos*, *Carcharhinus limbatus*, *Stegostoma tigrinum*, *Taeniurops meyeri*, *Neotrygon caeruleopunctata*, *Pateobatus jenkinsii*, *Megatrygon microps*, *Mobula alfredi*, *M. birostris*, *Mobula kuhlii*, *Aetobatus ocellatus*, *Acroteriobatus leucospilus*, *Rhina ancylostoma*, *Rhynchobatus djiddensis*, *Torpedo sinuspersici*) per deployment was included as the model response term, and the reef location was included as the explanatory variable with Poisson error distributions applied^{40,41}. All the data that was used in the analysis of variance models had approximately normal distributions and the models were summarised, plotted, and checked⁴¹. No issues were detected with model convergence, overdispersion, zero inflation or sphericity^{40,42}.

A Tukey post hoc comparison was applied to the results of each of the analysis of variance models (coral/fish metrics & elasmobranch species counts) to examine if the calculated means varied between the four monitored reefs^{43,44}. The confidence interval was set based on the Studentized range statistic and Tukey's Honest Significant Difference was applied^{43,44}.

To investigate if the fish, coral, and elasmobranch communities varied between the four monitored reefs, two-dimensional nonmetric multidimensional scaling (NMDS) ordinations were fitted to each community's relative abundance data^{45–47}. Each NMDS ordination for each community (fish, coral, elasmobranch) was applied with the Sorenson Bray Curtis distance measures to calculate the dissimilarity matrix^{40,47}. To account for potential outliers, Sorenson Bray outlier analysis was applied which indicated that no species' relative abundance should be transformed⁴⁸. The ordination was structured using "autotransform" set to false and was set to run for 100 iterations using several random starting points⁴⁷. The three NMDS ordinations were plotted and checked. No issues were found regarding convergence and all stress values were < 0.20 ^{40,47}. To avoid localised minima, stress vs. iteration comparisons confirmed that each ordination stress value had stabilized, that their final instability was < 15.50 , and that the deviation was < 0.001 over the final 20 iterations^{40,48}.

Three permuted multivariate analyses of variance models were used to examine variations in the coral, fish, and elasmobranch relative abundance distance matrix across the four sampled reefs^{40,49}. Each model was run across 999 permutations and Sorenson Bray Curtis distance measures were applied⁴⁰. A secondary analysis of variance using the function "betaspider" was applied to each model to examine if variances in the calculated Bray Curtis distances were equal among the studied reefs^{36,40,49}. For each model, Bray Curtis distances did not vary between the studied sites indicating that including the reef as the explanatory factor in the permuted multivariate analysis of variance models sufficiently explains the variation in each community's ordination^{36,40,49}.

Vector fitting was used to examine the effects of the metrics describing the coral and fish communities (the relative abundance of live coral, dead coral, soft coral, hard coral, fish species, herbivorous fish, coralivorous fish, cleaner fish, and piscivorous fish, richness of fish, coral, and soft coral) on the elasmobranch communities ordination in the two-dimensional NMDS ordination space^{50,51}. The "envfit" function fitted vectors for each of the metrics to the ordination, scaling the lengths of their effects to their correlation (square root of the calculated r^2 value) with the ordination^{50–52}. The rate of false discovery was controlled using the Benjamini Hochberg procedure operating under the assumption that a false discovery rate above 0.1 was significant⁵².

Results

The species accumulation curves trended towards asymptotic following 17 samples for corals, 20 samples for teleost fish and 37 for elasmobranchs species. This indicated that most of the coral, fish, and elasmobranch communities had been sampled. Across the transects on the four studied reefs, 21 genera of corals were observed, comprising of 16 genera of hard coral and five genera of soft coral (Supplementary Table 1.). In total, 63 species of fish were observed on the reef sites, including 47 species of teleost and 16 species of elasmobranch (Supplementary Table 1.; Table 1.). The teleost fish were further split into 15 species of herbivorous fish, seven species of piscivorous fish, and nine species of both cleaner and corallivorous fish (Table 1.). Species' mean average abundance (\pm SE), taxonomy, richness, and distribution between the monitored reef sites can be found in Supplementary Table 1.

Analyses of variance modelling indicated that the percentage cover ($F(3) = 10.7$, $p < 0.001$) and richness ($F(3) = 12.389$, $p = 0.003$) of live coral and the percentage cover ($F(3) = 10.27$, $p < 0.001$) and richness ($F(3) = 5.857$, $p = 0.002$) of hard corals varied between the monitored reefs (Fig. 2.). The percentage cover of dead corals ($F(3) = 1.354$, $p = 0.269$) and the richness ($F(3) = 0.52$, $p = 0.671$) and percentage cover ($F(3) = 1.679$, $p = 0.185$) of soft corals did not vary between the monitored reefs (Fig. 2., Table 1.). Post hoc comparisons indicated that the mean score for the percentage cover and richness of live and hard coral was significantly lowest on the shallow reef (Fig. 2., Table 1.). The abundance ($F(3) = 6.601$, $p < 0.001$) and richness ($F(3) = 7.329$, $p < 0.001$) of fish were found to be highest on the northern reef, which also had the most abundant piscivorous fish ($F(3) = 5.66$, $p = 0.003$; Fig. 2.). Teleost fish were more abundant on the southern reef than on the shallow reef ($F(3) = 6.601$, $p < 0.001$; Fig. 2.; Table 1.) as were cleaner fish species ($F(3) = 24.69$, $p < 0.001$; Fig. 2.). The abundance of herbivorous ($F(3) = 1.708$, $p = 0.179$) and corallivorous ($F(3) = 0.845$, $p = 0.488$) fish did not vary between the reefs (Fig. 2.; Table 1.). Outputs from the non-metric multidimensional scaling and permuted multivariate analysis of variance modelling matched the results stemming from the ANOVA models. The NMDS models indicate that the relative abundance of coral families (dimensions = 2, stress = 0.184; $F(3) = 3.855$, $p = 0.001$), fish species (dimensions = 2, stress = 0.139; $F(3) = 10.408$; $p < 0.001$), and elasmobranch species (dimensions = 2, stress = 0.117; $F(3) = 10.35$, $p = 0.001$) differed between the reefs in ordination space, suggesting vector fitting can be applied to estimate how the functional metrics explain the variability in each community (Fig. 2.; Table 1.).

Class	Order	Family	Species	Common Name	Northern	Central	Shallow	Southern
Chondrichthyes	Carcharhiniformes	Carcharhinidae	<i>Triakonodon obesus</i>	Whitetip reef shark	0 ± 0	7.83 ± 1.49	0.17 ± 0.11	0 ± 0
			<i>Carcharhinus amblyrhynchos</i>	Grey reef shark	0 ± 0	2.92 ± 0.66	0 ± 0	0.5 ± 0.29
			<i>Carcharhinus limbatus</i>	Oceanic blacktip shark	0.17 ± 0.17	1.75 ± 0.59	0 ± 0	0.17 ± 0.11
	Orectolobiformes	Stegostomatidae	<i>Stegostoma tigrinum</i>	Zebra shark	0.17 ± 0.11	3.33 ± 0.78	0 ± 0	0.25 ± 0.25
	Myliobatiformes	Dasyatidae	<i>Taeniurops meyeri</i>	Blotched fantail ray	2.58 ± 1.31	1.75 ± 0.73	0 ± 0	1 ± 0.46
			<i>Neotrygon caeruleopunctata</i>	Kuhl's ray	0 ± 0	0 ± 0	1.08 ± 0.43	0 ± 0
			<i>Pateobatus jenkinsii</i>	Jenkin's Whiptail ray	0 ± 0	1.5 ± 0.77	0.33 ± 0.19	0 ± 0
		Mobulidae	<i>Megatrygon microps</i>	Smalleye stingray	0.33 ± 0.19	0.17 ± 0.11	0 ± 0	1.25 ± 0.45
			<i>Mobula alfredi</i>	Reef manta ray	0.17 ± 0.11	0.17 ± 0.11	0 ± 0	3.33 ± 1.1
			<i>Mobula birostris</i>	Giant manta ray	0.42 ± 0.26	0.5 ± 0.23	0.17 ± 0.11	4.17 ± 1.31
		Myliobatidae	<i>Mobula kuhlii</i>	Shortfin devil ray	1.25 ± 1.25	2.67 ± 1.17	0 ± 0	6.67 ± 1.65
			<i>Aetobatus ocellatus</i>	Eagle ray	1.92 ± 0.77	1.42 ± 1.02	0.08 ± 0.08	1.33 ± 0.48
			Rhinopristiformes	Rhinobatidae	<i>Acroteriobatus leucospilus</i>	Grey spot guitarfish	0 ± 0	0 ± 0
		Rhinidae	<i>Rhina ancylostoma</i>	Bowmouth guitarfish	0.33 ± 0.19	0 ± 0	0 ± 0	0.83 ± 0.34
			<i>Rhynchobatus djiddensis</i>	White spotted wedge fish	0 ± 0	0 ± 0	0 ± 0	1.33 ± 0.56
Torpediniformes			Torpedinidae	<i>Torpedo sinuspersici</i>	Electric torpedo ray	0 ± 0	0 ± 0	1.25 ± 0.54

Class	Order	Functional Metric	Unit of Measurement	Northern	Central	Shallow	Southern
Anthozoa	<i>Hexacorallia</i> & <i>Octocorallia</i>	Live corals	Percentage cover	31.34 ± 4.85	48.1 ± 4.96	15.87 ± 2.49	41.21 ± 4.33
		Dead corals	Percentage cover	2.65 ± 0.67	1.84 ± 0.57	4.88 ± 1.55	2.59 ± 1.39
		Coral species richness	Number of species	4.25 ± 0.52	5 ± 0.35	2.58 ± 0.4	4.17 ± 0.47
		Hard corals	Percentage cover	25.49 ± 4.02	36.12 ± 3.35	10.4 ± 2.45	30.49 ± 3.75
		Soft corals	Percentage cover	5.84 ± 1.25	11.97 ± 4.11	5.47 ± 1.26	10.72 ± 2.51
Osteichthyes	<i>Actinopterygii</i>	Live fish	Abundance of individuals	29.05 ± 3.18	42.04 ± 3.9	23.36 ± 2.47	37.31 ± 3.28
		Herbivorous fish	Abundance of individuals	15.96 ± 2.22	17.91 ± 2.08	12.69 ± 1.48	18.59 ± 2.22
		Coralivorous fish	Abundance of individuals	6.93 ± 1.06	6.75 ± 1.05	5.06 ± 0.98	5.63 ± 0.79
		Cleaner fish	Abundance of individuals	4.31 ± 0.51	10 ± 1.36	1.12 ± 0.36	15.77 ± 2.13
		Piscivorous fish	Abundance of individuals	7.54 ± 1.47	10.06 ± 1.87	4.26 ± 1	7.73 ± 1.38
		Fish species richness	Number of species	16 ± 1.38	21.92 ± 1.92	12.83 ± 1.08	15.08 ± 1.2

Table 1. Mean numbers (\pm standard error (SE)) of elasmobranch species recorded by the remote camera during deployments across the four monitored reef sites in Southern Mozambique. A zero value indicates that a species was not observed on a reef site. Mean numbers (\pm standard error (SE)) of recorded values for each of the modelled functional metrics are also provided as well as the units in which each metric was measured.

Analyses of variance and Tukey post hoc comparisons indicated that zebra (*S. tigrinum*) ($F(3) = 14.93$, $p < 0.001$), common blacktip (*C. limbatus*) ($F(3) = 6.936$, $p < 0.001$), grey reef (*C. amblyrhynchos*) ($F(3) = 15.13$, $p < 0.001$), and white tip reef (*T. obesus*) ($F(3) = 27.23$, $p < 0.001$) sharks were observed more on the northern reef (Fig. 2.). The models also suggested that bowmouth guitarfish (*R. ancylostoma*) ($F(3) = 4.861$, $p = 0.003$), white spotted wedge fish (*R. djiddensis*) ($F(3) = 5.333$, $p = 0.002$), small eye stingrays (*M. microps*) ($F(3) = 5.055$, $p = 0.004$), devil rays (*M. kuhlii*) ($F(3) = 5.929$, $p = 0.002$), reef manta rays (*M. alfredi*) ($F(3) = 8.48$, $p < 0.001$), and giant manta rays (*M. birostris*) ($F(3) = 7.902$, $p < 0.001$) were observed most on the southern reef (Fig. 2.). Kuhl's rays (*N. caeruleopunctata*) ($F(3) = 7.592$, $p < 0.001$), grey spot guitarfish (*A. leucospilus*) ($F(3) = 4.661$, $p = 0.006$), and torpedo rays (*T. sinuspersici*) ($F(3) = 4.8$, $p = 0.005$) were most observed on the shallow reef (Fig. 2.). The models did not indicate any difference in the numbers of blotched fantail rays (*T. meyeri*) ($F(3) = 1.962$, $p = 0.134$), Jenkin's Whiptail ray (*P. jenkinsii*) ($F(3) = 3.199$, $p = 0.082$) or eagle rays (*A. ocellatus*) ($F(3) = 7.299$, $p = 0.287$; Fig. 2.) across the study sites.

Cluster analyses indicated that the northern, central, and southern reefs have similar coral communities whilst the shallow reef was distinct in its relative abundance of corals (Fig. 3(a.)). The shallow reef cluster also contained the most distinct community of fish species, whilst the southern and northern reef clusters were the most similar (Fig. 3(b.)). Cluster analyses also indicated that the elasmobranch community on both the northern and shallow reefs were distinct from the central and southern reefs (Fig. 3(c.)). The observed overlap in the southern and central clusters within the ordination space indicated a degree of similarity in the elasmobranch community on these reefs (Fig. 3(c.)). Vector fitting indicated that four of the calculated fish and coral metrics explained the plotted variations in elasmobranch species and their relative abundance on the monitored reefs (Fig. 3(c.)). The abundance of cleaner fish explained the variation in the species composition and relative abundance of the southern and (to some extent) central elasmobranch communities ($R^2 = 0.205$, $p = 0.007$; Fig. 3(c.)). The total abundance of corals explained some of the variation in the species composition and relative abundance of the central reef elasmobranch community ($R^2 = 0.16$, $p = 0.022$; Fig. 3(c.)). The variation in the species composition and relative abundance of the northern reef elasmobranchs appeared to be correlated with the richness of fish ($R^2 = 0.222$, $p = 0.003$; Fig. 3(c.)) species and the abundance of piscivorous fishes ($R^2 = 0.121$, $p = 0.006$; Fig. 3(c.)).

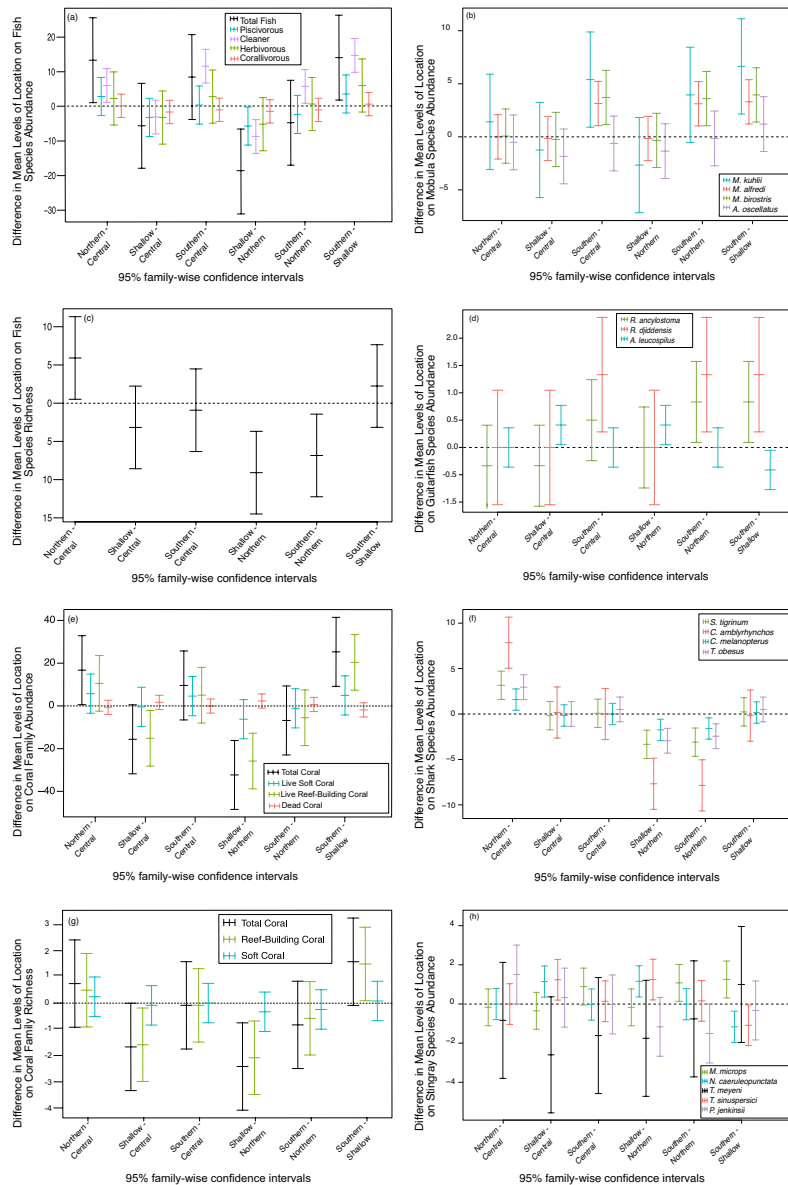


Fig. 2. Pairwise comparisons between the four sampled reefs of the mean recorded numbers of functional metrics of the fish community (a), the richness of the fish community (c), and the percentage cover (e) of live, dead, hard and soft corals and the species richness (g) of live, hard and soft corals. Pairwise comparisons of the mean numbers of Mobuliid rays (b), guitarfish (d), sharks (f) and stingrays (h) are also compared between the monitored reefs. Vertical lines in the centre and ends of the bars represent the mean and 95% family-wise confidence interval for each pairwise comparison.

Discussion

Our study represents the first attempt to investigate links between the composition of a reef’s fish and coral community and its assemblage of elasmobranchs in southeast Africa^{2,8,10}. The results indicated that a reef’s teleost fish community has an important influence on the abundance and distribution of elasmobranch species. This should provide environmental managers with novel information as to how the biological state of a reef community influences the relative abundance of multiple threatened elasmobranch species^{2,10,53}.

Many corals will not grow outside of certain depth limits due to the photosynthetic requirements of the zooxanthellae that they host in their polyps^{16,25,54} and are therefore constrained in terms of where they can settle and successfully develop^{16,25,54}. Such limitations occur alongside natural variation in a reef’s physical location or from alterations in the intensity of pressures that are levied against it (e.g., fishing, pollution, sediment deposits etc.) and affect its biology^{14,16,40}. Reef fish communities are intrinsically linked to benthic communities which also creates natural variability within regional reef fish communities^{1,9,23,25,54}.

The abundance of herbivorous and corallivorous fish species is influenced by the presence of grazing habitat^{2,25,54,55}. However, populations of piscivorous fish require abundant herbivorous and corallivorous fish

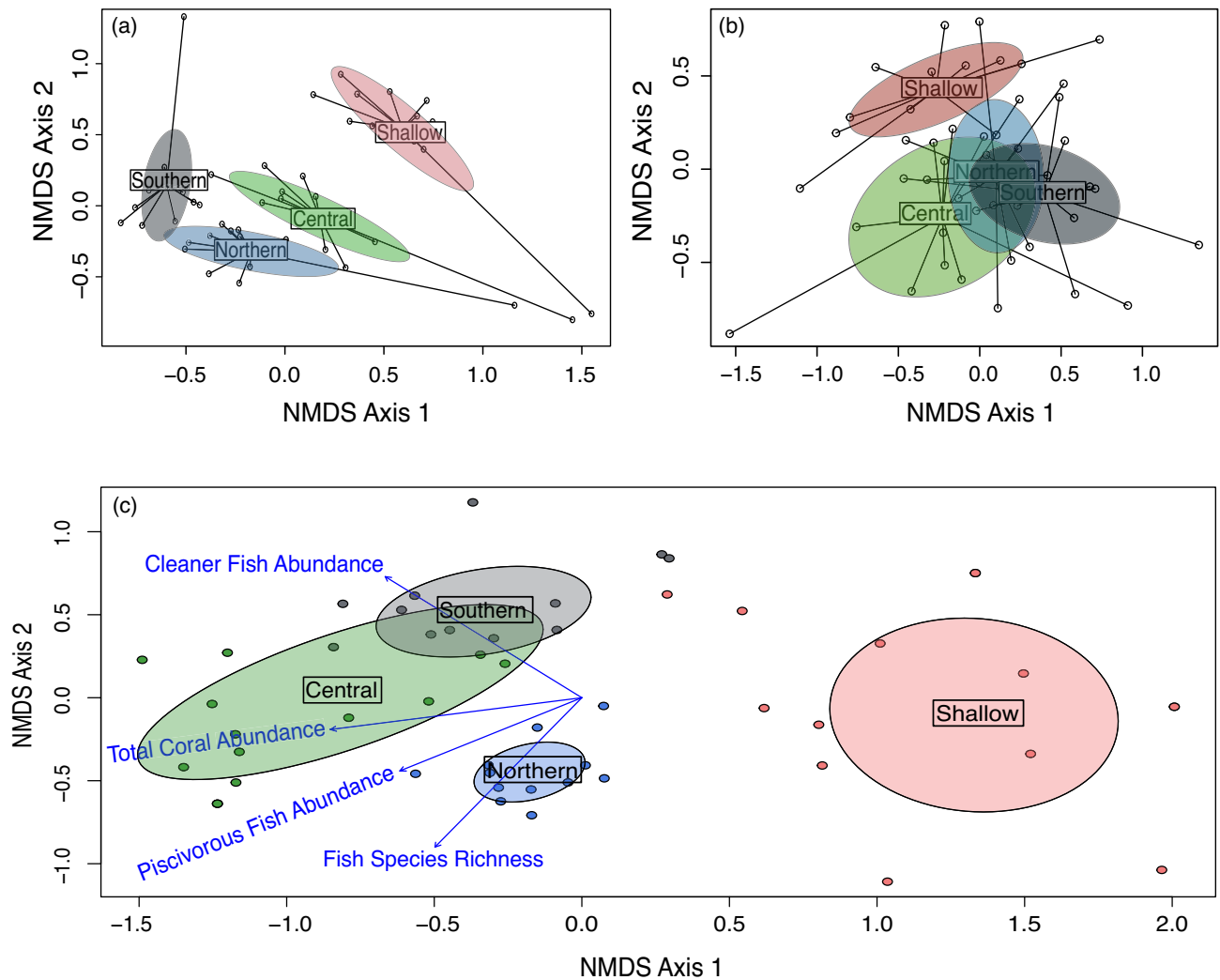


Fig. 3. Two-dimensional non-metric multidimensional scaling (NMDS) elliptical plot based on Bray Curtis dissimilarities. Data is derived from fish species (a), coral genera (b), and elasmobranch species (c) abundances recorded from belt transects and benthic images captured by a remote camera system positioned on four reef crests in southern Mozambique. Inset labels refer to the sampled reef sites. Ellipses surrounding inset labels indicate the space occupied by the elasmobranch community (95%), compared across the sampled sites. Blue arrows and labels represent the significant influences of functional metrics explaining the variance in ordination space. The length and direction of the arrows relative to each reef's ellipses indicates their degree of influence on the composition of each reef's elasmobranch community.

for consumption^{2,25,54,55}. If a reef cannot support abundant populations of herbivorous, corallivorous, and piscivorous teleost fish species, then it is unlikely to support many elasmobranch species since they generally occupy high trophic levels^{10,16,25,54}.

Many reef shark species occupy apex or meso-predator positions within the dynamics of a reef's ecology^{56–58}. The reef fish and elasmobranch communities on the northern reef were distinct from those we observed at the other three reefs^{14,16,40}. The richness and abundance of reef fish and the abundance of piscivorous fish were all found to be highest on the northern reef^{2,15,16}. The richness of reef fish and the abundance of piscivorous fish were identified as the principal factors underpinning the structure of the northern reefs' elasmobranch community which was found to be principally composed of reef sharks^{7,9,16}. As apex predator's reef sharks principally rely on a reef's teleost fish populations for daily foraging^{7,9,12,59}. Reef fish account for over 75% of the diet of grey reef (*C. amblyrhynchos*) and white tip (*T. obesus*) reef sharks which were the most abundant sharks that we observed overall^{7,9,12}. Studies in an Australian marine protected area have concluded that the predator-prey relationship between grey reef and white tip reef sharks is determined by the abundance and richness of reef teleosts^{7,9,10,12}, and our evidence supports these findings^{2,7,9,10,12,14–16}.

Mobula rays (*M. kuhlii*, *M. alfredi*, *M. birostris*), small eye stingrays (*M. microps*), white spotted guitarfish (*R. djiddensis*), bowmouth guitarfish (*R. ancylotoma*), and cleaner fish were most abundant on the southern reef^{5,60}. Mobula rays, small-eye stingrays, white-spotted guitarfish, and bowmouth guitarfish are regularly observed interacting with cleaner fish for long periods (hours) of time across the globe^{28,60,61}. Previous investigations

in our study area showed that these species are frequently observed in the vicinity of the southern reef^{5,60,61}. Mobuliids spend a lot of their time on reefs in southern Mozambique interacting with cleaner fish^{5,60} that provide services to remove ectoparasites^{5,28,60,62}.

The ecological composition of reef communities can be linked to physical characteristics such as the water depth and the proximity to the shore^{23–25}. Our analyses showed that the coral, fish, and elasmobranch communities on the shallow reef were distinct from those on the northern, central, and southern reefs^{2,10,16}. All the metrics that were used to describe the fish and coral communities (abundance of total coral, soft coral, hard coral, herbivorous fish, corallivorous fish, piscivorous fish, cleaner fish) were lowest on the shallow reef which is consistent with prior investigations^{23,54}. Three species (*N. caeruleopunctata*, *T. sinuspersici*, *A. leucospilus*) of ray were more likely to be observed on the shallow reef. These rays appear to be most abundant on shallow (< 30 m) inshore reefs close to the intertidal sandy substratum on which they forage^{55,63–65}.

The relative abundance of herbivorous fish and the coral community did not differ between the deeper/oceanic reefs (northern reef, central reef, southern reef)^{24,55,65}. Herbivorous fish consume algae that compete with corals for space^{16,65}. Losses in the abundance of herbivorous fish can trigger an overabundance of macroalgae which can suffocate the coral community [1^{9,15,16}]. That the relative abundance of corals and herbivorous fish was found to be consistent between our study sites indicates that their benthic communities may be in a similar condition^{15,16}. These results support the notion that the region's coral communities are generally in a state of good health^{1,9,16,40}.

Understanding how a reef's biological characteristics influence the structure of its elasmobranch community can help to identify the biological requirements of elasmobranchs that use reef habitats^{1,9}. Our study aimed to investigate the bioecological characteristics of coral reefs in southern Mozambique (Western Indian Ocean – WIO – region) to assess if they affect the habitat use of regional elasmobranch species. The shallow reef had a coral community that was independent from the reefs fringing the oceanic drop-off suggesting that the structure of the benthic community on reefs in Inhambane vary across the depth gradient^{23,24}, which led to differences in elasmobranch diversity⁹. The richness and relative abundance of fish species were assessed to be highest on the northern reef, which also hosted the highest abundance of piscivorous fish, including reef sharks^{7,9,16}. The southern reef hosted the second-highest abundance of fish and the greatest abundance of cleaner species^{2,9,10,16}. The elasmobranch community on the southern reef was mostly composed of Mobula rays and guitarfish, which are regularly observed interacting with cleaner species on reef systems for hours at a time^{5,60,61}.

Alterations in the functional metrics (e.g., relative abundance of fish, corals, herbivorous, corallivorous, piscivorous species etc.) of a reef's ecosystem can have dramatic implications for elasmobranch species^{7,9,16,40} by reducing the availability of prey, increasing competition, and in the long term, eliminate the reef as a viable habitat^{2,7,10,16}. Our results indicate that several functional metrics describing a reef's bioecological structure influence the shape of its associated elasmobranch community (2, 8, 12, 13). It appears that across relatively small spatial scales (< 50 km), the ecological state of a reef may alter the richness and abundance of elasmobranch species. As certain elasmobranch species appear to visit specific reefs with specific biological features in southern Mozambique, adopting regional coastal management strategies that reflect this reality would benefit vulnerable elasmobranch populations^{5,7,9,60}.

Data availability

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

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Author contributions

The investigation was developed and conceived by C.M. & S.O. L.G. & M.L. assisted with analysis, figure preparation and in developing the manuscript. No authors have competing interests.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to C.J.M.

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