



Elasmobranch species richness and assemblage composition in the world's largest shark sanctuary

Naomi F. Farabaugh^{1,*}, Mark E. Bond¹, Demian Chapman^{1,2}, Eric Clua^{3,4},
Simon Dedman¹, Alastair R. Harborne¹, Jeremy J. Kiszka¹, Michelle Heupel,⁵
Michael R. Heithaus¹

¹Institute of Environment, Department of Biological Sciences, Florida International University, Miami, FL 33199, USA

²Center for Shark Research, Mote Marine Laboratory, Sarasota, FL 34236, USA

³PSL, EPHE, CRIOBE USR3278 EPHE-CNRS-UPVD, P.O. Box 1013, 98729 Papetooi, French Polynesia

⁴Labex CORAIL, Université de Perpignan, 58 Avenue Paul Alduy, 66850 Perpignan, France

⁵Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania 7004, Australia

ABSTRACT: Indo-Pacific coral reefs host diverse assemblages of elasmobranchs from small-bodied mesopredators to apex predators that may vary in the amount of time they spend on reefs. Reef sharks and rays as a group are threatened by human activities and are facing widespread population declines, primarily due to fishing. These human factors may affect not only elasmobranch abundance, but also their assemblage composition. Thus, a better understanding of the factors associated with differences in species-specific abundances and assemblage structure across multiple spatial scales in relatively undisturbed systems could enhance the conservation of shark and ray populations on reefs generally. Here, we used baited remote underwater video stations to examine species richness and assemblage composition of elasmobranchs across forereefs in French Polynesia, the world's largest shark sanctuary. Boosted regression tree models revealed that island group, latitude, and island geomorphology had the greatest effect on elasmobranch species richness. Assemblages at most islands were dominated by blacktip reef sharks *Carcharhinus melanopterus* and grey reef sharks *C. amblyrhynchos*, while rays were generally rare, although there was significant spatial variation in elasmobranch assemblage composition. This variation was not associated with human factors, and appears to reflect species interactions and species-specific responses to environmental variation. Further studies on species interactions (facilitation, competition, and predation) among elasmobranchs will provide a better functional understanding of drivers of elasmobranch species composition on individual coral reefs.

KEY WORDS: Baited remote underwater video station · BRUVS · Species richness · Marine predators · Boosted regression tree · BRT

1. INTRODUCTION

Local assemblages are composed of subsets of species that are part of a regional species pool (Cornell & Harrison 2014). Elucidating how environmental conditions influence the composition and abundance of these local assemblages is important to better understanding ecosystem function (e.g. Gagné et al. 2020). Furthermore, investigations of how multiple factors interact to determine community composition in the

absence of human impacts will help in developing realistic targets for restoration of degraded systems (e.g. Prach et al. 2019)

In coral reef ecosystems, previous studies have shown that local species assemblages can be influenced by the scale of investigation, species-specific adaptations to environmental conditions, mobility of taxa, larval supply, and species interactions (Cornell & Harrison 2014). For example, benthic community composition and structure (Graham & Nash

2013), sea surface temperature (SST), exposure to extreme events (Ceccarelli et al. 2023), net primary productivity (NPP) (e.g. Williams et al. 2015), fishing (e.g. Guillemot et al. 2014), and the abundance and biomass of predators (Boaden & Kingsford 2015) can drive teleost assemblage abundance and structure.

Indo-Pacific coral reefs host an array of both resident and transient elasmobranchs (sharks and rays) that occupy multiple ecological roles from small-bodied to apex predators (Osgood & Baum 2015, Chapman et al. 2022). As a group, reef sharks (the species that are mostly resident on reefs) are threatened by human activities, particularly fishing, and have experienced widespread population declines (e.g. Robbins et al. 2006, Ferretti et al. 2010, Roff et al. 2018). A recent global survey of coral reefs found that reef sharks were absent on almost 20% (69 of 371) of reefs sampled, and over half of the nations sampled (34 of 58) had abundances lower than regional expectations (MacNeil et al. 2020). Lower abundances of sharks occurred in areas where gillnets and longlines are used and where fisheries management policy and/or enforcement is relatively weak. Even relatively common species have experienced widespread declines, with blacktip reef sharks *Carcharhinus melanopterus* and grey reef sharks *C. amblyrhynchos* being absent from 46.9 and 40.8% of reefs, respectively (Simpfendorfer et al. 2023). Conversely, well designed protected areas and effective fisheries management, especially in conjunction with one another, have strong conservation benefits for reef sharks (Goetze et al. 2024). Additionally, management and socio-economic factors also influence assemblage composition, with heavily impacted reefs showing a shift from shark-dominated assemblages to ray-dominated ones (Simpfendorfer et al. 2023). At the highest levels of human impact, even rays become scarce (Simpfendorfer et al. 2023).

While these studies provide an important global perspective, it is important to understand the factors driving the relative abundance and assemblage composition of elasmobranch species across multiple spatial scales. While the abundance of reef predators, including elasmobranchs, is associated with variation in teleost assemblages (e.g. Boaden & Kingsford 2015, Barley et al. 2017, Desbiens et al. 2021), the importance of various elasmobranch predators on reefs remains uncertain (e.g. Roff et al. 2016, Ruppert et al. 2016, Heithaus et al. 2022). Part of the challenge in assessing the ecological roles and importance of elasmobranchs on reefs is that the widespread declines of predators may have led to the degradation of their impacts on reefs before data to assess the importance

of these predators to reefs could be acquired (e.g. Roff et al. 2016, Desbiens et al. 2021, Heithaus et al. 2022, Dedman et al. 2024). To set appropriate restoration targets, it is therefore also of value to understand factors associated with variation in relative abundance and assemblage composition of elasmobranchs when human impacts are relatively low.

French Polynesia is the world's largest shark sanctuary. It banned lethal shark fishing and the trade and export of shark products, with the exception of a single species, in 2006. In 2012, this exception was removed and even sharks caught as bycatch must be immediately released (Ward-Paige 2017). French Polynesia supports robust shark populations that are minimally impacted by anthropogenic factors (MacNeil et al. 2020, Farabaugh et al. 2024). Despite apparently small human impacts, there is marked variation in the relative abundance of reef sharks, in general, across French Polynesia that is associated with environmental factors, especially island geomorphology (e.g. atolls vs. high islands) (Farabaugh et al. 2024). However, species richness and assemblage composition across the array of reef types and environmental conditions in French Polynesia remain poorly understood.

Here, we expand upon previous studies using baited remote underwater video stations (BRUVVs) to assess species richness, assemblage composition, and species-specific patterns of association of elasmobranchs across environmental and anthropogenic gradients on forereefs in the Indo-Pacific coral reef system of French Polynesia, which features low human impacts and no current direct fishing pressure on sharks.

2. MATERIALS AND METHODS

2.1. Site description

French Polynesia, in the south-central Pacific (Fig. 1), has an exclusive economic zone covering ca. 5 030 000 km². It consists of 5 archipelagos: the Marquesas Islands, the Tuamotu Archipelago, the Society Islands, the Gambier Islands, and the Austral Islands (Fig. 1). For this study, the islands were divided into 6 groups based on geography: Marquesas, Leeward Society Islands, Windward Society Islands, West Tuamotus, East Tuamotus (including the Gambier Islands), and Austral Islands. Briefly, the Windward Society Islands have the highest human population. The majority of islands in the Society and Austral Islands are high islands, but each features

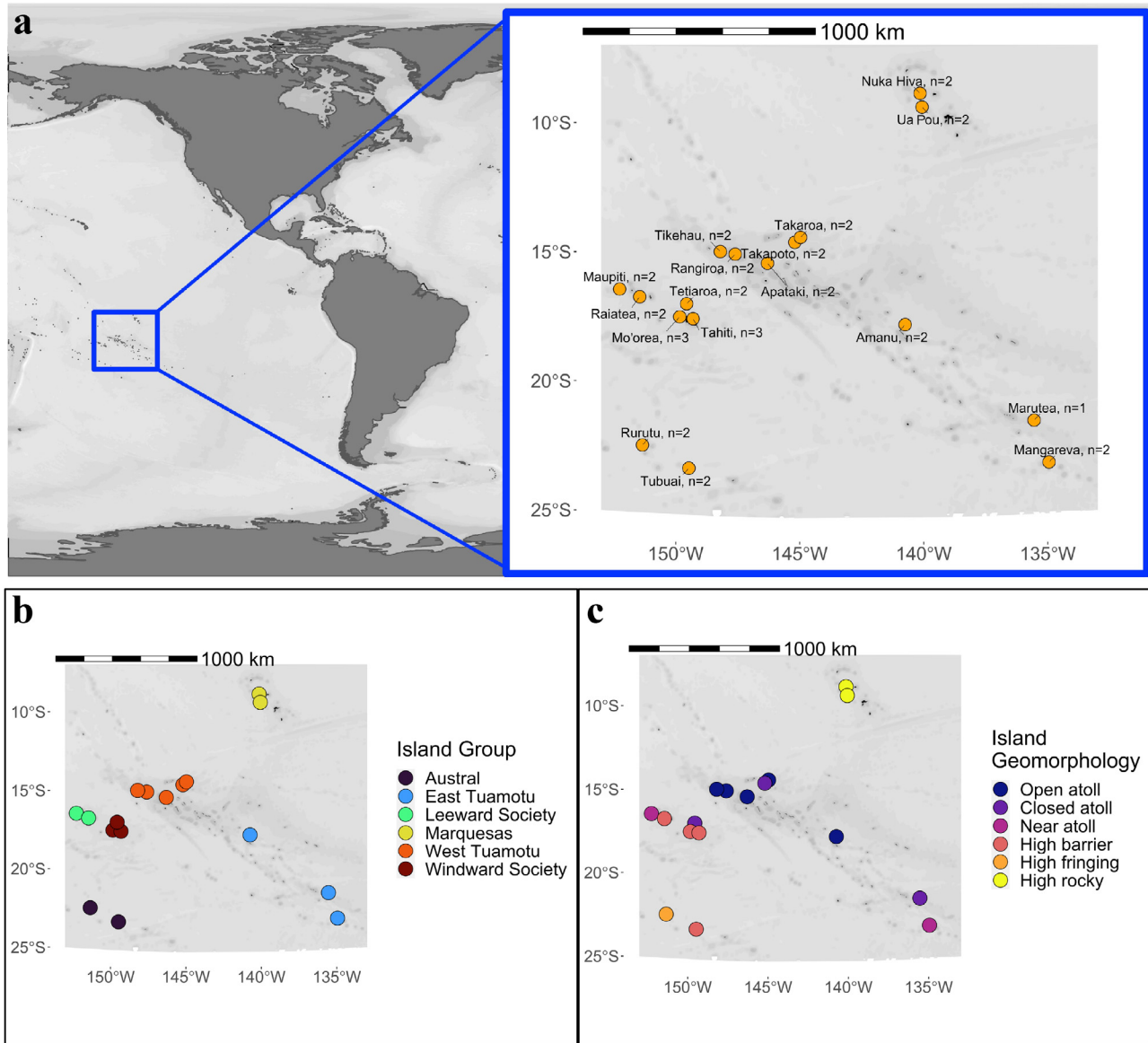


Fig. 1 continued on next page

Fig. 1. Sampling locations in (a) French Polynesia, representing (b) 6 island groups, with (c) varied geomorphologies, that included (d) atolls and high islands. Locations varied in (e) net primary productivity (NPP), (f) mean sea surface temperature (SST), and (g) market gravity

several atolls. In contrast, the Tuamotus are composed largely of atolls and near atolls. The Marquesas Islands are distinct in being high islands with rocky, rather than coral, reefs and much greater productivity than other island groups. The high relative abundances of sharks in French Polynesia (Ward-Paige & Worm 2017, MacNeil et al. 2020, Farabaugh et al. 2024) suggest that the shark sanctuary has been broadly successful. Furthermore, reconstructed shark catches indicate that French Polynesia has lower shark catches than other shark sanctuaries in the region, despite having a large EEZ (Ward-

Paige 2017). Even before the sanctuary was implemented, elasmobranchs only made up a small percentage of total marine fisheries catches (Farabaugh et al. 2024, see Fig. S1 in their Supplement). A more detailed site description can be found in Farabaugh et al. (2024).

2.2. Field methods

BRUVSs were used to survey 35 reefs, defined as an area of ca. 4 km² with continuous coral reef

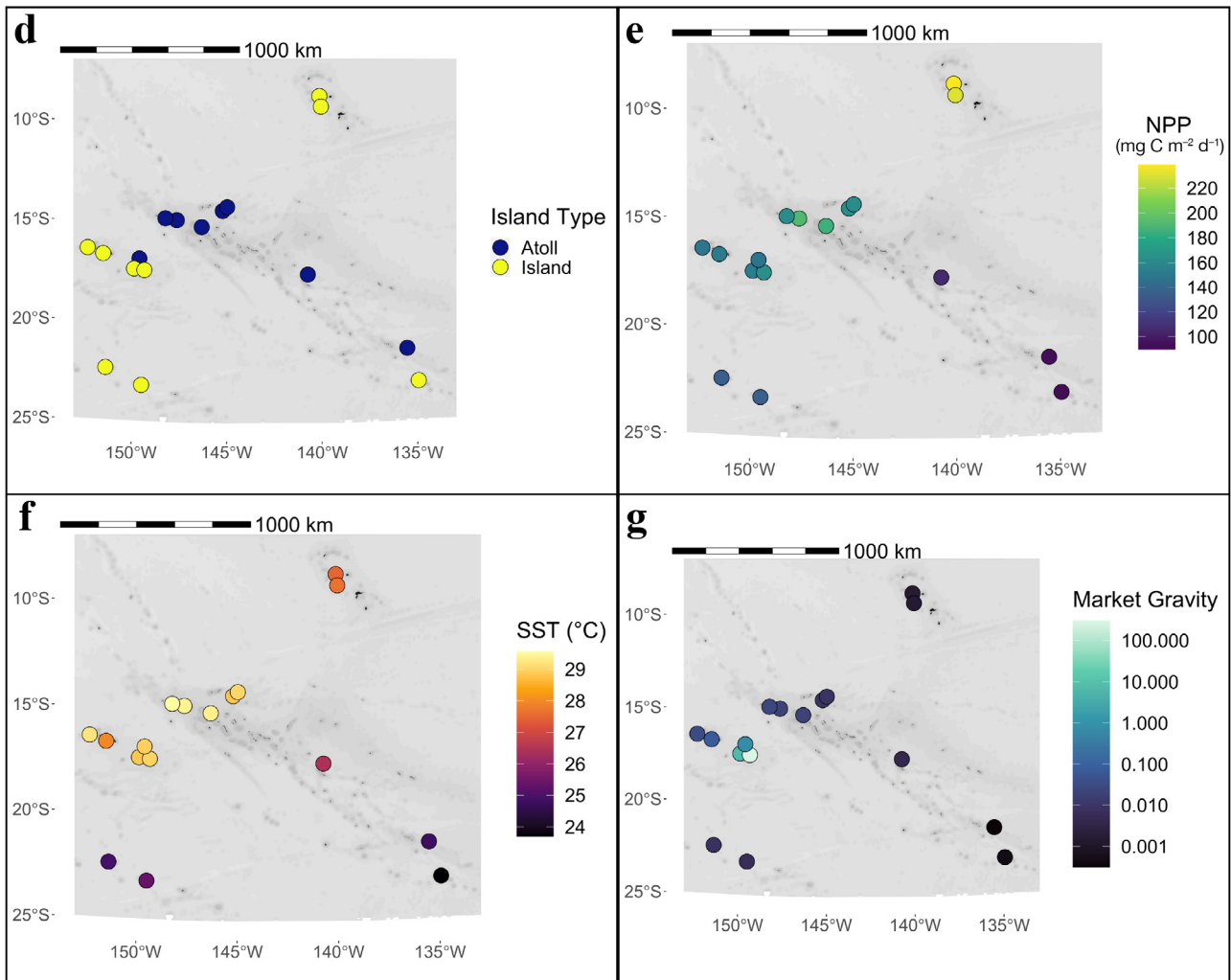


Fig. 1. (continued)

habitat, across 17 different islands/atolls (hereafter 'islands') (Fig. 1, Table 1). Islands were categorized according to their geomorphology as open atoll, closed atoll, near atoll, high barrier, high fringing, or high rocky. Open atolls have boat-navigable passages. Closed atolls lack such passages, although smaller shallow-water passes still allow more limited movement of water and animals between the forereef and lagoon. Near atolls, sometimes called 'pseudo-atolls,' are high islands that occupy a very small area of the lagoon inside their annular reef (Davis 1928, Goldberg 2016). Other high islands were classified by their reef types: barrier reefs with lagoons, fringing reefs with no lagoon, and rocky instead of coral reefs (Table 1).

Each BRUVS consisted of a GoPro Hero4 Silver or GoPro Hero+ action camera (<https://www.gopro.com>) mounted to an aluminum frame with a bait arm (ca. 1.5 m in length) extending in front of the

camera with a container holding ca. 1 kg of oily fish bait (yellowfin tuna, small inshore fish, fish heads and scraps, typically tuna or sardines). Current direction was determined using dye tabs, and BRUVSs were positioned so the camera faced down-current. Deployment of BRUVSs occurred during daylight hours on forereefs at depths of 9–35 m. Each BRUVS set had a minimum soak time of 60 min, with deployments up to 90 min. No 2 BRUVSs were deployed within 500 m of one another within a sampling day to prevent autocorrelation, and each reef had a minimum of 42 deployments (mean = 58; max = 70).

All sampling took place in 2016 and 2017. Sampling at individual reef locations usually took place over a single period of <10 d (max. 37 d). During deployment of each set, the bottom depth was recorded, SST was measured using a YSI Pro 2030 model (<https://www.ysi.com/>), and water visibil-

Table 1. Characteristics of the sampled islands

Site	No. of reefs sampled	Island geomorphology	Island group	Market gravity	Season sampled	Lagoon size (km ²)	Sets per island
Amanu	2	Open atoll	East Tuamotu	0.0041	Dry	240	117
Apataki	2	Open atoll	West Tuamotu	0.0182	Wet	706	134
Mangareva	2	Near atoll	East Tuamotu	0.0005	Dry	407	108
Marutea	1	Closed atoll	East Tuamotu	0.0003	Dry	112	55
Maupiti	2	Near atoll	Leeward Society	0.0330	Wet	44	113
Mo'orea	3	High barrier	Windward Society	6.6582	Wet	382	184
Nuka Hiva	2	High rocky	Marquesas	0.0015	Wet	0	106
Raiatea	2	High barrier	Leeward Society	0.0690	Dry	198	124
Rangiroa	2	Open atoll	West Tuamotu	0.0199	Wet	1446	119
Rurutu	2	High fringing	Austral Islands	0.0077	Wet	0	103
Tahiti	3	High barrier	Windward Society	303.9799	Wet	154	172
Takapoto	2	Closed atoll	West Tuamotu	0.0095	Dry	85	122
Takarua	2	Open atoll	West Tuamotu	0.0086	Dry	93	109
Tetiaroa	2	Closed atoll	Windward Society	0.7265	Wet	16	115
Tikehau	2	Open atoll	West Tuamotu	0.0239	Wet	461	122
Tubuai	2	High barrier	Austral Islands	0.0060	Dry	85	104
Ua Pou	2	High rocky	Marquesas	0.0016	Wet	0	110

ity was visually estimated to the nearest meter up to 15 m.

2.3. Video data extractions

Using the FinPrint Annotator (v1.1.44.0) (<https://github.com/GlobalFinPrint/Finprint-Annotator>), each video was viewed to 90 min or to the end of the video with a minimum length of 60 min. Videos were reviewed by at least 2 annotators, and all observations were checked by an expert reviewer to confirm identifications and resolve inconsistencies. Animal identifications were made to the species level in 3340 of 3485 (95.8%) of observations.

Relative abundance was measured using the maximum number of individuals of each target species seen in a single frame for each video (MaxN). MaxN avoids double counting the same individual that might enter and exit the field of view multiple times, and is the standard for reporting relative abundance for BRUVS data (Cappo et al. 2004, MacNeil et al. 2020). Overall MaxN for each set was calculated by summing the MaxN for each species seen in that set. The number of unique elasmobranch species seen in each set was counted for each set. Individuals that could not be identified down to species (e.g. 'unknown shark', 'unknown ray', 'unknown mobulid ray') were only included in species counts and MaxN calculations if there was no other observation of that type during a set. For instance, an observation of an unknown mobulid would only be included if no other

mobulid rays were seen in that set. The number of unique species seen at each reef was also calculated using this method.

2.4. Other environmental and anthropogenic data

Open-access satellite-based observations (Ocean Productivity, Oregon State University, <http://orca.science.oregonstate.edu/index.php>) using the vertically generalized production model (Behrenfeld & Falkowski 1997) were used to determine NPP. NPP values of each reef were averaged over the 2 sampling years (2016–2017) from the nearest neighbor pelagic cell for each location (Gove et al. 2013). SST was taken during each deployment and then averaged to obtain an average SST per reef. Market gravity (Cinner et al. 2018) was selected as the metric for human pressure because it outperformed other metrics (human population density and human population size) in preliminary analyses. Consistent with Cinner & Maire (2018), market gravity was calculated as the population of the nearest settlement divided by the squared travel time to that reef location. Gravity values for each reef were produced by averaging gravity values from individual BRUVS sets. These covariates were chosen to be consistent with previous studies on shark relative abundance in French Polynesia (Farabaugh et al. 2024) as well as wider literature on factors that influence assemblage and community composition of predators on coral reefs.

2.5. Assessing co-occurrence and species habitat associations

Pairwise chi-squared testing using presence/absence was done to examine if species co-occurred on sets more than expected. To avoid unequal sample sizes, we standardized sets to 60 min soak times. Based on preliminary analysis, and due to infrequency of sightings, the 2 stingray species (pink whiprays *Pateobatis fai* and blotched fantail rays *Taeniurops meyeri*) were grouped together, as were all mobulid ray species (oceanic manta *Mobula birostris*, manta *M. alfredi*, and Chilean devil ray *M. tarapacana*). We used a significance level of $\alpha = 0.05$, and Pearson's residuals were used to determine where species had positive and negative associations.

Species' associations with individual islands and island groups were examined using chi-squared tests on the sum of MaxN for abundance and species richness. We took a random subsample of each of these groups to avoid unequal sampling sizes so that the same number of sets were examined for each island ($n = 103$) and island group ($n = 207$). Marutea was excluded from the island analysis due to low sample sizes. All sets were standardized to have a 60 min soak time and Pearson's residuals were used to examine species associations with locations.

2.6. Assessing similarity of species assemblages

To examine the similarity of species assemblages across reefs, hierarchical cluster analysis of mean MaxN was performed using the R packages 'vegan' (Oksanen et al. 2012) and 'Pvclust' (Suzuki & Shimodaira 2006). 'Pvclust' allowed us to determine significance of splits in the dendrogram by applying bootstrapping resampling techniques to obtain a p-value corrected for bias (Suzuki & Shimodaira 2006). The correlation distance method was used.

2.7. Modeling species richness

Boosted regression trees (BRTs) were used to determine the relative influence of predictor variables on the number of unique elasmobranch species seen at each reef. BRTs are a machine learning technique that accounts for high proportions of variability despite complex multivariate relationships by using boosting algorithms to create an ensemble from many regression trees (Elith et al. 2008). BRTs can handle complex non-linear relationships, are not sensitive to collinearity among variables, and account for interac-

tions between predictor variables (Elith et al. 2008, Abeare 2009, Jouffray et al. 2019). Island geomorphology, island group, latitude, market gravity, NPP, SST, water visibility, lagoon size, and lagoon depth were used as predictor variables. Sampling season and the time that BRUVSs were without bait (in rare instances where bait was broken and removed by animals) were also included as predictor variables.

Models were fitted using R version 4.0.2 (R Core Team 2022) with the package 'gbm.auto' (Dedman et al. 2017). This package automates the analysis, model evaluation, and plotting processes for BRTs. The Poisson distribution was selected based on visual inspection. We determined optimal model parameters (hyperparameters) for tree complexity, bag fraction, and learning rate by testing across a series of values (1, 2, 3, 4, 5 for tree complexity; 0.0005, 0.001, 0.005, 0.01 for learning rate; and 0.5, 0.55, 0.60, 0.65, 0.7, 0.75 for bag fraction). We used the combination of model parameters that yielded the smallest model deviance and the best correlation score between training data and testing data for final models. We focus only on variables with relative influences above that expected by chance (100/number of variables) for discussion purposes (Müller et al. 2013). Soak time was used to apply an offset to account for differences in video length from set to set. All values are reported as means \pm SD.

2.8. Modeling assemblages

To link the multivariate shark and ray assemblage to the environmental variables considered for species richness, we used distance-based linear models (DISTLMs) and visualized the models using distance-based redundancy analysis (dbRDA) (Legendre & Anderson 1999, McArdle & Anderson 2001). Similarity values among all individual BRUVSs were calculated using the Bray-Curtis statistic without any data transformation. DISTLMs used the 11 biophysical variables described for the BRT analyses, with data blocked at the reef and island group scale as necessary. Models were selected using the 'BEST' procedure based on values of Akaike's information criterion (AIC). Analyses were conducted using the DISTLM and dbRDA routines in PRIMER v 7.0.23 with PERMANOVA (Clarke & Gorley 2015).

3. RESULTS

A total of 16 species of elasmobranchs, including 10 shark and 6 ray species, were recorded on the 2017

BRUVSs analyzed. Sharks were more abundant than rays at all islands, and at least 1 shark was seen at every reef. Rays were absent from 16 of 35 (45.7%) reefs and 4 islands. On one island (Ua Pou), more ray species were observed than shark species, despite the fact that sharks were overall more abundant (Fig. 2). There was a general latitudinal pattern in island-level species richness, with lower species richness at southern islands (Tubuai, Rurutu, and Mangareva) and highest species richness to the north (Nuka Hiva, Ua Pou, and Tikehau). The average number of elasmobranch species seen at each BRUVS was 1.67 ± 0.99 , with up to 5 species being sighted in a single video. The number of elasmobranch species sighted at each reef ranged from 2 to 11, with just under 6 elasmobranch species seen on average at each reef (5.91 ± 2.16).

Blacktip reef sharks were the most abundant and frequently sited species, followed by grey reef sharks (Table 2). Both species were recorded at all islands and on 34 of the 35 reefs. Great hammerheads *Sphyrna mokarran* were the least abundant species and were only seen in the West Tuamotus. No species were seen at fewer than 2 separate islands, although 4 other species (Chilean devil ray, oceanic manta, blotched

fantail ray, and silvertip shark *Carcharhinus albimarginatus*) were seen at only 2 islands. Of these species, 3 were only seen within a single island group. Blotched fantail rays and oceanic manta were only positively identified in the Marquesas, where rays were more abundant overall and made up a higher proportion of observations than in any other location (Fig. 3).

3.1. Species assemblages

Hierarchical cluster analysis examining species assemblages separated reefs into 5 significant clusters (Fig. 4). All nodes within each cluster had p-values ≤ 0.05 , indicating that all nodes within clusters were significantly different from other outgroups within that cluster. While reefs from the same island were always in the same overall cluster, they were not always the most closely related reef within that cluster. All reefs from the Windward Society Islands and the Eastern Tuamotus had assemblages that clustered together, although this pattern did not hold for other island groups. Rurutu and Tubuai in the Austral islands were separated, for example, with species

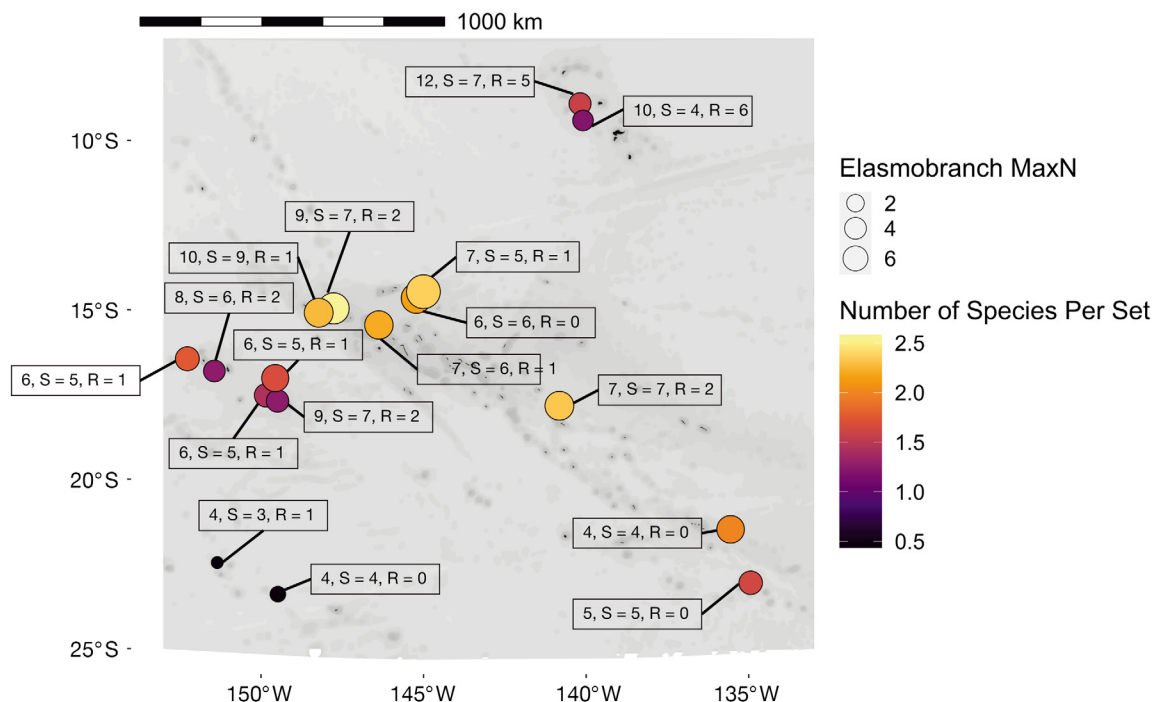


Fig. 2. Relative abundance and number of elasmobranch species observed at sampling islands in French Polynesia. Mean MaxN (i.e. the maximum number of individuals of each target species seen in a single frame for each video) of elasmobranchs at each island is represented by the size of the point, while the point color represents the mean number of species observed per set. The number of species observed in total at each island is indicated via the label and then broken down into total number of shark (S) and ray (R) species

Table 2. Elasmobranch species observed on baited remote underwater video stations. IUCN: International Union for Conservation of Nature and Natural Resources; MaxN: maximum number of individuals of each target species seen in a single frame for each video; LC: Least concern; NT: Near Threatened; VU: Vulnerable; EN: Endangered; CR: Critically Endangered; NA: not applicable. Primary habitats determined by the habitat description of Ebert et al. (2021), and consistent with the definition of reef sharks and rays by Chapman et al. (2022)

Scientific name	Common name	Primary habitat	IUCN status	Mean MaxN	SD MaxN	% Sets present	% of observations	# Reefs present
<i>Carcharhinus melanopterus</i>	Blacktip reef shark	Reef	VU	1.541	1.394	77.54	44.88	34
<i>Carcharhinus amblyrhynchos</i>	Grey reef shark	Reef	EN	0.890	1.514	42.29	24.48	34
<i>Triaenodon obesus</i>	Whitetip reef shark	Reef	VU	0.259	0.492	23.80	13.77	33
<i>Negaprion acutidens</i>	Sicklefin lemon shark	Reef	EN	0.109	0.366	9.27	5.37	26
Shark spp.	Unknown shark	NA	NA	0.059	0.261	5.55	3.21	30
<i>Nebrius ferrugineus</i>	Tawny nurse shark	Reef	VU	0.046	0.254	3.72	2.15	12
<i>Aetobatus ocellatus</i>	Ocellated eagle ray	Pelagic	VU	0.028	0.238	2.13	1.23	19
<i>Carcharhinus limbatus</i>	Common blacktip shark	Transient	VU	0.025	0.172	2.28	1.32	11
<i>Taeniurops meyeri</i>	Blotched fantail ray	Benthic	VU	0.017	0.134	1.69	0.98	4
Ray spp.	Unknown ray	NA	NA	0.010	0.210	0.55	0.32	7
<i>Pateobatis fai</i>	Pink whipray	Benthic	VU	0.006	0.086	0.59	0.34	5
<i>Mobula birostris</i>	Oceanic manta	Pelagic	EN	0.006	0.083	0.55	0.32	3
Manta spp.	Unknown manta	Pelagic	NA	0.006	0.083	0.55	0.32	4
<i>Mobula</i> spp.	Unknown mobulid	Pelagic	NA	0.006	0.083	0.55	0.32	5
<i>Sphyrna lewini</i>	Scalloped hammerhead	Pelagic	CR	0.005	0.077	0.45	0.26	6
<i>Galeocerdo cuvier</i>	Tiger shark	Transient	NT	0.004	0.063	0.40	0.23	7
<i>Carcharhinus albimarginatus</i>	Silvertip shark	Reef	VU	0.003	0.054	0.30	0.17	3
<i>Mobula alfredi</i>	Reef manta	Pelagic	VU	0.002	0.050	0.25	0.14	4
<i>Mobula tarapacana</i>	Chilean devil ray	Pelagic	EN	0.002	0.044	0.20	0.11	3
<i>Sphyrna mokarran</i>	Great hammerhead	Transient	CR	0.001	0.039	0.15	0.09	2

assemblages from Rurutu being distinct. The reefs from Tubuai formed a cluster with Takaroa in the Western Tuamotus, even though these islands have very different total abundances of elasmobranchs. Takaroa had the highest mean MaxN (6.75 ± 4.15) of any island and Tubuai was the second lowest (0.63 ± 0.83). Furthermore, these 2 sites had very different species richness overall, with 7 different species seen at Takaroa and only 4 at Tubuai, and the sites are around 1100 km apart. However, assemblages at both sites were dominated by grey reef sharks and were the only islands where grey reef sharks accounted for more than half of the total MaxN (Fig. 3).

With the exception of Maupiti, which had assemblages more similar to those in the Tuamotus, all islands in the Society Islands clustered together and were dominated by blacktip reef sharks with a higher proportion of sicklefin lemon sharks *Negaprion acutidens* than recorded at other islands. Nuka Hiva (Marquesas Islands) showed similar patterns and clustered with the Society Islands. Ua Pou, the other island in the Marquesas, formed a unique cluster that featured a very high proportion of rays (Figs. 3–5).

Chi-squared analyses revealed spatial patterns of species relative abundance (Fig. 5; Figs. S2–S7 in the

Supplement at www.int-res.com/articles/suppl/m753p155_supp.pdf). Rays, common blacktip sharks *Carcharhinus limbatus*, silvertip sharks, and scalloped hammerhead sharks *Sphyrna lewini* were strongly associated with the Marquesas and exhibited no significant positive associations with any other island groups. Grey reef sharks occurred far less than expected in the Marquesas (Fig. 5a; Fig. S2) and Society Islands (Fig. 5d,e; Figs. S3 & S4), but more often than expected in the Tuamotus (Fig. 5b,c; Figs. S5 & S6). Blacktip reef sharks showed the opposite pattern, being more common than expected in the Society Islands and less common in the Tuamotus and Austral Islands (Fig. 5). This pattern was also present at the island level. Grey reef sharks and blacktip reef sharks had significant and inverse patterns of presence or absence at 7 of the 16 analyzed islands, and inverse associations, though not strong ones, at another 7 islands (Figs. S2–S7). Sicklefin lemon sharks and grey reef sharks appear to have largely inverse distributions. Sicklefin lemon sharks were seen less than expected in the Tuamotus and more than expected in the Windward Society Islands (Fig. 5). At the island level, sicklefin lemon sharks and grey reef sharks showed negative associations at all but 1 island, although not all of these associations were strong (Figs. S2–S7).

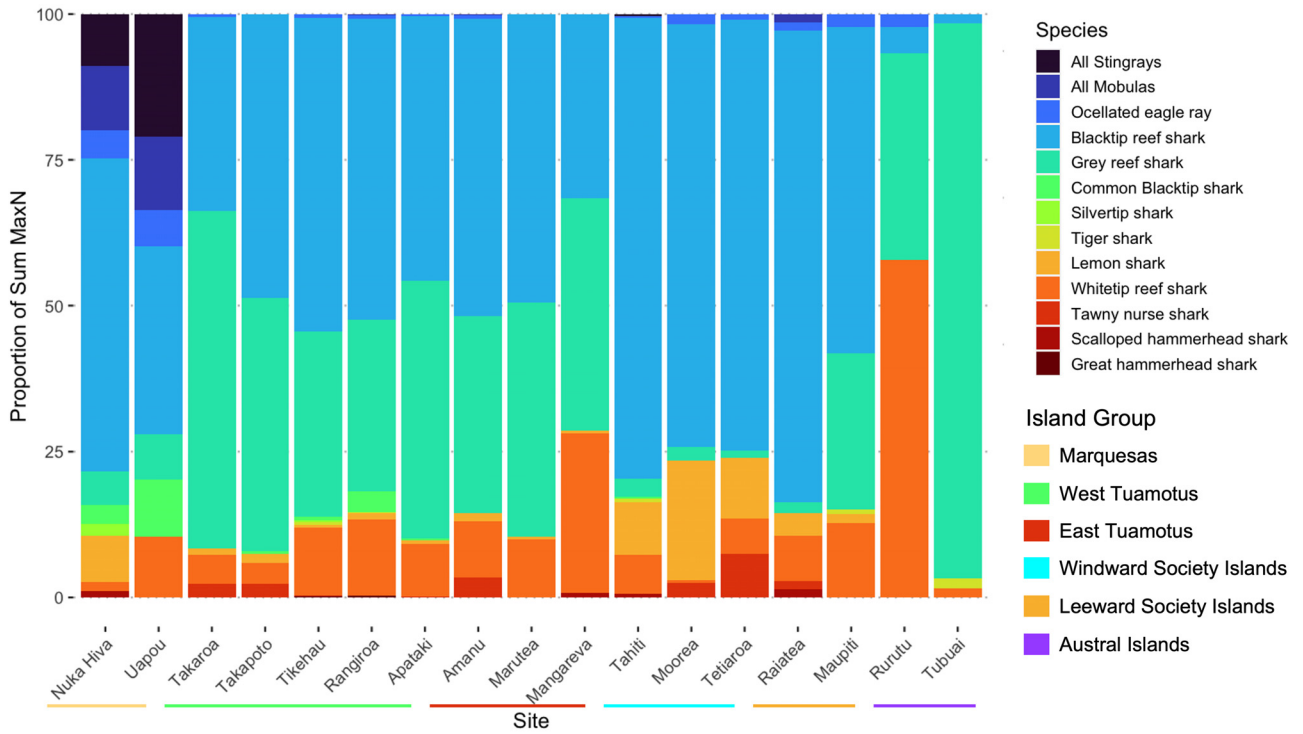


Fig. 3. Proportion of relative abundance made up by elasmobranch species observed at islands in French Polynesia. Island groups are denoted by colored lines under each site

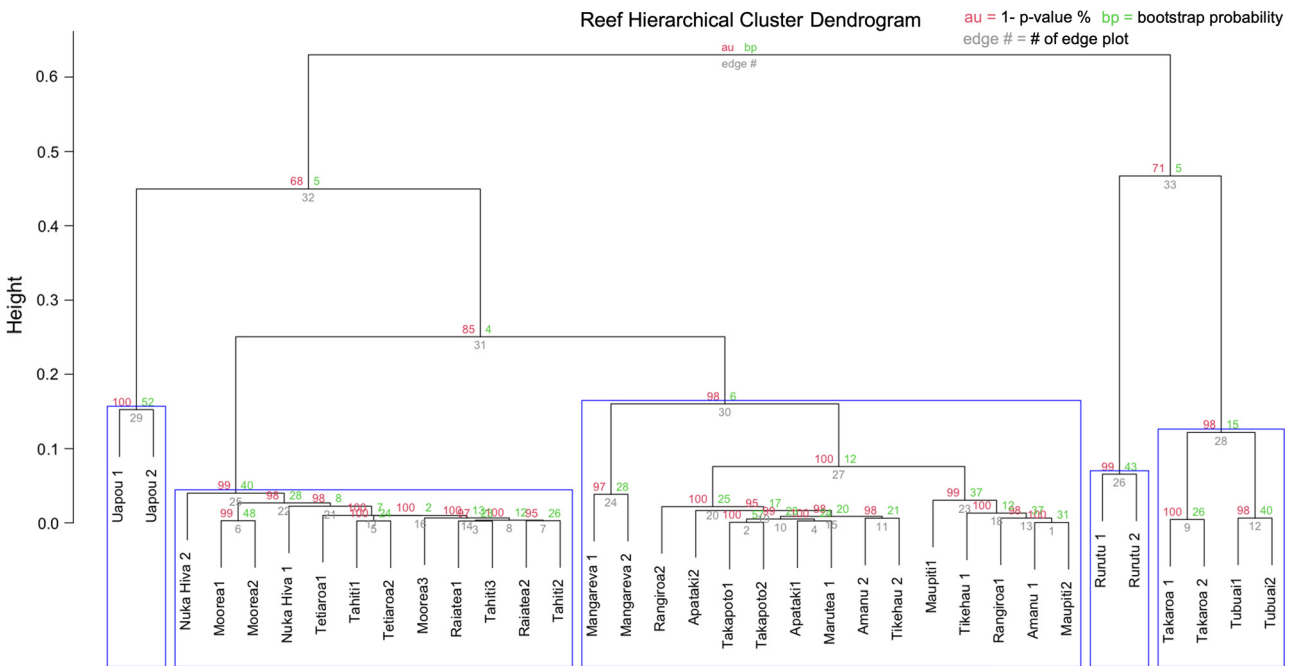


Fig. 4. Hierarchical cluster dendrogram examining species assemblages as determined by mean MaxN for each reef. The significance of each split is assessed by an approximately unbiased (AU) p-value and represented as 1 minus the p-value, noted on the upper left of each node in red. On the right in green is the bootstrapping probability (BP), the frequency a cluster appears in the bootstrapping replicates. The largest cluster with a node with a significant p-value (at $\alpha = 0.05$) is boxed in blue. Additional information about curve fitting for clusters is provided in Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m753p155_supp.pdf; the plot number for this can be found below each node in gray

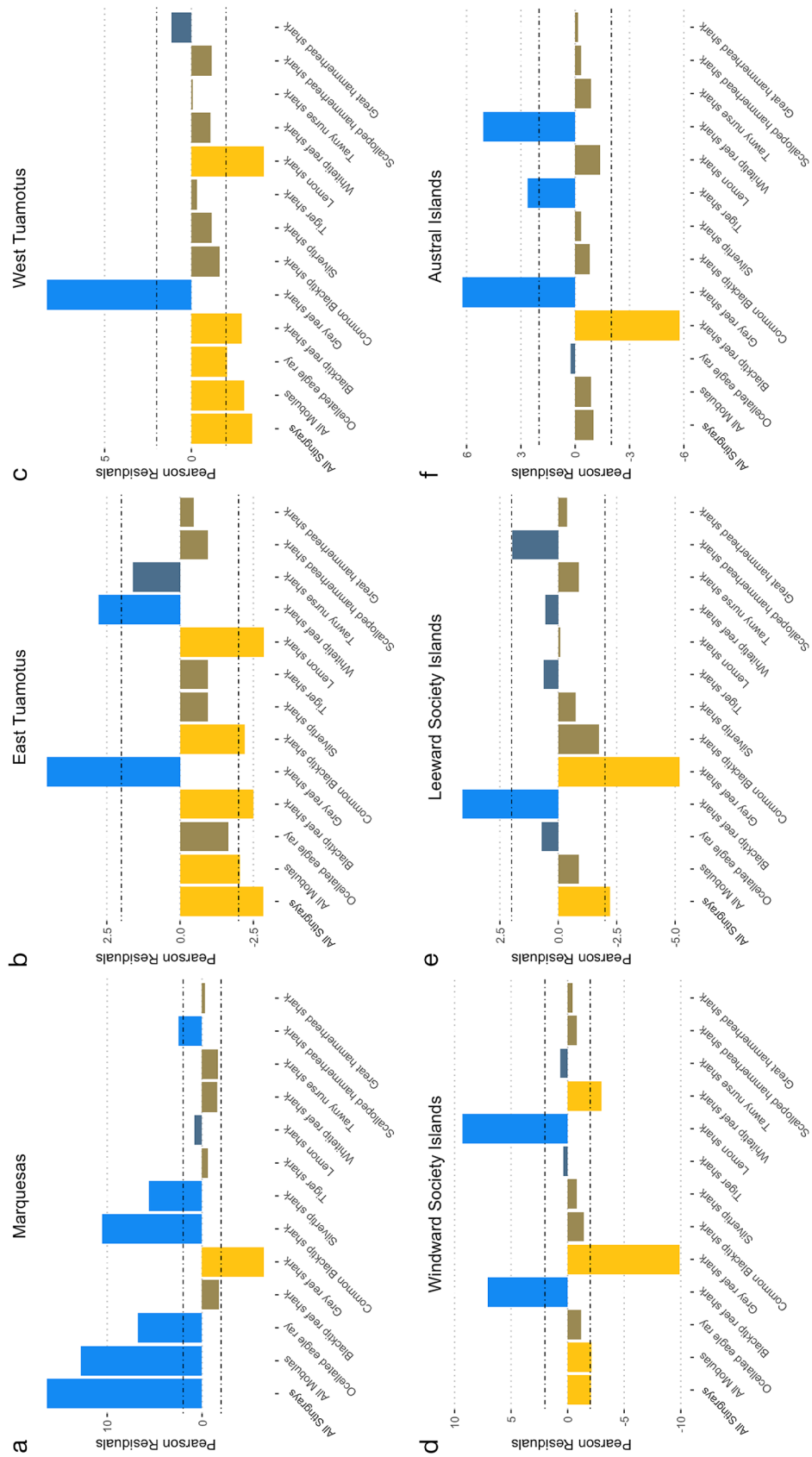


Fig. 5. Pearson's residuals from chi-squared test comparing species mean MaxN at different island groups. Dot-dash lines indicate thresholds: Pearson's >2 indicates a significant positive association (shown in bright blue), indicating that a species was observed at that island more than expected; conversely, Pearson's <-2 indicates a significant negative association (shown in bright yellow), indicating that the species was observed at that island less than expected. Species that showed no significant association are in dull blue and yellow

3.2. Species co-occurrence

Pairwise chi-squared comparisons of species presence on individual videos revealed that several species co-occurred significantly more than expected (Fig. 6). Blacktip reef sharks, grey reef sharks, and whitetip reef sharks *Triaenodon obesus*, the most abundant species, were strongly positively associated with one another. Grey reef sharks also co-occurred with tawny nurse sharks *Nebrius ferrugineus* more than expected, while blacktip reef sharks co-occurred significantly with sicklefin lemon sharks. However, sicklefin lemon sharks and grey reef sharks showed a strong disassociation, occurring together on individual videos far less than would be expected (Fig. 6). Common blacktip sharks, mobulid rays, and stingrays had strong positive associations (Fig. 6).

3.3. Drivers of species richness

The BRT model exploring the number of elasmobranch species per reef was not zero-inflated and accounted for ~67% of the variation seen among reefs (Fig. 7). Island group was the most influential factor, with a relative influence of 32% (Fig. 7). The Marquesas had the most species observed per reef, with a mean 10.25 ± 0.96 and 13 species seen overall. The West Tuamotus (mean species per reef = 6.4 ± 1.23) and Leeward Society Islands (mean species per reef = 5.8 ± 1.0) had 12 and 9 species of elasmobranchs, respectively. The Windward Society Islands had fewer elasmobranch species seen on average per reef (5.5 ± 0.9) and 9 elasmobranch species overall. The East Tuamotus (mean species per reef = 4.6 ± 1.5) had 8 species overall, while the least speciose island

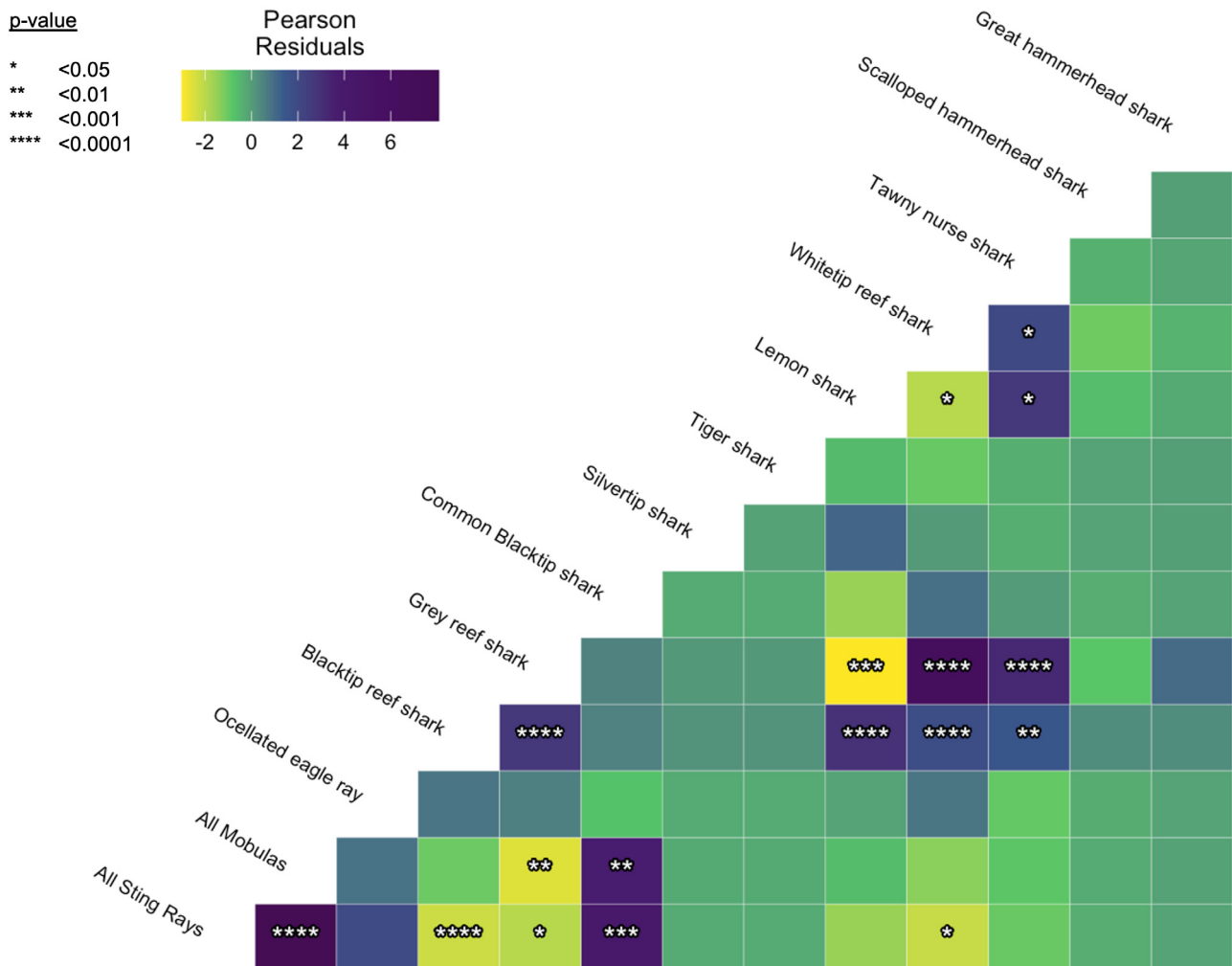


Fig. 6. Heatmap of Pearson's residuals for pairwise chi-squared testing examining species co-occurrence on sets using presence/absence data. Species pairs with a significant association ($p < 0.05$) are indicated by a star and the number of stars indicates the level of significance

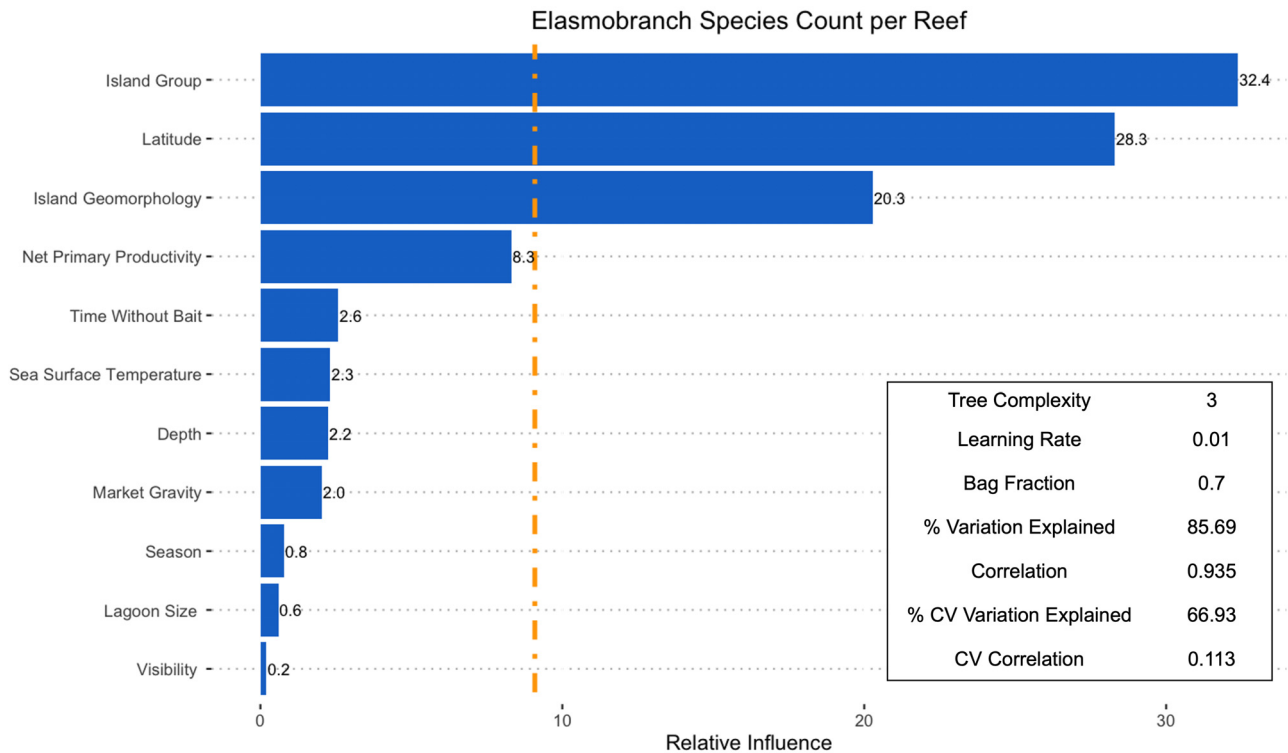


Fig. 7. Relative influence of all predictor variables in boosted regression tree models of total number of elasmobranch species seen per reef. Variables with relative influence greater than that indicated by the orange line have influence above that expected by chance ($100/\text{number of variables}$). Box shows model parameters and performance statistics. CV: cross validated

group, the Austral Islands, had only 6. On average, the Austral islands had 3 times fewer elasmobranch species per reef (mean species per reef = 3.0 ± 0.8) than the Marquesas.

Latitude was the second most influential factor, with a relative influence of ca. 28%. More northerly reefs tended to have greater species richness of elasmobranchs, with a sharp increase in number of species seen on reefs around 17° S, around the Society Islands, followed by a plateau at latitudes north of 15° S, which is around the northernmost islands of the Western Tuamotus (Fig. 8b).

Island geomorphology had a relative influence of ca. 20% (Fig. 7), with rocky reefs on high islands being the most speciose (mean species per reef = 10.2 ± 1.0), almost twice the average of open atolls (6.3 ± 1.5). These were followed by closed atolls (5.60 ± 0.89), high islands with barrier reefs (5.0 ± 1.6), and near atolls (4.5 ± 1.0). High islands with fringing reefs were the least speciose, with only an average of 3.5 ± 0.7 species per reef.

3.4. PERMANOVA models

Two model solutions could not be separated by AIC and included all variables or all variables except visibility ($R^2 = 0.300$). Other models within 2 AIC units of

these best models cannot be discounted (Burnham & Anderson 2004), but were similar and included most variables with the exception of dropping combinations of visibility, time without bait, market gravity, and depth. Marginal tests indicated that island group and island geomorphology were the most important variables ($>17\%$ of deviance explained, $p = 0.001$). Consequently, model visualization using dbRDA demonstrated the clustering of BRUVSs within the same reef and island group, and the first 2 axes explained 27.3% of the variation in the data and 90.9% of the variation explained by the fitted model (Fig. 9).

4. DISCUSSION

We found significant variation of elasmobranch assemblages within French Polynesia, which can broadly be characterized as having high abundances and species richness of elasmobranchs, and sharks in particular. Blacktip reef sharks and grey reef sharks were the 2 most common shark species, and they dominated assemblages at many islands. Of shark species with ranges in French Polynesia (Siu et al. 2017), only 1 species of reef shark (Galapagos shark *Carcharhinus galapagensis*) and 1 transient species that occupies primarily nearshore habitats (bull shark

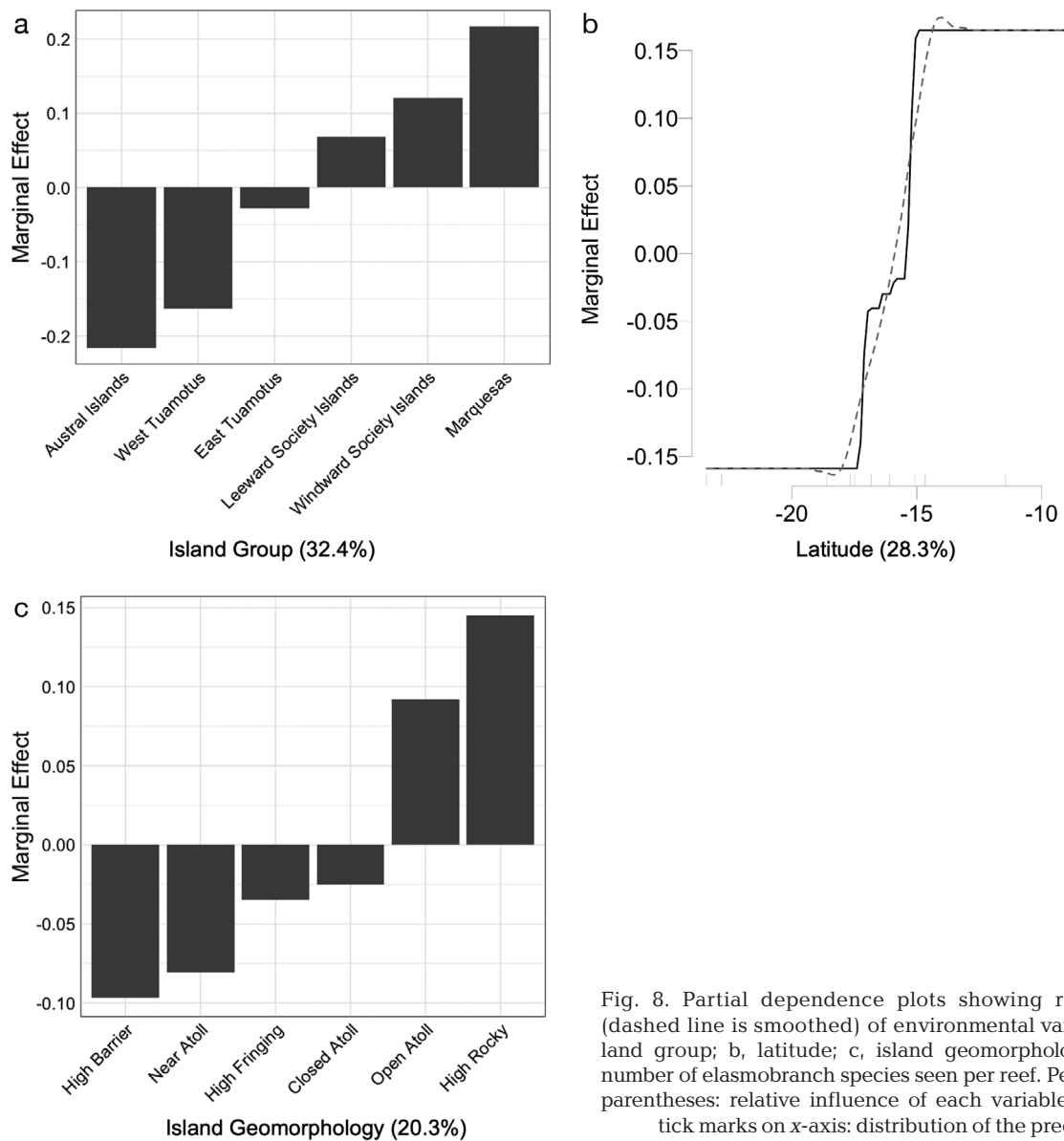


Fig. 8. Partial dependence plots showing relationships (dashed line is smoothed) of environmental variables (a, island group; b, latitude; c, island geomorphology) to total number of elasmobranch species seen per reef. Percentages in parentheses: relative influence of each variable. Light grey tick marks on x-axis: distribution of the predictors

C. leucas) did not appear on our BRUVSs. Low occurrence of these species, however, is not likely due to depletion. Indeed, bull sharks have very rarely been observed in French Polynesia, with only 1 individual scientifically verified (Nelson & Johnson 1980). The range of Galapagos sharks only includes the Austral and Gambier archipelagos, and the island of Rapa Iti (Siu et al. 2017). Furthermore, this species generally occurs in waters deeper than we sampled (Meyer et al. 2010). The rest of the shark species known to occur in French Polynesia but that were not sighted occur primarily in pelagic or deep oceanic habitats. Six of the 8 ray species documented in French Polynesia (Siu et al. 2017) were seen at our BRUVSs. The only species not observed, the deep-water stingray

Plesiobatis davies and pelagic stingray *Pteroplatytrygon violacea*, are not expected to occur in fore-reef habitats.

As with relative abundances of sharks overall (e.g. Farabaugh et al. 2024), the species richness of elasmobranchs in French Polynesia is equivalent to or higher than richness seen in comparable studies elsewhere in the Indo-Pacific, such as the Great Barrier Reef (Australia) (Espinoza et al. 2014) and New Caledonia (Juhel et al. 2018). However, species assemblages were not always similar to those seen elsewhere. For instance, French Polynesia had a paucity of large-bodied transient/pelagic shark species such as tiger sharks *Galeocerdo cuvier*, scalloped hammerhead sharks, and great hammerhead sharks, as well as sil-

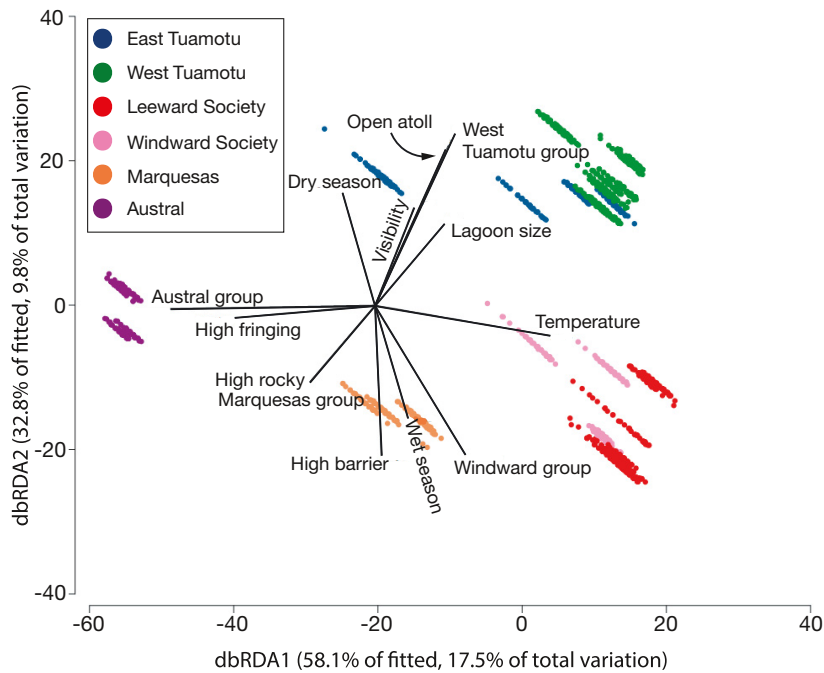


Fig. 9. Visualization of distance-based linear models (DISTLMs) using distance-based redundancy analysis (dbRDA). Dot color indicates island group

vertip sharks, when compared to the same studies done on the Great Barrier Reef and in New Caledonia (Espinoza et al. 2014, Juhel et al. 2018). Although it is likely that these shark species, which are more pelagic and typically occur at low densities, are under-sampled by the BRUVS methods in all of these studies, the deeper maximum depths of BRUVSs in the Great Barrier Reef and New Caledonia studies may contribute to this pattern. Additionally, large-bodied transient/pelagic shark species may have patchy distributions within French Polynesia as they have been seen in abundance in certain areas. For instance, tiger sharks have been the target of eco-tourism shark dives in Tahiti (e.g. Séguigne et al. 2023b), and hammerhead sharks have been seen frequently in Rangiroa. Furthermore, both tiger sharks and great hammerhead sharks have demonstrated seasonal patterns of abundance in Rangiroa (Boube et al. 2023, Séguigne et al. 2023a). This, along with the inclusion of seasonality in the top performing DISTLMs, indicates that season may have an influence on elasmobranch assemblage composition. However, our BRT models showed no evidence that season had any influence on patterns of species richness, nor have BRT models shown any evidence that season has any impact on broadscale patterns of shark abundance in French Polynesia (Farabaugh et al. 2024). Further work at key sights, with an emphasis on time series sampling, could provide further

insights into the influence of seasonality on elasmobranch communities in French Polynesia.

Similar to many other nations in the Indo-Pacific (e.g. Simpfendorfer et al. 2023), elasmobranch assemblages in French Polynesia were dominated by sharks, with a general paucity of rays. While we would not expect planktivorous rays to be attracted to bait in the way sharks and carnivorous rays are, the relative attractiveness of bait to these groups should not vary across locations. Therefore, it is possible to make comparisons about the relative ratios of sharks vs. rays spatially. The Marquesas were an exception to the relative lack of rays seen elsewhere in French Polynesia. Rays accounted for ca. 30% of the elasmobranch assemblage seen in the Marquesas. Their abundance there may be due to marked habitat differences at this island group. The Marquesas are the only location

in French Polynesia that lacks developed coral reefs. Instead, the benthic community is composed mostly of microalgae and algal turf on a benthos dominated by rocky habitats (Payri et al. 2016). Marquesan waters also have nitrate and phosphate concentrations 100 times that of the adjacent subtropical gyre, leading to high phytoplankton and zooplankton biomass. (e.g. Martinez et al. 2016). This is likely the reason for the high abundance of planktivorous mobulid rays seen here. Indeed, both primary productivity and zooplankton abundance are positively correlated with reef and oceanic manta abundance in many locations including the Great Barrier Reef in Australia, the Maldives, and coastal Ecuador and Mexico (e.g. Jaime et al. 2012, Armstrong et al. 2016, 2021, Fonseca-Ponce et al. 2022, Harty et al. 2022).

The Marquesas are also one of the most isolated island groups in the world, being farther away from any continental land mass than any other archipelago. Its rocky reefs, productive waters, and high latitude make it very distinct from the other archipelagos of French Polynesia. This suite of characteristics may account for the increased presence of scalloped hammerheads and silvertip sharks that prefer access to deeper waters (Tickler et al. 2017). Other known hotspots for scalloped hammerheads sharks, such as the Galapagos islands (e.g. Hearn et al. 2010), Malpelo Island (e.g. Bessudo et al. 2011), and Revillagigedo National Park (e.g. Aldana-Moreno et al. 2020), are

similar to the Marquesas in many respects, being remote islands with rocky reefs and productive waters.

The 2 most common species seen in French Polynesia, blacktip reef sharks and grey reef sharks, had high probabilities of being seen together on the same video, which is not surprising given their abundance. However, their patterns of relative abundance at the scale of reefs were not similar. Blacktip reef sharks were often seen less than expected at islands where grey reef sharks were seen more than expected, and vice versa. These results align with other studies that have found niche partitioning between these 2 species arising from interspecific competition (e.g. Papastamatiou et al. 2018, Sabando et al. 2020). Blacktip reef sharks rely more on reef-associated than pelagic food webs compared to grey reef sharks at Palmyra atoll (McCauley et al. 2012). This may be the result of differential habitat use, with grey reef sharks favoring forereef habitats and blacktip reef sharks spending time in forereef, backreef, and lagoon habitats even as adults (Heupel et al. 2018, Papastamatiou et al. 2018). When observed together, however, blacktip reef sharks generally give way to grey reef sharks, suggesting some level of competitive dominance (Papastamatiou et al. 2018, Sabando et al. 2020) that could lead to the inverse patterns of relative abundance at the reef level that were observed.

Interestingly, patterns of relative abundance or absence of whitetip reef sharks were not closely aligned with those of blacktip reef sharks and grey reef sharks at the level of island groups, but they had strong positive patterns of association at the level of individual videos. The positive association at the video level might be driven by a benefit to an association while foraging. Labourgade et al. (2020) found that grey reef sharks can benefit by foraging in the presence of whitetip reef sharks. The latter can access reef crevices and often flush prey, making those prey available to grey reef sharks. Whitetip reef sharks did not appear to benefit from this association, with the foraging outcome of the associations being neutral (commensalistic) or kleptoparasitic. However, it is possible that elsewhere, fish fleeing grey reef sharks that try to shelter in reef structure may become more available to whitetip reef sharks, thus resulting in a by-product mutualism for both species. Therefore, while dietary overlap may suggest a degree of competition, specific behaviors appear to alleviate potentially negative consequences of competition and may actually lead to commensalism or mutualism. It is possible that such specific foraging consequences could drive other patterns of species co-occurrence and abundance in French Polynesia. Indeed, abun-

dance of shark predators has been found to have a positive relationship with that of teleost predators (Farabaugh 2023).

Sicklefin lemon sharks were the largest-bodied shark commonly observed at our BRUVSs. Though limited work has been done examining diets of adults, the diets of juvenile sicklefin lemon sharks have been shown to be dominated by teleosts, and at larger size classes they can feed on other elasmobranch species, rays in particular (e.g. Cortés 1999, White et al. 2004). While the degree of foraging on other sharks is unknown, lemon sharks *Negaprion brevirostris* in the Atlantic Ocean, which grow to similar adult body sizes, are established predators of smaller sharks (e.g. Guttridge et al. 2012). Stable isotope analysis of adult sicklefin lemon sharks suggests that they have a higher trophic position (4.5) than smaller reef sharks, and may fill the role of apex predators (Frisch et al. 2016). As such, they may be dominant competitors or predators of smaller reef sharks such as grey reef sharks, with which they were seen together in individual videos much less often than expected. These results were mirrored at the island level, with sicklefin lemon sharks being positively associated with islands and in island groups where grey reef sharks often had negative associations and vice versa. While little work has been done on the interactions between adults of these species, in the Seychelles, grey reef sharks and sicklefin lemon sharks use very different habitats across all age ranges (Lea et al. 2016). Grey reef sharks primarily inhabit fore-reef and slope habitats, while sicklefin lemon sharks remained primarily within the lagoon of the atoll. However, this contrasts with observations in French Polynesia, where sicklefin lemon sharks are seen frequently on the forereef (e.g. Clua et al. 2010, Mourier et al. 2013), although lagoons and backreef areas are important nursery habitats for sicklefin lemon sharks (e.g. Mourier & Planes 2013, Mourier et al. 2013) but are not used as nursery habitats for grey reef sharks. Unlike grey reef sharks, blacktip reef sharks use similar nursery habitats as lemon sharks (e.g. Matich et al. 2017) and demonstrated a strong positive association with many of the same islands and island groups that sicklefin lemon sharks did, in addition to being seen more often than expected in the same videos. It is also possible that this pattern of disassociation between grey reef sharks and sicklefin lemon sharks, and association of blacktip reef sharks with sicklefin lemon sharks, is due to differing habitat preferences. Grey reef sharks were strongly associated with islands that were open atolls, whereas sicklefin lemon sharks and blacktip reef sharks tended to be strongly associated with high

islands with barrier reefs. Furthermore, island biogeography was a significant driver of both grey reef shark abundances and blacktip reef shark abundances in French Polynesia (Farabaugh et al. 2024), although it was a stronger predictor of blacktip reef shark abundances than of grey reef shark abundances.

Overall patterns of species richness of elasmobranchs varied considerably across the broad geographic range of the world's largest shark sanctuary in French Polynesia. However, islands with high species richness were not necessarily the places with highest overall abundance of elasmobranchs. Furthermore, while the drivers of these patterns of species richness were similar to those driving the overall abundance of sharks, they were not the same. For example, while island geomorphology is the overwhelming driver of overall shark abundance (Farabaugh et al. 2024), it was less important in driving patterns of species richness. Instead, island group and latitude were the variables that explained the most variation in our BRT models. However, island geomorphology and island group were the most important variables in our DISTLMs of elasmobranch assemblages.

Latitude is a well known driver of shark species richness globally, with shark species richness tending to peak around 30–40° N or S (e.g. Tittensor et al. 2010, Lucifora et al. 2011, Guisande et al. 2013). This pattern, however, is often complicated by other factors at regional scales. For example, Espinoza et al. (2014) found increased shark species richness at the northern and southern edges of the Great Barrier Reef compared with intermediate latitudes. Another reason for the latitudinal trend displayed here may be overall abundance patterns, as many of the southern islands where we found fewer species also had lower abundance. However, this is not the case for all islands. The Marquesas, which contained the northernmost islands, had intermediate-to-low overall abundance compared to the rest of French Polynesia (Fig. 2), but were the most speciose islands.

Island group had the largest effect on species richness and elasmobranch assemblages within our study, and was likely a result of islands within a group being spatially clustered and often with similar bathymetry and disturbance histories that are not accounted for elsewhere in our models. While species assemblages from the same island group were often clustered together in hierarchical cluster analysis, this was not always the case. Where this was not the case, interesting patterns of species assemblages emerged. For instance, reefs from Rurutu, the only high island with a fringing reef sampled, formed their own unique cluster, and had unique species assemblages dom-

inated by whitetip reef sharks. It is notable that reefs of the same island were always found within the same broad clusters, though not always as nearest neighbors, indicating that spatial patterns were prominent not only in the number of elasmobranch species found on reefs, but also in the species assemblages found at those reefs. Factors operating at finer spatial scales, like distance to reef pass, leeward vs. windward, proximity to shark feeding/ecotourism operations, bathymetry, and coral cover, may influence shark abundance and assemblage structure. While analyses of these factors are beyond the scope of the current study, this effort would provide further insight into the drivers of elasmobranch species assemblages.

Interestingly, human factors (i.e. market gravity) did not influence elasmobranch species richness. This is consistent with patterns of total shark abundance in French Polynesia, where market gravity was not a significant factor (Farabaugh et al. 2024). Some species (e.g. grey reef sharks), however, may be more sensitive to human influences than other species, but still persist even at the highest levels of market gravity in French Polynesia (Farabaugh et al. 2024), suggesting that even for species that are negatively associated with human impact, overall anthropogenic effects are relatively small. Furthermore, it is possible that while human factors did not have an influence on overall species richness, they may impact the species composition of elasmobranch assemblages since market gravity was included in the top performing DISTLMs. However, the lack of inclusion of market gravity in models within 2 AIC units of the best models, paired with its lack of significance in species richness BRT models, suggests that any effects on elasmobranch assemblages in French Polynesia are likely limited. This lack of human impacts in French Polynesia contrasts with global patterns where anthropogenic factors often drive elasmobranch diversity (e.g. Simpfendorfer et al. 2023), although gradients of human pressure within the world's largest shark sanctuary of French Polynesia are much lower than those found globally.

5. CONCLUSIONS

Here we found that French Polynesia overall is characterized by high abundances and species richness of elasmobranchs, sharks in particular. Although assemblages at most islands were dominated by blacktip reef sharks and grey reef sharks, and demonstrated a paucity of rays, we found significant variation in elasmobranch assemblages. While some of this

variation appears to be driven by habitat features, spatial dynamics, and history, models found that island geomorphology, latitude, and island group were the primary drivers of species richness. Species assemblages and associations at smaller scales may be driven by species interactions, both positive and negative, that warrant further investigation.

Acknowledgements. This work was funded by Paul G. Allen Philanthropies and the Pew Charitable Trust. We thank Serge Planes, Gilles Siu, Adeline Goyard, Clément Ameil, Nicolas Bureau, Noémie Jublier, Alisson Bordeaux, Matthis Jorge, the Tetiaroa Society, the Brando Hotel, Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE), and many generous individuals across French Polynesia for their logistical support and help in the field. Patricia Heithaus, Riki Bonnema, Erin McCombs, Eva Maire, and numerous volunteers at Florida International University (FIU) and Aquarium of the Pacific provided invaluable assistance in video data extraction. N.F.F. was supported by an FIU Presidential Fellowship, FIU Dissertation Year Fellowship, and McKnight Dissertation Fellowship during this project. Work was conducted under FIU IACUC Committee authorization and special permit from the Environment Department of French Polynesia. The present work was part of N.F.F.'s PhD dissertation. This is contribution #1794 from the Institute of Environment at FIU. All sampling was conducted in compliance with FIU's Animal Care & Use Committee (IACUC) protocols (15-022, 18-028, 21-025), and special permit (Ref. 5129/MCE/ENV, 22 June 2016).

LITERATURE CITED

- Abear S (2009) Comparisons of boosted regression tree, GLM and GAM performance in the standardization of yellowfin tuna catch-rate data from the Gulf of Mexico longline fishery. MSc thesis, Louisiana State University and Agricultural and Mechanical College, Baton Rouge, LA
- ✦ Aldana-Moreno A, Hoyos-Padilla EM, González-Armas R, Galván-Magaña F and others (2020) Residency and diel movement patterns of the endangered scalloped hammerhead *Sphyrna lewini* in the Revillagigedo National Park. *J Fish Biol* 96:543–548
- ✦ Armstrong AO, Armstrong AJ, Jaine FRA, Couturier LIE and others (2016) Prey density threshold and tidal influence on reef manta ray foraging at an aggregation site on the Great Barrier Reef. *PLOS ONE* 11:e0153393
- ✦ Armstrong AO, Stevens GMW, Townsend KA, Murray A and others (2021) Reef manta rays forage on tidally driven, high density zooplankton patches in Hanifaru Bay, Maldives. *PeerJ* 9:e11992
- ✦ Barley SC, Meekan MG, Meeuwig JJ (2017) Species diversity, abundance, biomass, size and trophic structure of fish on coral reefs in relation to shark abundance. *Mar Ecol Prog Ser* 565:163–179
- ✦ Behrenfeld MJ, Falkowski PG (1997) Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol Oceanogr* 42:1–20
- ✦ Bessudo S, Soler GA, Klimley AP, Ketchum JT, Hearn A, Arauz R (2011) Residency of the scalloped hammerhead shark (*Sphyrna lewini*) at Malpelo Island and evidence of migration to other islands in the Eastern Tropical Pacific. *Environ Biol Fishes* 91:165–176
- ✦ Boaden AE, Kingsford MJ (2015) Predators drive community structure in coral reef fish assemblages. *Ecosphere* 6:46
- ✦ Boube T, Azam CS, Guilbert A, Huveneers C and others (2023) First insights into the population characteristics and seasonal occurrence of the great hammerhead shark, *Sphyrna mokarran* (Rüppell, 1837) in the Western Tuamotu archipelago, French Polynesia. *Front Mar Sci* 10:1234059
- ✦ Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociol Method Res* 33:261–304
- ✦ Cappo M, Speare P, De'ath G (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *J Exp Mar Biol Ecol* 302:123–152
- ✦ Ceccarelli DM, Evans RD, Logan M, Jones GP and others (2023) Physical, biological and anthropogenic drivers of spatial patterns of coral reef fish assemblages at regional and local scales. *Sci Total Environ* 904:166695
- Chapman DD, MacNeil MA, Heupel MR, Meekan M, Harvey ES, Simpfendorfer CA, Heithaus MR (2022) The elasmobranchs of coral reefs. In: Carrier JC, Simpfendorfer CA, Heithaus MR, Yopak KE (eds) *Biology of sharks and their relatives*, 3rd edn. CRC Press, Boca Raton, FL, p 635–655
- Cinner J, Maire E (2018) Global gravity of coral reefs spatial layer (data set). James Cook University. <https://researchdata.edu.au/global-gravity-coral-spatial-layer/1330462>
- ✦ Cinner JE, Maire E, Huchery C, MacNeil MA and others (2018) Gravity of human impacts mediates coral reef conservation gains. *Proc Natl Acad Sci USA* 115:E6116–E6125
- Clarke KR, Gorley RN (2015) *Getting started with PRIMER v7*. PRIMER-e: Plymouth Marine Laboratory, Plymouth
- ✦ Clua E, Buray N, Legendre P, Mourier J, Planes S (2010) Behavioural response of sicklefin lemon sharks *Negaprion acutidens* to underwater feeding for ecotourism purposes. *Mar Ecol Prog Ser* 414:257–266
- ✦ Cornell HV, Harrison SP (2014) What are species pools and when are they important? *Annu Rev Ecol Evol Syst* 45:45–67
- ✦ Cortés E (1999) Standardized diet compositions and trophic levels of sharks. *ICES J Mar Sci* 56:707–717
- Davis WM (1928) *The coral reef problem*. American Geographical Society, New York, NY
- ✦ Dedman S, Officer R, Clarke M, Reid DG, Brophy D (2017) Gbm.auto: a software tool to simplify spatial modelling and marine Protected Area planning. *PLOS ONE* 12:e0188955
- ✦ Dedman S, Moxley JH, Papastamatiou YP, Braccini M and others (2024) Ecological roles and importance of sharks in the Anthropocene Ocean. *Science* 385:adl2362
- ✦ Desbiens AA, Roff G, Robbins WD, Taylor BM, Castro-Sanguino C, Dempsey A, Mumby PJ (2021) Revisiting the paradigm of shark-driven trophic cascades in coral reef ecosystems. *Ecology* 102:e03303
- Ebert DA, Dando M, Fowler S (2021) *Sharks of the world: a complete guide*. Princeton University Press, Princeton, NJ
- ✦ Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. *J Anim Ecol* 77:802–813

- Espinoza M, Cappel M, Heupel MR, Tobin AJ, Simpfendorfer CA (2014) Quantifying shark distribution patterns and species-habitat associations: implications of marine park zoning. *PLOS ONE* 9:e106885
- Farabaugh NF (2023) Reef shark and predatory teleost abundance and assemblage composition in the world's largest shark sanctuary. PhD dissertation, Florida International University, Miami, FL
- Farabaugh NF, Bond ME, Chapman D, Clua E and others (2024) Incorporating environmental factors is critical for determining conservation baselines for relative abundance of sharks on coral reefs. *Mar Ecol Prog Ser* 736: 93–105
- Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecol Lett* 13:1055–1071
- Fonseca-Ponce IA, Zavala-Jiménez AA, Aburto-Oropeza O, Maldonado-Gasca A, Galván-Magaña F, González-Armas R, Stewart JD (2022) Physical and environmental drivers of oceanic manta ray *Mobula birostris* sightings at an aggregation site in Bahía de Banderas, Mexico. *Mar Ecol Prog Ser* 694:133–148
- Frisch AJ, Ireland M, Rizzari JR, Lönnstedt OM, Magnenat KA, Mirbach CE, Hobbs JPA (2016) Reassessing the trophic role of reef sharks as apex predators on coral reefs. *Coral Reefs* 35:459–472
- Gagné TO, Reygondeau G, Jenkins CN, Sexton JO, Bograd SJ, Hazen EL, Houtan KSV (2020) Towards a global understanding of the drivers of marine and terrestrial biodiversity. *PLOS ONE* 15:e0228065
- Goetze JS, Heithaus MR, MacNeil MA, Harvey E and others (2024) Directed conservation of the world's reef sharks and rays. *Nat Ecol Evol* 8:1118–1128
- Goldberg WM (2016) Atolls of the world: revisiting the original checklist. *Atoll Res Bull* 610:1–47
- Gove JM, Williams GJ, McManus MA, Heron SF, Sandin SA, Vetter OJ, Foley DG (2013) Quantifying climatological ranges and anomalies for Pacific coral reef ecosystems. *PLOS ONE* 8:e61974
- Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32: 315–326
- Guillemot N, Chabanet P, Kulbicki M, Vigliola L, Léopold M, Jollit I, Le Pape O (2014) Effects of fishing on fish assemblages in a coral reef ecosystem: from functional response to potential indicators. *Ecol Indic* 43:227–235
- Guisande C, Patti B, Vaamonde A, Manjarrés-Hernández A and others (2013) Factors affecting species richness of marine elasmobranchs. *Biodivers Conserv* 22:1703–1714
- Guttridge TL, Gruber SH, Franks BR, Kessel ST and others (2012) Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. *Mar Ecol Prog Ser* 445:279–291
- Harty K, Guerrero M, Knochel AM, Stevens GMW, Marshall A, Burgess K, Stewart JD (2022) Demographics and dynamics of the world's largest known population of oceanic manta rays *Mobula birostris* in coastal Ecuador. *Mar Ecol Prog Ser* 700:145–159
- Hearn A, Ketchum J, Klimley AP, Espinoza E, Peñaherrera C (2010) Hotspots within hotspots? Hammerhead shark movements around Wolf Island, Galapagos Marine Reserve. *Mar Biol* 157:1899–1915
- Heithaus MR, Dunn RE, Farabaugh NF, Lester E and others (2022) Advances in our understanding of the ecological importance of sharks and their relatives. In: Carrier JC, Simpfendorfer CA, Heithaus MR, Yopak KE (eds) *Biology of sharks and their relatives*, 3rd edn. CRC Press, Boca Raton, FL, p 487–521
- Heupel MR, Lédée EJI, Simpfendorfer CA (2018) Telemetry reveals spatial separation of co-occurring reef sharks. *Mar Ecol Prog Ser* 589:179–192
- Jaine FRA, Couturier LIE, Weeks SJ, Townsend KA, Bennett MB, Fiora K, Richardson AJ (2012) When giants turn up: sighting trends, environmental influences and habitat use of the manta ray *Manta alfredi* at a coral reef. *PLOS ONE* 7:e46170
- Jouffray JB, Wedding LM, Norström AV, Donovan MK and others (2019) Parsing human and biophysical drivers of coral reef regimes. *Proc R Soc B* 286:20182544
- Juhel JB, Vigliola L, Mouillot D, Kulbicki M, Letessier TB, Meeuwig JJ, Wantiez L (2018) Reef accessibility impairs the protection of sharks. *J Appl Ecol* 55:673–683
- Labourgade P, Ballesta L, Huvenciers C, Papastamatiou Y, Mourier J (2020) Heterospecific foraging associations between reef-associated sharks: first evidence of kleptoparasitism in sharks. *Ecology* 101:e03117
- Lea JSE, Humphries NE, von Brandis RG, Clarke CR, Sims DW (2016) Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. *Proc R Soc B* 283:20160717
- Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol Monogr* 69:1–24
- Lucifora LO, García VB, Worm B (2011) Global diversity hotspots and conservation priorities for sharks. *PLOS ONE* 6:e19356
- MacNeil MA, Chapman DD, Heupel M, Simpfendorfer CA and others (2020) Global status and conservation potential of reef sharks. *Nature* 583:801–806
- Martinez E, Rodier M, Maamaatuaiahutapu K (2016) *Environnement océanique des Marquises*. In: Galzin R, Duron SD, Meyer JY (eds) *Biodiversité terrestre et marine des îles Marquises, Polynésie Française*. Société Française d'Ichtyologie, Paris, p 123–136
- Matich P, Kiszka JJ, Mourier J, Planes S, Heithaus MR (2017) Species co-occurrence affects the trophic interactions of two juvenile reef shark species in tropical lagoon nurseries in Moorea (French Polynesia). *Mar Environ Res* 127:84–91
- McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290–297
- McCauley DJ, Young HS, Dunbar RB, Estes JA, Semmens BX, Micheli F (2012) Assessing the effects of large mobile predators on ecosystem connectivity. *Ecol Appl* 22: 1711–1717
- Meyer CG, Papastamatiou YP, Holland KN (2010) A multiple instrument approach to quantifying the movement patterns and habitat use of tiger (*Galeocerdo cuvier*) and Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. *Mar Biol* 157:1857–1868
- Mourier J, Planes S (2013) Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. *Mol Ecol* 22:201–214
- Mourier J, Buray N, Schultz JK, Clua E, Planes S (2013) Genetic network and breeding patterns of a sicklefin lemon shark (*Negaprion acutidens*) population in the Society Islands, French Polynesia. *PLOS ONE* 8:e73899

- ✦ Müller D, Leitão PJ, Sikor T (2013) Comparing the determinants of cropland abandonment in Albania and Romania using boosted regression trees. *Agric Syst* 117:66–77
- ✦ Oksanen J, Blanchet FG, Kindt R, Legendre P and others (2012) *Vegan: community ecology package*. R package version 2.0-2. <https://cran.r-project.org/web/packages/vegan/index.html>
- ✦ Osgood GJ, Baum JK (2015) Reef sharks: recent advances in ecological understanding to inform conservation. *J Fish Biol* 87:1489–1523
- ✦ Papastamatiou YP, Bodey TW, Friedlander AM, Lowe CG and others (2018) Spatial separation without territoriality in shark communities. *Oikos* 127:767–779
- ✦ Payri CE, De Ramon N'Yeurt A, Fiat S, Andréfouët S (2016) La macroflore marine de l'archipel des Marquises. In: Galzin R, Duron SD, Meyer JY (eds) *Biodiversité terrestre et marine des îles Marquises, Polynésie française*. Société française d'Ichtyologie, Paris, p 207–219
- ✦ Prach K, Durigan G, Fennessy S, Overbeck GE, Torezan JM, Murphy SD (2019) A primer on choosing goals and indicators to evaluate ecological restoration success. *Restor Ecol* 27:917–923
- ✦ R Core Team (2022) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- ✦ Robbins WD, Hisano M, Connolly SR, Choat JH (2006) Ongoing collapse of coral-reef shark populations. *Curr Biol* 16:2314–2319
- ✦ Roff G, Doropoulos C, Rogers A, Bozec YM and others (2016) The ecological role of sharks on coral reefs. *Trends Ecol Evol* 31:395–407
- ✦ Roff G, Brown CJ, Priest MA, Mumby PJ (2018) Decline of coastal apex shark populations over the past half century. *Commun Biol* 1:223
- ✦ Ruppert JLW, Fortin MJ, Meekan MG (2016) The ecological role of sharks on coral reefs: response to Roff et al. *Trends Ecol Evol* 31:586–587
- ✦ Sabando MA, Rieucou G, Bradley D, Caselle JE, Papastamatiou YP (2020) Habitat-specific inter and intraspecific behavioral interactions among reef sharks. *Oecologia* 193:371–376
- ✦ Séguigne C, Bègue M, Meyer C, Mourier J, Clua É (2023a) Provisioning ecotourism does not increase tiger shark site fidelity. *Sci Rep* 13:7785
- ✦ Séguigne C, Mourier J, Clua É, Buray N, Planes S (2023b) Citizen science provides valuable data to evaluate elasmobranch diversity and trends throughout the French Polynesia's shark sanctuary. *PLOS ONE* 18:e0282837
- ✦ Sempendorfer CA, Heithaus MR, Heupel MR, MacNeil MA and others (2023) Widespread diversity deficits of coral reef sharks and rays. *Science* 380:1155–1160
- ✦ Siu G, Bacchet P, Bernardi G, Brooks AJ and others (2017) Shore fishes of French Polynesia. *Cybium* 41:245–278
- ✦ Suzuki R, Shimodaira H (2006) *Pvclust: an R package for assessing the uncertainty in hierarchical clustering*. *Bioinformatics* 22:1540–1542
- ✦ Tickler DM, Letessier TB, Koldewey HJ, Meeuwig JJ (2017) Drivers of abundance and spatial distribution of reef-associated sharks in an isolated atoll reef system. *PLOS ONE* 12:e0177374
- ✦ Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Berghe EV, Worm B (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature* 466:1098–1101
- ✦ Ward-Paige CA (2017) A global overview of shark sanctuary regulations and their impact on shark fisheries. *Mar Policy* 82:87–97
- ✦ Ward-Paige CA, Worm B (2017) Global evaluation of shark sanctuaries. *Glob Environ Change* 47:174–189
- ✦ White WT, Platell ME, Potter IC (2004) Comparisons between the diets of four abundant species of elasmobranchs in a subtropical embayment: implications for resource partitioning. *Mar Biol* 144:439–448
- ✦ Williams ID, Baum JK, Heenan A, Hanson KM, Nadon MO, Brainard RE (2015) Human, oceanographic and habitat drivers of Central and Western Pacific coral reef fish assemblages. *PLOS ONE* 10:e0120516

*Editorial responsibility: Peter Corkeron,
Nathan, Queensland, Australia
Reviewed by: M. Royer and 2 anonymous referees*

*Submitted: June 20, 2024
Accepted: December 4, 2024
Proofs received from author(s): January 22, 2025*