

FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

REEF SHARK & PREDATORY TELEOST ABUNDANCE AND ASSEMBLAGE
COMPOSITION IN THE WORLD'S LARGEST SHARK SANCTUARY

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

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BIOLOGY

by

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To: Dean Michael Heithaus
College of Arts, Sciences and Education

This dissertation, written by Naomi Frances Farabaugh, and entitled Reef Shark & Predatory Teleost Abundance and Assemblage Composition in the World's Largest Shark Sanctuary having been approved in respect to style and intellectual content, is referred to you for judgment.

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DEDICATION

For mom & pops who have been my biggest cheerleaders, my strongest supporters and who taught me to chase my dreams. For C.J. the world's best brother and pusher of buttons, who always has my back. For my friends who got me through good times and bad with game nights, good meals, long chats and incredible adventures - both real and imagined. For Popi the world's best paddleboat co-captain. To all my family, by blood and by choice, who have loved me and carried me, who have laughed with me and cried with me. Thank you.

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ABSTRACT OF THE DISSERTATION

REEF SHARK & PREDATORY TELEOST ABUNDANCE AND ASSEMBLAGE
COMPOSITION IN THE WORLD'S LARGEST SHARK SANCTUARY

by

Naomi Frances Farabaugh

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Professor Michael Heithaus, Major Professor

Populations of sharks and other marine predators have declined dramatically worldwide. Because sharks play a role in the dynamics of their ecosystems and there is increasing interest in rebuilding populations, understanding the factors influencing their abundances and assemblage structure are important for proper conservation management. French Polynesia is the world's largest shark sanctuary and features gradients of environmental and anthropogenic factors; it therefore provides a model system for elucidating the factors that affect the abundance and assemblage compositions of elasmobranchs and large teleost predators. Using ~3000 hours of baited remote underwater video data collected across 17 islands and 35 reefs, I found that the relative abundances of sharks at high islands were only one third of that on atolls, and open atolls had abundances nearly 20% higher than closed atolls. Therefore, realistic conservation targets for reef sharks in the Indo-Pacific should account for island geomorphology. Other environmental factors had smaller effects and human pressures (market gravity) did not significantly influence abundances. Assemblages at most islands generally lacked rays and were dominated by blacktip reef sharks (*Carcharhinus melanopterus*) and grey reef sharks (*Carcharhinus amblyrhynchos*). There was, however, significant variation in

elasmobranch assemblages across French Polynesia. Species assemblages and associations, particularly at smaller scales, may be shaped by species interactions. Relative abundances of predatory teleosts from the families Lutjanidae, Scombridae, Megalopidae, Carangidae, Sphyraenidae, Serranidae, and Lethrinidae on 19 reefs across 11 different islands/atolls varied positively with net primary productivity. Island geomorphology, human population density, relative abundance of sharks, and sea surface temperature, also influenced predatory teleost abundances. Interestingly, higher abundances of teleosts were found on reefs with higher abundances of sharks. However, unlike sharks, predatory teleosts appear to be sensitive to fishing pressure at even low human population densities. Higher abundances of predatory teleosts and sharks, together, are generally positively associated with healthier reefs as measured by percent cover of hard corals and crustose coralline algae. The relationships between coral health, small teleosts, and both groups of predators, however, were non-linear and it is unclear if the presence of predators helps facilitate reef health or if healthier reefs attract greater abundances of predators.

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PREFACE

The following chapter has been submitted for publication and is in review in *Journal of Applied Ecology* and has been formatted for that publication:

CHAPTER II

INCORPORATING ENVIRONMENTAL FACTORS IS CRITICAL FOR
DETERMINING CONVERSATION BASELINES FOR SHARK RELATIVE
ABUNDANCE OF CORAL REEFS

The following chapters are in advanced preparation to be submitted for review in *Marine Ecology Progress Series* and has been formatted for that publication:

CHAPTER III

VARIATION IN PREDATORY FISH ABUNDANCES ACROSS HUMAN AND
ENVIRONMENTAL GRADIENTS ON REMOTE CORAL REEF IN THE SOUTH
PACIFIC

CHAPTER IV

ELASMOBRANCH SPECIES RICHNESS AND ASSEMBLAGE COMPOSITION IN
THE WORLD'S LARGEST SHARK SANCTUARY

CHAPTER I

GENERAL INTRODUCTION

Marine predator populations, including sharks are undergoing dramatic global declines. (Ferretti et al., 2010; Myers & Worm, 2003; Pacoureau et al., 2021). One third of sharks and their relatives are threatened with extinction and the primary driver of these declines is overexploitation, through both incidental catch and targeted fishing (Dulvy et al., 2021). In coral reefs around the globe, a recent survey (Global Fingerprint) reported that sharks were absent on nearly 20% (69 of 371) of surveyed reefs across the Atlantic and Indo-Pacific regions, and over half of the nations sampled (34 of 58) had abundances lower than regional expectation (MacNeil et al. 2020).

While sharks can play diverse roles in ecosystems as predators, competitors, facilitators of other species, and in nutrient transport, the relative importance of sharks in structuring communities and ecosystem processes remains poorly resolved (e.g. Heithaus et al. 2022). In some situations, sharks may be important to ecosystem processes. (e.g. Frid et al. 2008; Heithaus et al. 2008, 2010; Burkholder et al. 2013; Estes et al. 2016; Moxley et al. 2019). For example, in Shark Bay Western Australia tiger sharks (*Galeocerdo cuvier*) structure seagrass systems, primarily through risk effects on megagrazers that are transmitted to seagrasses (e.g. Burkholder et al. 2013, Nowicki et al. 2021, see also Heithaus et al. 2022). Similarly, white sharks (*Carcharodon carcharias*) may limit recovery of kelp forests by suppressing sea otter (*Enhydra lutris*) populations (Moxley et al. 2019). Despite these examples, our understanding of the ecological importance of sharks in structuring ecosystems remains incomplete (Heithaus et al. 2022). This is particularly true in coral reef systems, where interaction strength is reduced by complex and diffuse food webs (Rizzari et al. 2014; Frisch et al. 2016; Roff et al. 2016; Desbiens

et al. 2021; Chapman et al. 2022). While theoretical models suggest sharks may be important in stabilizing coral reef systems (Kondoh 2008), empirical studies suggest that this may not universally be the case and there remains considerable uncertainty about their ecological importance in these habitats (Heupel et al. 2014, 2019; Desbiens et al. 2021; Chapman et al. 2022; Heithaus et al. 2022; Sandin et al. 2022). While there is likely a degree of context dependence of shark importance to reef health, a lack of studies in areas where there are natural gradients in shark relative abundance has hindered our ability to address this question.

French Polynesia is an overseas collectivity of France encompassing five archipelagos in the south central Pacific. It contains over 2% of the world's living coral reef area (Spalding et al., 2001) inside its ~5,030,000 km² exclusive economic zone (EEZ). Prohibitions on shark fishing, trade, and export in 2006 and 2012 have resulted in French Polynesia becoming the world's largest shark sanctuary. Global surveys suggest that the sanctuary is largely successful in maintaining high shark abundances (Ward-Paige & Worm, 2017, MacNeil et al. 2020). However, French Polynesia contains gradients in human and environmental factors that can provide insights that make it an ideal place to examine how environmental and anthropogenic factors might influence shark communities in relatively pristine to moderately impacted states and to lay the foundation for gaining insights into the functional significance of sharks and predatory teleosts in coral reef systems. As such, data from French Polynesia could provide important insights for determining if shark conservation is important to the health of coral reefs and what targets of relative abundance might be reasonable for management efforts.

Based on the suitability of French Polynesia as a study site, this project employed from baited remote underwater video stations (BRUVs), and underwater visual censuses to measure critical variables to help determine the occurrence and potential role of sharks and predatory teleosts in this model system.

In Chapter 2, I use data from baited remote underwater video stations (BRUVs) to assess the relative abundance of sharks across the majority of French Polynesia's range. I extend the dataset presented by MacNeil et al. (2020) by expanding the spatial scale of sampling with more than 800 additional BRUV sets, by exploring additional environmental factors, including those that could be easily incorporated into conservation planning, and by conducting species-specific analyses to determine if there is interspecific variation in responses to environmental factors.

In Chapter 3 I use data from BRUVS to assess the relative abundances of predatory teleosts from the families Lutjanidae, Scombridae, Megalopidae, Carangidae, Sphyraenidae, Serranidae and Lethrinidae on 19 reefs across 11 islands/atolls. I use boosted regression trees to model the environmental and anthropogenic factors that have the largest influence on relative abundances of predatory teleost as a whole, and abundances of the most common families - Lutjanidae (snappers), Serranidae (groupers), Carangidae (jacks) - separately.

In Chapter 4, I quantify species richness and assemblage composition of elasmobranchs across environmental and anthropogenic gradients present in the full BRUVS dataset and examine patterns of co-occurrence and avoidance in species pairs.

In Chapter 5, I integrate data on the relative abundance of predatory teleosts and sharks with data on the abundances of smaller fishes and coral reef health to explore whether reef health and fish assemblages are correlated with the abundances of predatory teleosts, sharks or their combined abundances.

Finally, in Chapter 6, I synthesize the information from my dissertation and suggest avenues for future research.

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CHAPTER II

INCORPORATING ENVIRONMENTAL FACTORS IS CRITICAL FOR DETERMINING CONVERSATION BASELINES FOR SHARK RELATIVE ABUNDANCE OF CORAL REEFS

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Abstract

1. Populations of sharks, including those inhabiting coral reefs, have experienced dramatic global declines. Setting appropriate targets for restoring reef shark populations requires estimates of expected relative abundances in the absence of intense fishing. Thus, it is important to identify factors that drive the carrying capacity of sharks in relatively intact reef systems and to determine whether expected shark abundance varies according to easy to assess variables that could be used by managers for setting restoration targets, or prioritizing resource allocation, for particular areas in the absence of detailed data.
2. French Polynesia, the world's largest shark sanctuary, provides a model system for addressing this question. I used baited remote underwater video surveys (BRUVS) to assess relative abundance of sharks on 35 reefs across the broad geographic range of French Polynesia.
3. Boosted regression tree models revealed that relative abundance of sharks varied significantly with island geomorphology. Overall shark relative abundances at high islands were nearly three times lower than on atolls, and open atolls had abundances nearly 20% higher than closed atolls.
4. Island group, temperature and net primary productivity had limited effects. Human pressure (market gravity) was not a significant factor.
5. *Synthesis and applications.* Although species-specific patterns varied, my findings suggest that environmental factors, particularly island geomorphology, should be taken into account when setting shark abundance recovery targets. Using this easy

to assess factor can facilitate the allocation of conservation effort and improve assessments of species recovery efforts for islands in the Indo-Pacific Region.

Introduction

Marine predator populations have experienced dramatic declines worldwide (Ferretti et al., 2010; Myers & Worm, 2003; Pacoureau et al., 2021). For sharks, the overwhelming driver of these declines is overexploitation through both incidental catch and targeted fishing (Dulvy et al., 2021). Data to track these global declines have been primarily focused on open-ocean systems targeted by industrial fisheries (e.g., Davidson et al. 2016; Pacoureau et al. 2021), but recent work suggests that shark population declines are also widespread in coastal and coral reef- associated systems (e.g. Ferretti et al., 2010; Robbins et al., 2006; Roff et al., 2018). For example, a recent global survey (Global Fingerprint) reported that sharks were absent on nearly 20% (69 of 371) of surveyed coral reefs and observed at low relative abundances at many others (MacNeil et al., 2020). At this global scale, human factors including the presence of longlines and gillnet fisheries, poor governance, and a lack of protections for sharks were associated with lower relative abundances. Given this reduction, conservation measures must go beyond merely halting population declines but aim to rebuild populations.

Currently, restoration targets (or estimates of population rebound potential) for reef sharks would have to be based on regional average abundances (e.g., MacNeil et al. 2020). While this approach can provide broad-scale insights into the potential effectiveness of restoration efforts or population status, data on carrying capacities – even

relative ones – across locations where restoration might occur would greatly enhance efforts to allocate conservation resources and set appropriate targets (e.g., Lotze et al., 2011; Micheli et al., 2004). Indeed, not understanding the carrying capacity of a habitat might lead to suboptimal allocation of resources, a failure to identify locations of high conservation potential, or inaccurate assessment of conservation outcomes. Thus, knowledge of abundances that might be expected based on the specific ecological conditions at particular sites are important. To be useful for conservation, however, the measured conditions should be those that are easily determined without costly or time-consuming field measurements.

To date, overfishing of sharks or their prey has been assumed to be the overwhelming driver of spatial variation in reef shark abundance across multiple scales (e.g., Clementi et al., 2021; Letessier et al., 2019; MacNeil et al., 2020; Nadon et al., 2012). Ecological conditions, however, may drive considerable variation in abundances of sharks across islands or reefs (e.g. Papastamatiou et al., 2006; Dunn et al, 2022) or even drive small-scale variation in shark abundance (e.g. Desbiens et al., 2021; Heupel & Simpfendorfer, 2014). Therefore, studies that investigate shark abundances across a range of conditions relatively free from human impacts would be useful for setting local and regional conservation targets, allocating conservation resources, and assessing management success.

French Polynesia is an excellent system to investigate variation in shark relative abundances across environmental gradients in the relative absence of shark fishing. Its

5,000,000 km² Exclusive Economic Zone includes over 2% of the world's living reef area (Spalding et al., 2001) and comprises the world's largest shark sanctuary. Also, gradients in human and environmental factors across islands allows the disentangling of anthropogenic and natural drivers of shark relative abundance. Finally, its nesting within the spatiotemporal footprint of a global survey of shark abundance (MacNeil et al. 2020) allows direct comparisons with other locations and allows results to be applied to conservation at the scale of the Indo-Pacific basin.

I used data from baited remote underwater video stations (BRUVS) to survey the relative abundance of sharks across the majority of French Polynesia's range relative to environmental and anthropogenic factors. I extend the dataset of MacNeil et al. (2020) to new locations and by >800 additional BRUV sets. Also, I assess additional environmental factors and conduct species-specific analyses to determine if there is interspecific variation in responses to environmental factors.

Methods

Site Description

French Polynesia lies in the south-central Pacific. An overseas collectivity of France, it is made up of five archipelagos: Marquesas Islands, Tuamotu Archipelago, Society Islands, Gambier Islands, and Austral Islands (Figure 1). For the purposes of this study, I subdivided the Society Islands into Windward and Leeward islands and the Tuamotus into eastern (including the Gambier Islands) and western groups (Figure 1b).

The Society Islands - the most populous island group - are mostly high islands with barrier reefs but include several small coral atolls. The Tuamotus are sparsely populated coral atolls. The Western Tuamotus feature more productive waters than the Eastern Tuamotus, which include the high islands with barrier reefs of the Gambier Archipelago. The Austral Islands are mostly high islands with either fringing reefs or barrier reefs and tend to have cooler and less productive waters. They are among the most remote islands in the world. The Marquesas have small populations and are generally high islands without developed coral reefs. Coastlines are characterized largely by rocky reefs and sea caves. The waters tend to be highly productive.

There are >30 species of sharks reported from French Polynesia, with seven commonly found in shallower reefs (Appendix S1). Global surveys suggest that the sanctuary is largely successful in maintaining high shark abundances (Ward-Paige & Worm, 2017; MacNeil et al. 2020). Even prior to the introduction of the shark sanctuary, shark and ray catches did not make up a large portion of total marine fisheries catches (Bale et al., 2009; Pauly et al., 2020; R. White et al., 2020) (Appendix S5). Current and historical cultural practices regarding the catching of sharks may contribute to their limited exploitation (Torrente et al., 2018).

Field Methods

From 2016-2017, BRUVS were used to survey 35 reefs across 17 sites in French Polynesia (Figure 1b). I defined a “reef” as *ca.* 4 km² of continuous coral reef habitat. All sites were grouped based on their geomorphology: open atoll, closed atoll, near atoll,

high barrier, high fringing, and high rocky. Open atolls ($n = 5$) have boat navigable passes, while closed atolls ($n = 3$) lack such passages. Water and animals may move between the open ocean and lagoon in closed atolls, but movement is restricted relative to open atolls. 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 characterized by their reef types, with many having barrier reefs and lagoons, one site featured a fringing reef and lacked a lagoon, and the Marquesas have rocky reefs.

BRUVS included a GoPro Hero4 Silver or GoPro Hero+ camera mounted to an aluminum frame with a *ca.* 1.5 m pole that held *ca.* 1 kg of oily fish bait (yellow fin tuna, small inshore fish, sardines, or fish heads and scraps- typically tuna) in a container in front of the camera. The camera and bait were positioned to face down current, which was determined using dye tabs. BRUVS were deployed during daylight hours on the forereef at 9 - 35 m depth. No two BRUVS were deployed within 500m of one another within a sampling day to reduce autocorrelation. Each BRUVS set had a minimum soak time of 60 minutes, with deployments up to 90 minutes. Each reef had at least 42 sets (Mean =58, Max =70; Appendix S2). At an individual reef, most sets were deployed over a single period of fewer than 10 days (max 37 days). For each set, sea surface temperature (SST) was taken using a YSI (Pro 2030 model), bottom depth recorded, and water visibility was visually estimated to the nearest meter up to 15 meters.

Work was conducted under FIU IACUC Committee authorization and special permit from the Environment Department of French Polynesia. All sampling was conducted in compliance with Florida International University's Animal Care & Use Committee (IACUC) protocols (15-022, 18-028, 21-025), and special permit (Ref. 5129/MCE/ENV, June 22nd, 2016).

Video Data Extractions

Videos were viewed and annotated in Fingerprint Annotator (v1.1.44.0). Each video was watched independently by at least two annotators. All observations were reviewed by an expert to verify identifications and resolve discrepancies. Identifications were made to the species level in 2,825 of 2,912 (97%) of observations. I calculated MaxN of each species on each BRUVS set and added these together to calculate overall elasmobranch MaxN for that set.

MaxN, the maximum number of individuals of each species seen in a single frame for each video, was used as the index for relative abundance. MaxN avoids recounting the same individuals that might enter and exit the field of view multiple times (Cappo et al. 2004). I calculated MaxN of each species on each BRUVS set and added these together to calculate overall shark MaxN for that set.

Other Environmental and Anthropogenic Data

Satellite-based observations of net primary productivity (NPP) were obtained from publicly available data (*Ocean Productivity Oregon State*, 2021) using the Vertically

Generalized Production Model (Behrenfeld & Falkowski, 1997). Values for each site were calculated based on the nearest neighbor pelagic cell for each reef location (Gove et al., 2013), then averaged over 2016 and 2017. Average SST was calculated from all SST measurements taken during BRUVS deployments at each reef. Market gravity (Cinner et al. 2018) was calculated as the population of the nearest settlement divided by the squared travel time to the reef location. Gravity values of individual BRUV sets were averaged to produce a single value for a reef (Cinner & Maire, 2018). Market gravity was selected as the metric for human pressure because it outperformed other metrics (human population density and human population size) in preliminary analysis.

Analysis

I used Boosted Regression Trees (BRTs) to determine the relative influence of predictor variables on the relative abundance of all sharks, and the three most abundant shark species alone. BRTs are a machine learning approach that uses both regression tree and boosted build algorithms to fit many models and combine them into a single model to account for high proportions of variability despite complex multivariate relationships (Elith et al., 2008). BRTs are insensitive to collinearity among variables, can handle complex non-linear relationships and account for interactions between predictors (Abeare, 2009; Elith et al., 2008; Jouffray et al., 2019).

Predictor variables were selected to focus on those that could be easily assessed for conservation planning and that are relevant to the biology of the focal species, almost entirely reef-resident ones, included in my sampling. Therefore, I did not include

variables like connectivity among islands because there is little dispersal between islands and low connectivity among island groups for many of the reef associated species considered here (e.g. Mourier et al., 2013; Mourier & Planes, 2013). Similarly, I did not include fine-scale predictor variables like rugosity or fish biomass because they are less available and more difficult to assess for rapid conservation planning. Future work will investigate these fine-scale variables. Initial variables included in my models were island geomorphology, island group, average net primary productivity, market gravity, sea surface temperature, water visibility, and the size of the lagoon. Season, depth of BRUVS, bait type, and time BRUVS was without bait (i.e., due to rare instances in which bait were broken and bait removed by animals), were also included in initial models.

Based on visual inspection of the distribution of response variable data, the Poisson distribution was used for all models except one, total shark MaxN by reef model, for which I used the Gaussian distribution. For each response variable, initial BRT models were run with all predictor variables plus a random variable. Any predictor variables with a relative influence value below the random variable were eliminated from the final models (Soykan et al., 2014). To account for variability, both initial and final models were run 100 times, and means taken to determine model results. Any models that explained less than 25% of the deviance of MaxN were excluded from further discussion. Models were run in R (version 4.0.2) using the *dismo* (Elith et al., 2008) and *ggBRT* packages (Jouffray et al., 2019). Optimal model parameters (tree complexity, bag fraction and learning rate) were determined by testing across a series of values, using those that gave the smallest model deviance, for each model. Spatial autocorrelation was

investigated using Moran's I method on each reef, with p-values Bonferroni corrected (for $\alpha_{\text{original}} = 0.05$ and $n = 35$, $\alpha_{\text{corrected}} < 0.0014$). I report MaxN $\pm$ sd, unless otherwise stated.

Results

A total of 2,111 BRUVS were set, but 96 were removed because the camera was obscured, or recordings corrupted. Sharks were observed on all sampled reefs, and at least one shark was sighted on 83.2% ($n = 1,676$ of 2,015) of sets. Overall, ten shark species representing four families and three orders were observed (Table 1). Blacktip reef sharks (*Carcharhinus melanopterus*), grey reef sharks (*Carcharhinus amblyrhynchos*), and whitetip reef sharks (*Triaenodon obesus*) were most common.

Mean MaxN for all shark species was 2.45 ± 2.27 . Sharks were most abundant at Takarua atoll (mean MaxN = 5.49 ± 3.21) in the Western Tuamotus and lowest at Rurutu (mean MaxN = 0.31 ± 0.49) in the Austral islands (Figure 2a). Reef-level MaxN ranged from 0.29 ± 0.51 (Rurutu 1) to 6.33 ± 3.36 (Takarua 2).

Blacktip reef sharks were most abundant at Tetiarua Atoll, Windward Society Islands (mean MaxN = 2.30 ± 1.58) and least abundant at Tubuai, Austral Islands (mean MaxN = 0.01 ± 0.1) (Figure 2b). Grey reef sharks were most abundant at Takarua (mean MaxN = 3.20 ± 2.31) and Takapoto (mean MaxN = 1.72 ± 1.44) in the Western Tuamotus. They were least abundant at Raiatea, Leeward Society Islands (mean MaxN = 0.016 ± 0.13) (Figure 2c). Whitetip reef sharks were less abundant than blacktip or grey reef sharks but

were most abundant at Rangiora, Western Tuamotus (mean MaxN = 0.60 ± 0.75) and least abundant at Tubuai, Austral Islands (mean MaxN = 0.01 ± 0.098) (Figure 2d).

All sharks

For total shark MaxN, only island geomorphology, NPP, island group and temperature were retained in the final model (Appendix S3, S4), which accounted for more than 50% of the variation among sets (Table 2). Island geomorphology was the most influential factor, with a relative influence of 55.4%, followed by NPP (20.1%), island group (12.7%), and temperature (11.8%) (Figure 3a).

Of the 35 reefs sampled, six showed some evidence of spatial autocorrelation (Moran's I; P values > 0.0014). To ensure results of the BRTs were not significantly influenced by spatial autocorrelation, a separate BRT analysis was conducted using the mean total shark MaxN for each reef. The same four explanatory variables were retained in the final model (Appendix S3, S4), which accounted for 80.2% of the variation seen among reefs (Table 2). Island geomorphology had a relative influence of 63.1%, followed by island group (21.2%), temperature (8.8%) and NPP (6.9%) (Figure 3b).

There was over a 10-fold difference between island types with the highest and lowest mean total MaxN. Sharks were most abundant on open atolls and least abundant on high islands with fringing reef (Figure 4a). At a broader level, sharks were about three times more abundant on atolls (mean MaxN = 3.88 ± 2.44) than high islands (mean MaxN = 1.31 ± 1.25).

Sharks were most abundant in the Tuamotus, and least abundant at the Austral Islands (Figure 4c). Sites with lower productivity tended to have lower shark abundance (Appendix S6, S7). Higher shark relative abundance was found with higher temperatures in general but was decreased at the highest temperatures sampled.

Blacktip reef sharks

Only island geomorphology and island group were retained in the final model for blacktip reef sharks (Appendix S3, S4), which accounted for >36% of the variation among sets (Table 2). Island geomorphology had a greater relative influence (56.0%) than island group (44.0%; Figure 3c). Blacktip reef sharks were most abundant on closed and open atolls and lowest on high rocky and fringing islands (Figure 5a). When grouped, blacktip reef shark abundance was more than twice as high on all atolls (mean MaxN = 1.91 ± 1.36) than all high islands (mean MaxN = 0.85 ± 0.93 ; $p < 0.001$). Blacktip reef sharks were more than an order of magnitude more abundant in the West Tuamotus (mean MaxN = 1.90 ; ± 1.30) than the Austral Islands (mean MaxN = 0.014 ; ± 0.12) (Figure 5b, Appendix S8).

Grey reef sharks

The final model for grey reef sharks, which accounted for 56.9% of variation in MaxN, retained island group, market gravity, lagoon size, temperature, and island geomorphology (Table 2). Island group was most influential, with a relative influence of 46.9%, followed by market gravity (16.7%), lagoon size (15.1%), temperature (11.9%)

and island geomorphology (9.4%) (Figure 3d). Grey reef shark MaxN in the West Tuamotus (mean MaxN = 1.78 ± 1.70) was more than twenty times that in the Marquesas (mean MaxN = 0.07 ± 0.29), and Windward Society Islands (mean MaxN = 0.04 ± 0.22) (Figure 6a, Appendix S9). They were least abundant on high islands and most abundant on open atolls. More broadly, grey reef sharks were eight times more abundant on atolls (mean MaxN = 1.44 ± 1.60) than on high islands (mean MaxN = 0.17 ± 0.49 , Figure 6e, Appendix S9). Market gravity had a slightly negative effect on MaxN. While lagoon size and temperature had generally positive effects (Figures 6b-d, Appendix S9).

Whitetip reef sharks

Both initial and final models predicted less than 25% of the variation in whitetip reef shark abundance MaxN values (Appendix S3).

Discussion

Across the broad range of ecological conditions found among the relatively undisturbed islands of French Polynesia, I found that shark relative abundance varied markedly. Indeed, differences in environmental conditions were associated with up to 10-fold differences in the relative abundances of specific species. Therefore, setting appropriate conservation and restoration targets for reef sharks of oceanic islands, and likely other habitat types, should incorporate realistic population baselines relative to local ecological conditions. Importantly in the context of this study, easily assessed broad indicators of ecological conditions (i.e., island geomorphology) explained considerable variation in shark relative abundances suggesting that conservation targets can be improved without a

need for a highly detailed understanding of local conditions. For example, in French Polynesia the reef with the highest abundance had a mean MaxN more than twenty times higher than the reef with the lowest MaxN. My results suggest this difference is not due to human pressures. The lack of human impacts on sharks in French Polynesia, despite its overwhelming importance at a global scale (MacNeil et al. 2020), is likely due to the relatively low human populations of French Polynesia, the presence of the shark sanctuary, and a local history of low exploitation of reef-associated sharks. Therefore, my results are likely to provide insights into the ecological factors influencing variation in reef shark relative abundance at island-associated reefs throughout the Indo-Pacific.

Reef shark relative abundances in French Polynesia are among the highest for Indo-Pacific nations sampled using similar methods (e.g., MacNeil et al. 2020). Countrywide, the mean sum of MaxN (2.45 ± 2.27) was greater than that found on BRUVS at the Solomon Islands (1.33 ± 0.12 SE) (Goetze et al., 2018), New Caledonia (1.5 ± 2.2 SD) (Juhel et al., 2018), Fiji (0.8, protected areas; 0.3, fished areas; Goetze & Fullwood, 2013), Indonesia (protected 0.8 and 0.6, fished 0.03; Jaiteh et al., 2016), and Tubbataha Reefs National Park in the Philippines (2.09; Murray et al., 2019).

Island geomorphology was the primary predictor of reef shark relative abundance across French Polynesia. Sharks were about three times more abundant on atolls than they were on high islands and open atolls had abundances nearly 20% higher than closed atolls. Therefore, the studies of sharks on remote atolls (Murray et al. 2019, Friedlander & Demartini 2002) cannot be used as an indicator of pristine abundances of sharks for other

island types and might overestimate the conservation potential of high islands. The high abundances of sharks at high islands in French Polynesia, however, still are among the highest in the region suggesting that there is considerable need for population rebuilding across island types in the region.

Atolls may support larger shark populations for a number of reasons. Phytoplankton biomass tends to be higher around larger islands ('island mass effect'), but atolls have more pronounced island mass effects than high islands (Gove et al., 2016). This is likely due to the export of nutrients from enclosed lagoons (Gove et al., 2016; Vollbrecht et al., 2021). Higher productivity could result in greater prey bases for sharks (e.g., Jennings et al., 2008; Chassot et al., 2010; Nadon et al., 2012), and NPP was a positive factor in my models of shark abundance. Reef sharks may require high proportions of reef productivity to support large populations (Dunn et al., 2022), so differences in productivity, or other factors affecting fish biomass, could be important determinants of carrying capacities.

Access to lagoon habitats may also explain higher abundances of sharks on atolls, particularly open atolls (e.g. Skinner et al. 2020). For example, high islands with the largest enclosed lagoons and near atolls had the highest relative abundances besides true atolls. Lagoon size itself was only retained in the grey reef shark model, suggesting that, for overall shark abundance, total area of lagoon is less important than access to an enclosed lagoon. Lagoons provide nursery habitats for several sharks (e.g., Heupel et al. 2018; Yates et al. 2015). For example, blacktip reef and sicklefin lemon sharks

(*Negaprion acutidens*) use shallow water nurseries in lagoons (e.g., Matich et al., 2017; Mourier et al., 2013; Mourier & Planes, 2013; Papastamatiou et al., 2009). As they grow, sicklefin lemon sharks move to waters along the forereef and beyond while adult blacktip reef sharks continue to use both forereef and lagoon waters frequently (Mourier et al., 2013; Mourier & Planes, 2013; Heupel et al., 2018). In the Line Islands, blacktip reef sharks have higher relative abundances in backreef habitats than forereef habitats (Papastamatiou et al., 2018) suggesting that greater availability of these habitats, that I did not sample, may increase overall population sizes at islands. It may also be that the reef passes, connecting lagoon and forereef habitats, facilitate high shark abundances. Indeed, these habitats can host fish spawning aggregations that support high abundances of sharks (Mourier et al. 2016).

Shark MaxN varied among island groups, which extend over a large latitudinal gradient. This, gradient, along with conditions not included in models, like bathymetry and shared disturbance histories may drive this pattern. Higher water temperatures were generally associated with higher MaxN values across the ranges I sampled. This is consistent with other studies (e.g. Schlaff et al. 2014). For instance, midwater BRUVS surveys in the Indo-Pacific found that SST was positively correlated with shark abundances at a large scale (Letessier et al., 2019). Similarly, towed-diver surveys of sharks across the Pacific found that shark densities increased with SST (Nadon et al., 2012). Higher temperatures, however, may not always benefit sharks (Rummer et al., 2022).

Although there were broad similarities in the factors associated with variation in abundance for the two most common species in my survey, there were also important differences between species. Only island group and island geomorphology were retained in the blacktip reef shark model, but island group was a more important factor in the grey reef shark model. Island geomorphology, the primary predictor for both total shark abundance and blacktip reef shark abundance, was the least influential of the significant factors for grey reef sharks. This interspecific variation in drivers of relative abundance may be due to spatial partitioning and differences in feeding ecology. Blacktip reef sharks occur in backreef, lagoon, and forereef habitats as adults while grey reef sharks favor forereef habitats (Heupel, Lédée, et al., 2018; Papastamatiou et al., 2018). Furthermore, in some locations grey reef sharks rely more on pelagic food webs than blacktip reef sharks (McCauley et al., 2012). Finally, while blacktip reef sharks use lagoon areas as nurseries (e.g., Papastamatiou et al. 2009; Mourier & Planes 2013; Matich et al. 2017) this does not appear to be the case for grey reef sharks.

Regardless of the reasons for interspecific variation in responses to environmental factors, my results suggest that easily determined environmental factors can be used to better set conservation targets for reef sharks generally and for abundant species in particular. For instance, if the countrywide mean MaxN in French Polynesia set expectations for shark relative abundances at all sites, it would overestimate potential abundances at some reefs by over a factor of eight. Also, this method would result in a target *ca.* 40% below the relative abundances I observed at reefs with high MaxN. Using broad geomorphological categories to set targets would reduce these errors dramatically

and facilitate more efficient use of conservation resources and effective management approaches.

While setting quantitative conservation targets is widely considered best practice, arriving at specific targets can be challenging, especially where data on historical baselines are unavailable or no longer realistic (Carwardine et al., 2009; Jachowski et al., 2015). Understanding how habitat and environmental features affect carrying capacity can help managers address some of these challenges. Efforts to base conservation on carrying capacity have been undertaken for both marine (Tinker et al., 2021) and terrestrial predators (Lyons et al., 2018). It may, however, be difficult to extrapolate findings from one study area to locations where conservation is being undertaken if the factors affecting carrying capacity are complex or difficult to measure, which is not the case for reef sharks of French Polynesia. Indeed, broad geomorphological characteristics of islands explained considerable variation in near natural reef shark relative abundances. Therefore, improving baseline predictions for similar islands in the Indo-Pacific would not require expensive monitoring or measurements. Further studies, exploring interspecific interactions in driving relative abundances in the absence of large anthropogenic effects, could enhance our understanding of the structure and abundance of natural reef shark communities.

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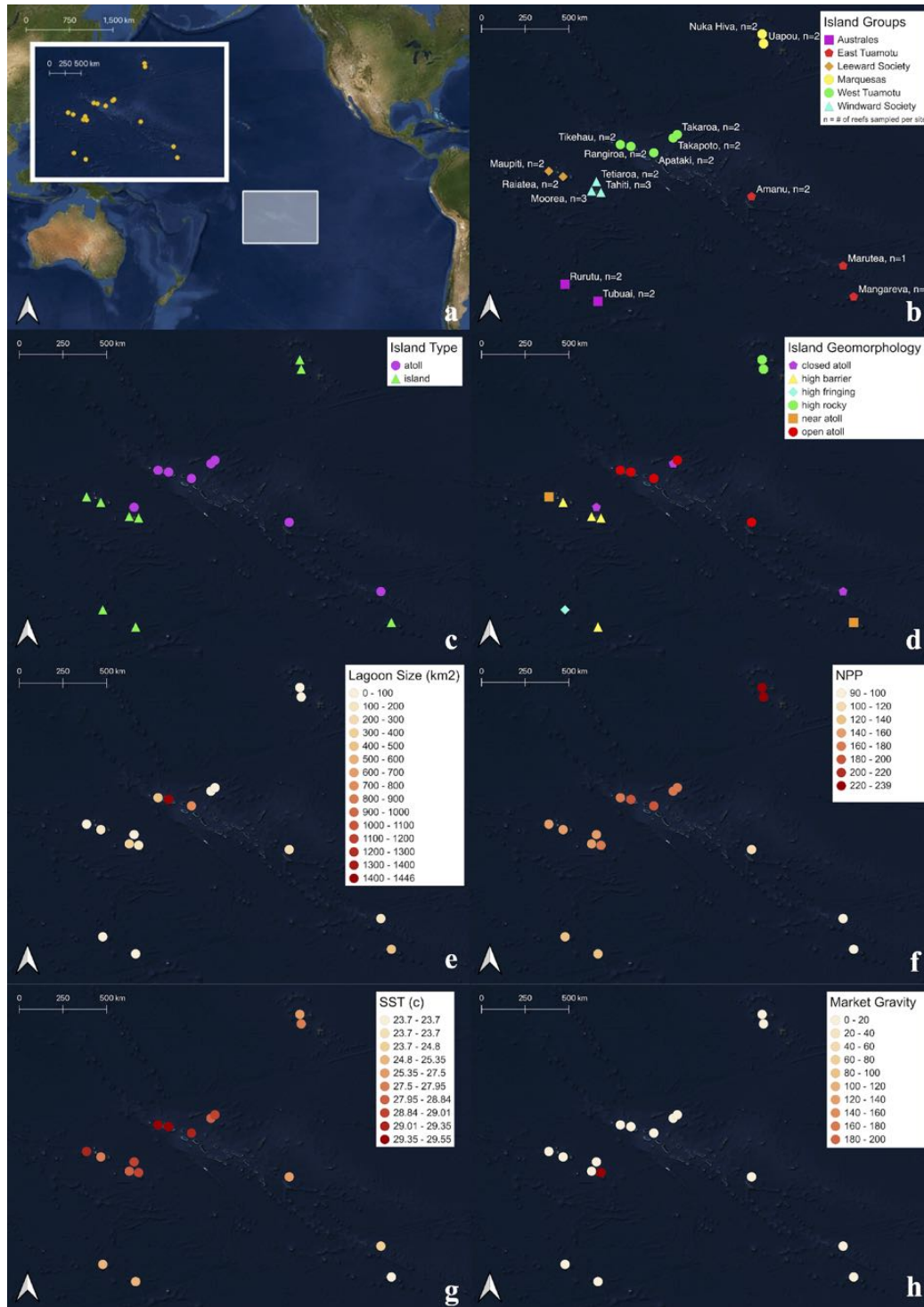
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Table 1: Shark species observed on BRUVS. LC =Least concern, NT =Near Threatened, VU =Vulnerable, EN =Endangered, CR =Critically Endangered.

Scientific Name	Common Name	Primary Habitat	IUCN Status	Mean MaxN	SD MaxN	% Sets Present	# Reefs Present
<i>Carcharhinus albimarginatus</i>	Silvertip shark	reef	VU	0.002	0.050	0.25	3
<i>Carcharhinus amblyrhynchos</i>	Grey Reef Shark	reef	EN	0.74	1.29	37.4	33
<i>Carcharhinus limbatus</i>	Common Blacktip Shark	transient	VU	0.02	0.15	1.6	10
<i>Carcharhinus melanopterus</i>	Blacktip reef shark	reef	VU	1.32	1.25	72.1	34
<i>Galeocerdo cuvier</i>	Tiger shark	transient	NT	0.002	0.05	0.17	5
<i>Negaprion acutidens</i>	Sicklefin lemon shark	reef	EN	0.08	0.32	6.8	25
<i>Sphyrna lewini</i>	Scalloped hammerhead	pelagic	CR	0.004	0.07	0.30	5
<i>Sphyrna mokarran</i>	Great hammerhead	transient	CR	0.0005	0.02	0.03	1
<i>Triaenodon obesus</i>	Whitetip reef shark	reef	VU	0.2	0.45	18.6	33
<i>Nebrius ferrugineus</i>	Tawny nurse shark	reef	VU	0.03	0.21	2.8	11

Table 2: Boosted regression tree parameters and mean model results for final models. CV = Cross Validated. Percent variation explained = 1- (residual deviance/total deviance).

Model Response Variable	Tree Complexity	Learning Rate	Bag Fraction	% Variation Explained	Correlation	CV % Variation Explained	CV Correlation
Total Shark MaxN	2	0.017	0.68	50.1	0.69	48.6	0.68
Reef Mean Shark MaxN	2	0.009	0.75	80.1	0.90	68.0	0.82
Blacktip Reef Shark MaxN	2	0.019	0.66	36.0	0.53	35.2	0.52
Grey Reef Shark MaxN	2	0.023	0.56	56.9	0.69	55.4	0.68
Whitetip Reef Shark MaxN	1	0.033	0.52	20.8	0.41	18.2	0.38



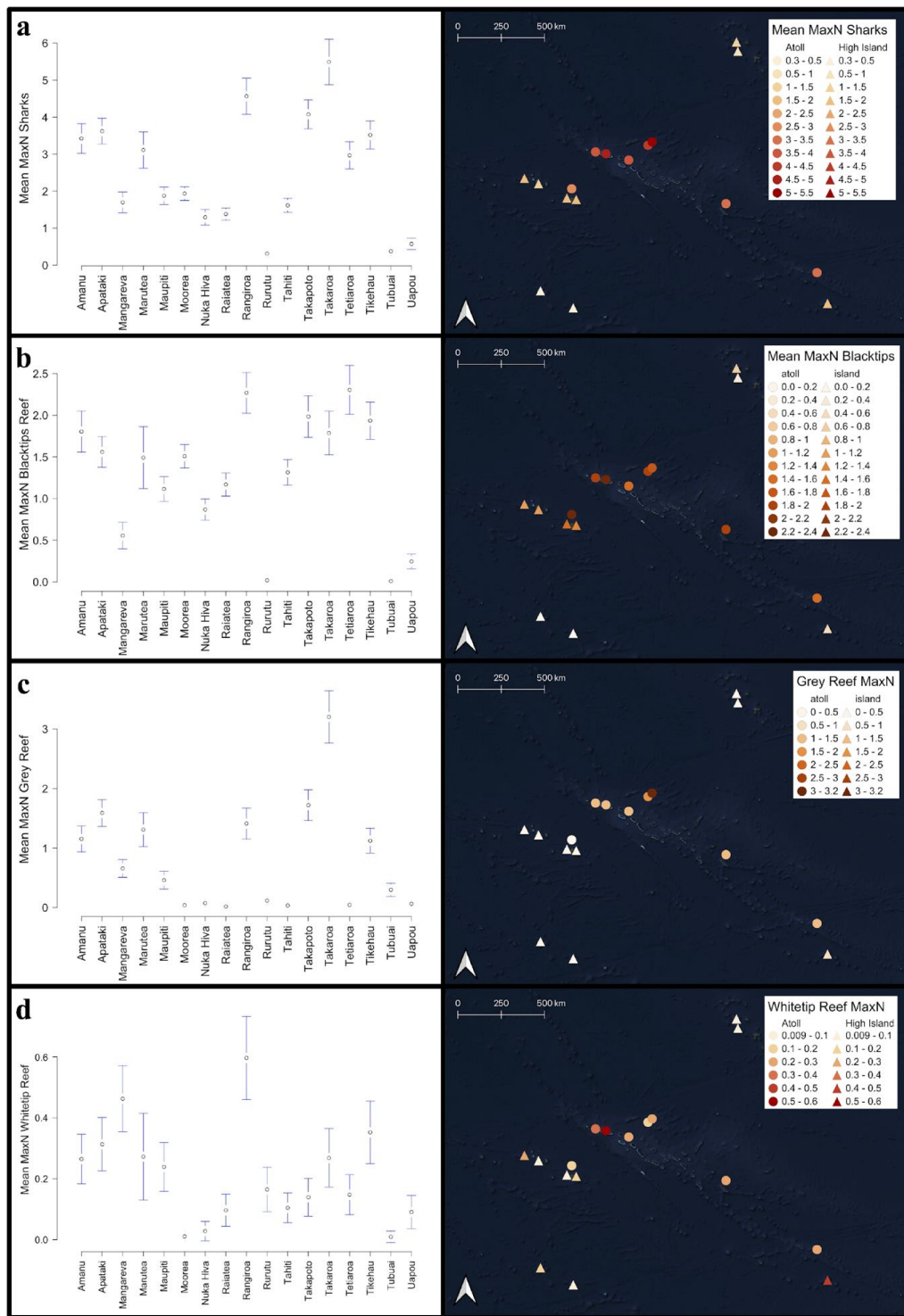


Figure 2: Spatial variation in relative shark abundance. Mean MaxN by site for a) all b) blacktip reef, c) grey reef, and d) whitetip reef sharks. Circles represent atolls and diamonds represent high islands.

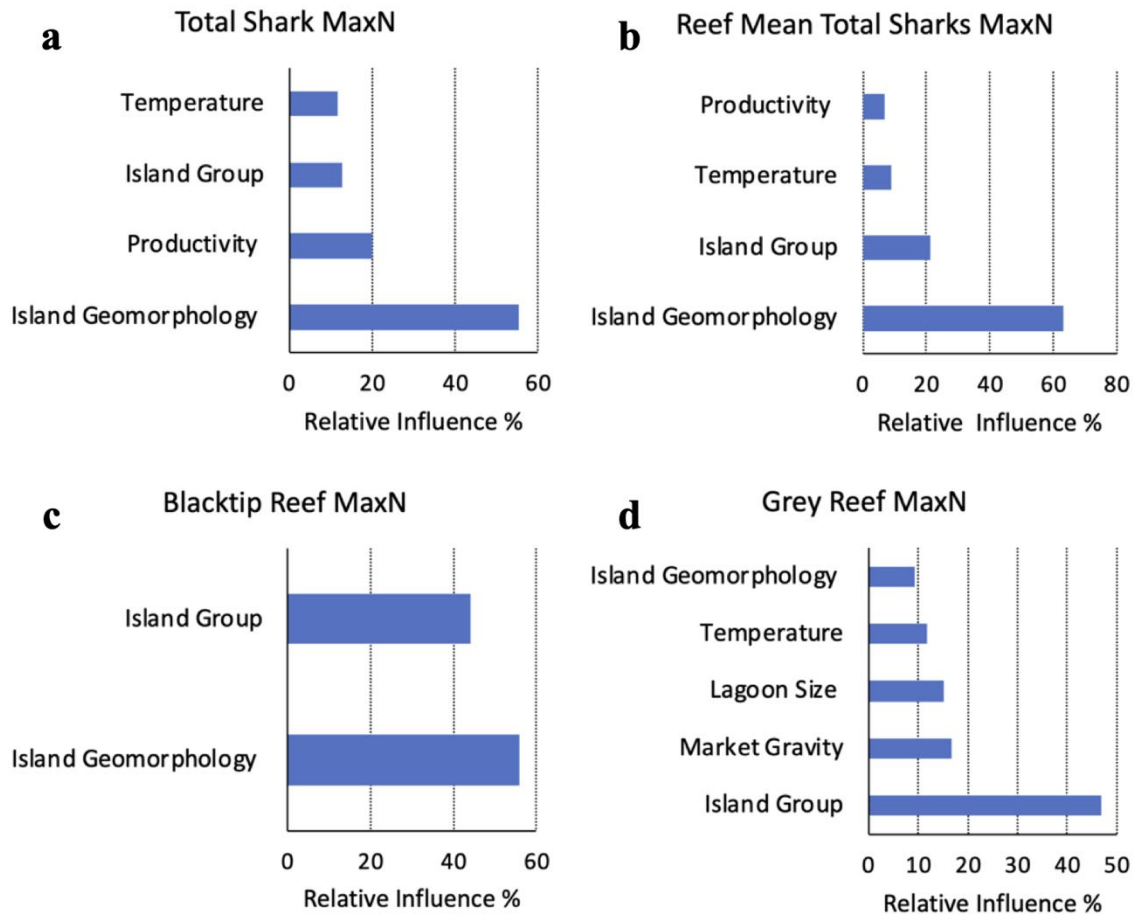


Figure 3: Mean relative influence of predictor variables in final BRT models of (a) total shark MaxN, (b) mean of total shark MaxN by reef, (c) blacktip reef shark MaxN, and (d) grey reef shark MaxN.

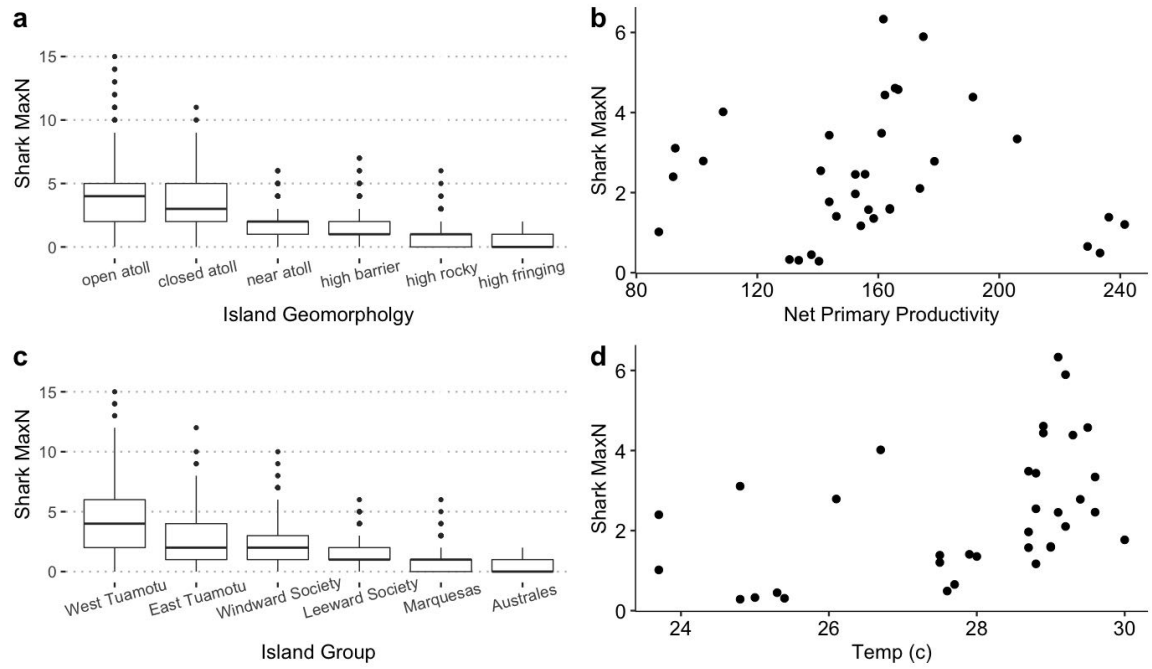


Figure 4: Relationship between mean MaxN and (a) island geomorphology, (b) net primary productivity, (c) island group, and (d) temperature.

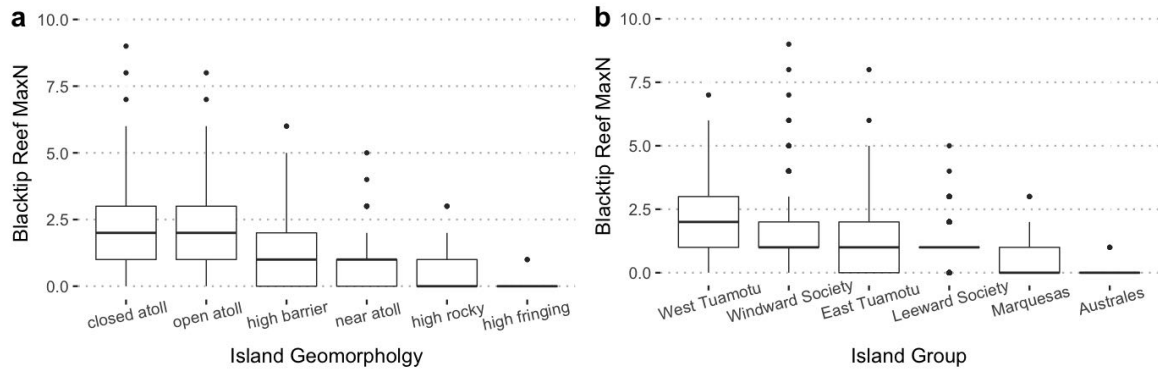


Figure 5: Relationship between blacktip reef shark mean MaxN and (a) island geomorphology and (b) island group.

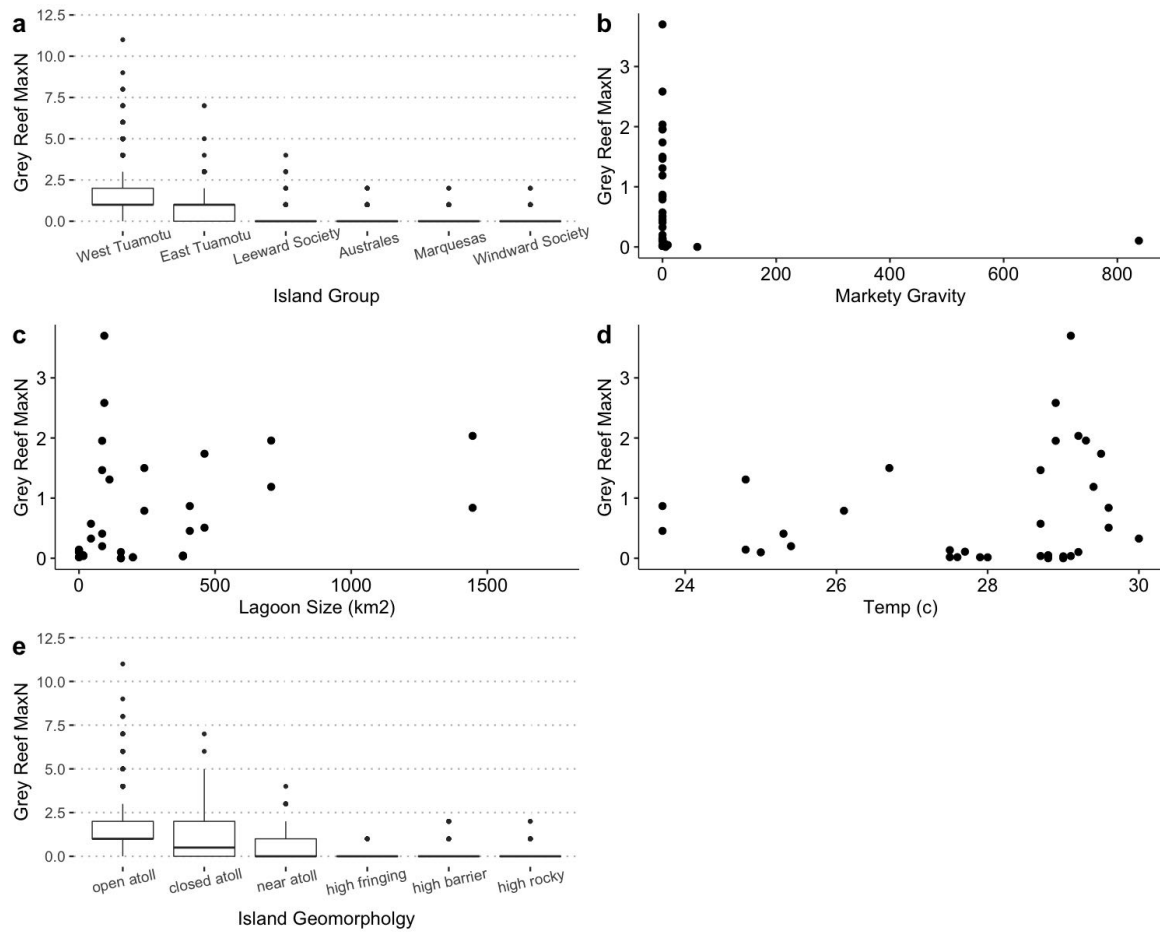


Figure 6: Relationship between grey reef shark mean MaxN and (a) island group, (b) market gravity, (c) lagoon size, (d) temperature and (e) island geomorphology.

Supplemental Material

Appendix S1: Shark species of French Polynesia (Clua et al. 2021, Siu et al., 2017), their IUCN protection status and their primary habitats as determined by habitat description Ebert et al. (2021), and being consistent with the definition of reef sharks as found in defined by Chapman et al. (2022). (LC= Least concern, NT= Near Threatened, VU= Vulnerable, EN= Endangered, CR= Critically Endangered, DD= Data Deficient).

Family	Scientific Name	Common Name	Primary Habitat	IUCN Status
Alopiidae	<i>Alopias pelagicus</i>	Pelagic thresher	pelagic	EN
Alopiidae	<i>Alopias vulpinus</i>	Thresher	pelagic	VU
Carcharhinidae	<i>Carcharhinus albimarginatus</i>	Silvertip shark	reef	VU
Carcharhinidae	<i>Carcharhinus amblyrhynchos</i>	Grey Reef Shark	reef	EN
Carcharhinidae	<i>Carcharhinus falciformis</i>	Silky shark	pelagic	VU
Carcharhinidae	<i>Carcharhinus galapagensis</i>	Galapagos shark	reef	LC
Carcharhinidae	<i>Carcharhinus leucas</i>	Bull shark	transient	VU
Carcharhinidae	<i>Carcharhinus limbatus</i>	Common Blacktip Shark	transient	VU
Carcharhinidae	<i>Carcharhinus longimanus</i>	Oceanic whitetip	pelagic	CR
Carcharhinidae	<i>Carcharhinus melanopterus</i>	Blacktip reef shark	reef	VU
Carcharhinidae	<i>Galeocerdo cuvier</i>	Tiger shark	transient	NT
Carcharhinidae	<i>Negaprion acutidens</i>	Sicklefin lemon shark	reef	EN
Carcharhinidae	<i>Prionace glauca</i>	Blue shark	pelagic	NT
Carcharhinidae	<i>Triaenodon obesus</i>	Whitetip reef shark	reef	VU
Dalatiidae	<i>Euprotomicrus bispinatus</i>	Pygmy shark	deep sea	LC
Dalatiidae	<i>Isistius brasiliensis</i>	Cookie cutter shark	deep sea	LC
Echinorhinidae	<i>Echinorhinus cookei</i>	Prickly shark	deep sea	DD
Etmopteridae	<i>Etmopterus lucifer</i>	Blackbelly lanternshark	deep sea	LC
Ginglymostomatidae	<i>Nebrius ferrugineus</i>	Tawny nurse shark	reef	VU
Hexanchidae	<i>Hexanchus nakamurai</i>	Bigeyed sixgill shark	deep sea	NT
Lamnidae	<i>Isurus oxyrinchus</i>	Shortfin mako	pelagic	EN
Pseudocarchariidae	<i>Pseudocarcharias kamoharai</i>	Crocodile shark	pelagic	LC
Rhincodontidae	<i>Rhincodon typus</i>	Whale shark	pelagic	EN
Scyliorhinidae	<i>Pseudotriakis microdon</i>	False catshark	deep sea	LC
Somniosidae	<i>Centroscymnus owstonii</i>	Roughskin dogfish	deep sea	NT
Sphyrnidae	<i>Sphyrna lewini</i>	Scalloped hammerhead	pelagic	CR
Sphyrnidae	<i>Sphyrna mokarran</i>	Great hammerhead	transient	CR
Squalidae	<i>Centrophorus atromarginatus</i>	Dwarf gulper shark	deep sea	CR
Squalidae	<i>Centrophorus moluccensis</i>	Smallfin gulper shark	deep sea	VU
Squalidae	<i>Centrophorus tessellatus</i>	Mosaic gulper shark	deep sea	EN
Squalidae	<i>Squalus megalops</i>	Shortnose spurdog	deep sea	LC
Squalidae	<i>Squalus melanurus</i>	Blacktailed spurdog	deep sea	DD
Squalidae	<i>Squalus mitsukurii</i>	Shortspine spurdog	deep sea	EN

Appendix S2: Sample sizes for sampled reefs, the sites and island groups where they are found, the type of island geomorphology of the site, and human population size (*Census Report 2017*, ISPF).

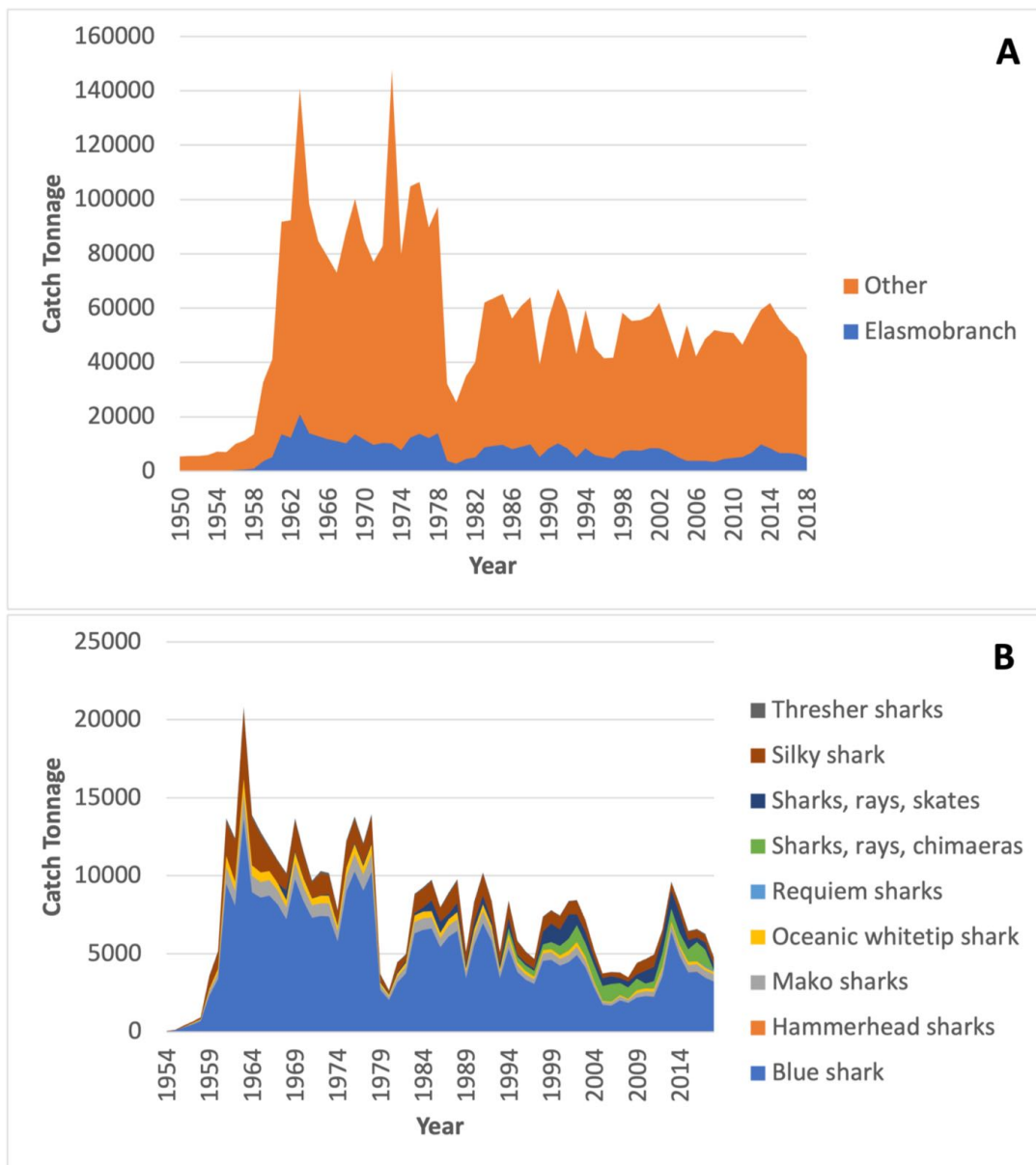
Reef	Site	Island Group	Island Geomorphology	Number of Sets	Human Population
Amanu 1	Amanu	East Tuamotu	open atoll	57	174
Amanu 2	Amanu	East Tuamotu	open atoll	60	174
Apataki1	Apataki	West Tuamotu	open atoll	70	442
Apataki2	Apataki	West Tuamotu	open atoll	64	442
Mangareva 1	Mangareva	East Tuamotu	near atoll	53	1384
Mangareva 2	Mangareva	East Tuamotu	near atoll	55	1384
Marutea 1	Marutea	East Tuamotu	closed atoll	55	104
Maupiti1	Maupiti	Leeward Society	near atoll	52	1295
Maupiti2	Maupiti	Leeward Society	near atoll	61	1295
Moorea1	Moorea	Windward Society	high barrier	66	18071
Moorea2	Moorea	Windward Society	high barrier	54	18071
Moorea3	Moorea	Windward Society	high barrier	63	18071
Nuka Hiva 1	Nuka Hiva	Marquesas	high rocky	54	3120
Nuka Hiva 2	Nuka Hiva	Marquesas	high rocky	52	3120
Raiatea1	Raiatea	Leeward Society	high barrier	65	12249
Raiatea2	Raiatea	Leeward Society	high barrier	59	12249
Rangiroa1	Rangiroa	West Tuamotu	open atoll	62	2709
Rangiroa2	Rangiroa	West Tuamotu	open atoll	57	2709
Rurutu 1	Rurutu	Austral Islands	high fringing	42	2574
Rurutu 2	Rurutu	Austral Islands	high fringing	61	2574
Tahiti1	Tahiti	Windward Society	high barrier	58	189277
Tahiti2	Tahiti	Windward Society	high barrier	59	189277
Tahiti3	Tahiti	Windward Society	high barrier	55	189277
Takapoto1	Takapoto	West Tuamotu	closed atoll	58	501
Takapoto2	Takapoto	West Tuamotu	closed atoll	64	501
Takaroa 1	Takaroa	West Tuamotu	open atoll	48	674
Takaroa 2	Takaroa	West Tuamotu	open atoll	60	674
Tetiaroa1	Tetiaroa	Windward Society	closed atoll	60	240
Tetiaroa2	Tetiaroa	Windward Society	closed atoll	55	240
Tikehau 1	Tikehau	West Tuamotu	open atoll	61	560
Tikehau 2	Tikehau	West Tuamotu	open atoll	61	560
Tubuai1	Tubuai	Austral Islands	high barrier	49	2217
Tubuai2	Tubuai	Austral Islands	high barrier	55	2217
Uapou 1	Uapou	Marquesas	high rocky	55	2213
Uapou 2	Uapou	Marquesas	high rocky	55	2213

Appendix S3: Boosted Regression Tree parameters and mean model results for initial models results. CV= Cross Validated. Percent variation explained = 1- (residual deviance/total deviance).

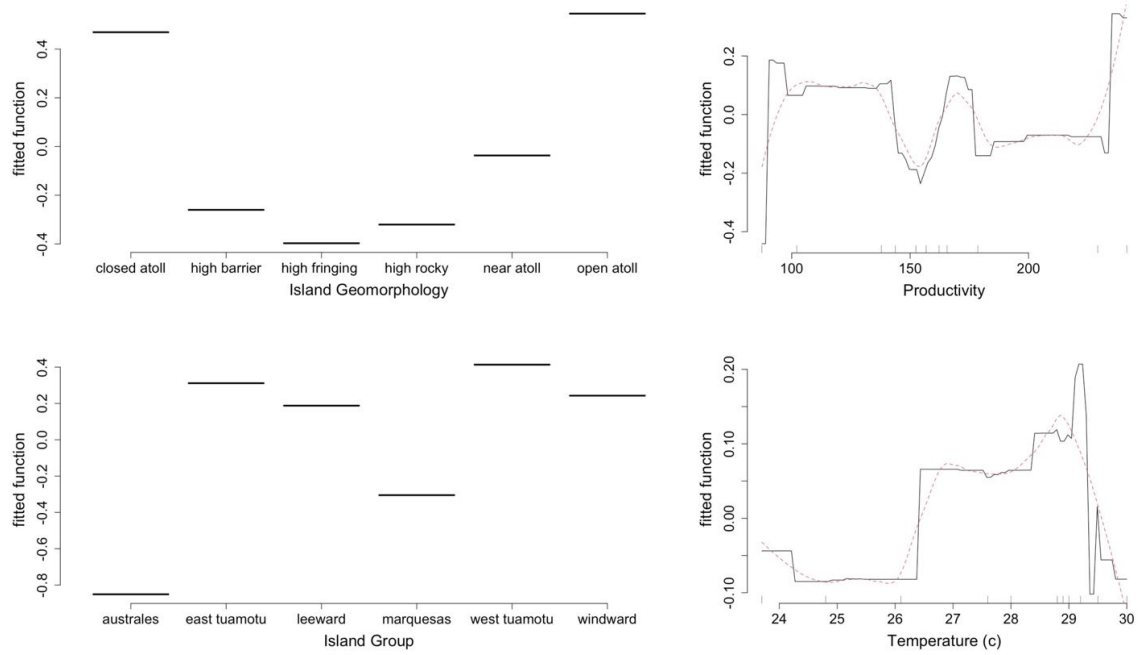
Model Response Variable	Tree Complexity	Learning Rate	Bag Fraction	% Variation Explained	Correlation	CV % Variation Explained	CV Correlation
Total Shark MaxN	2	0.017	0.685	53.38	0.728	48.22	0.677
Reef Mean Shark MaxN	2	0.009	0.750	80.48	0.909	65.73	0.796
Blacktip Reef Shark MaxN	2	0.019	0.655	44.43	0.629	38.72	0.563
Grey Reef Shark MaxN	2	0.023	0.560	58.60	0.726	54.15	0.675
Whitetip Reef Shark MaxN	1	0.033	0.525	19.69	0.413	16.18	0.366

Appendix S4: Mean relative influence of all model factors for initial model runs.

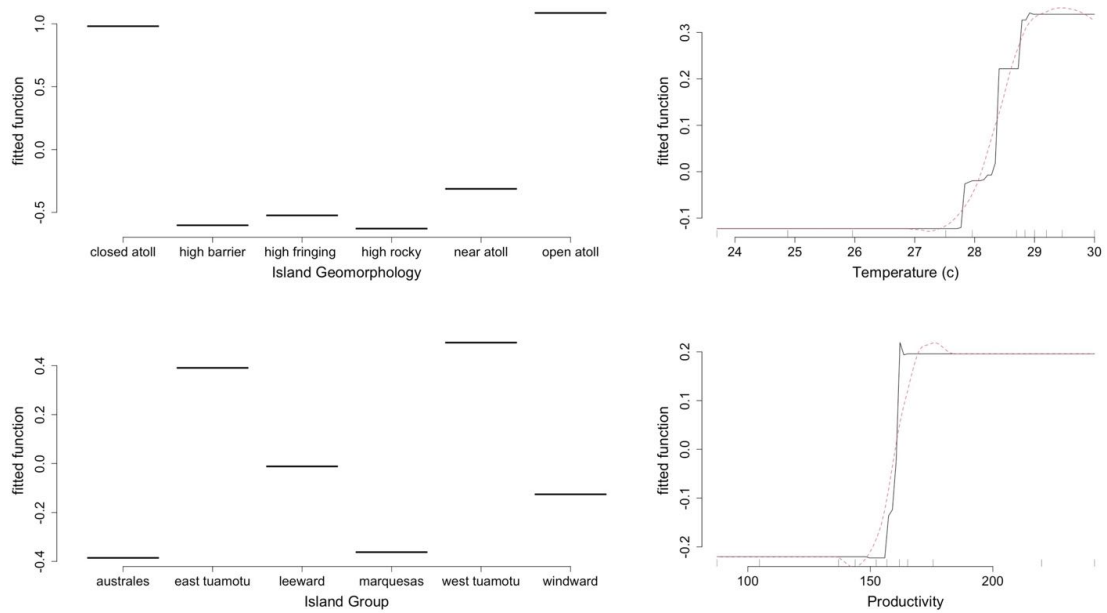
	Total Shark MaxN	Reef Mean Shark MaxN	Blacktip Reef Shark MaxN	Grey Reef Shark MaxN	Whitetip Reef Shark MaxN
Island Geomorphology	49.08	62.22	31.08	7.56	26.64
Island Group	11.44	18.96	18.04	47.89	4.70
Temperature	7.62	8.05	9.84	7.32	7.79
Net Primary Productivity	11.08	5.20	7.47	4.25	5.32
Random	7.52	2.37	11.16	5.84	7.95
Gravity	4.07	1.24	8.66	10.07	11.01
Lagoon Size	1.36	0.94	3.10	11.10	32.94
Season	0.09	1.22	0.13	0.28	0.02
Time without Bait	2.18	NA	2.97	1.93	2.54
Bait Type	3.45	NA	3.78	1.64	NA
Depth	1.60	NA	2.53	2.13	1.03
Visibility	0.51	NA	1.25	0.01	0.06



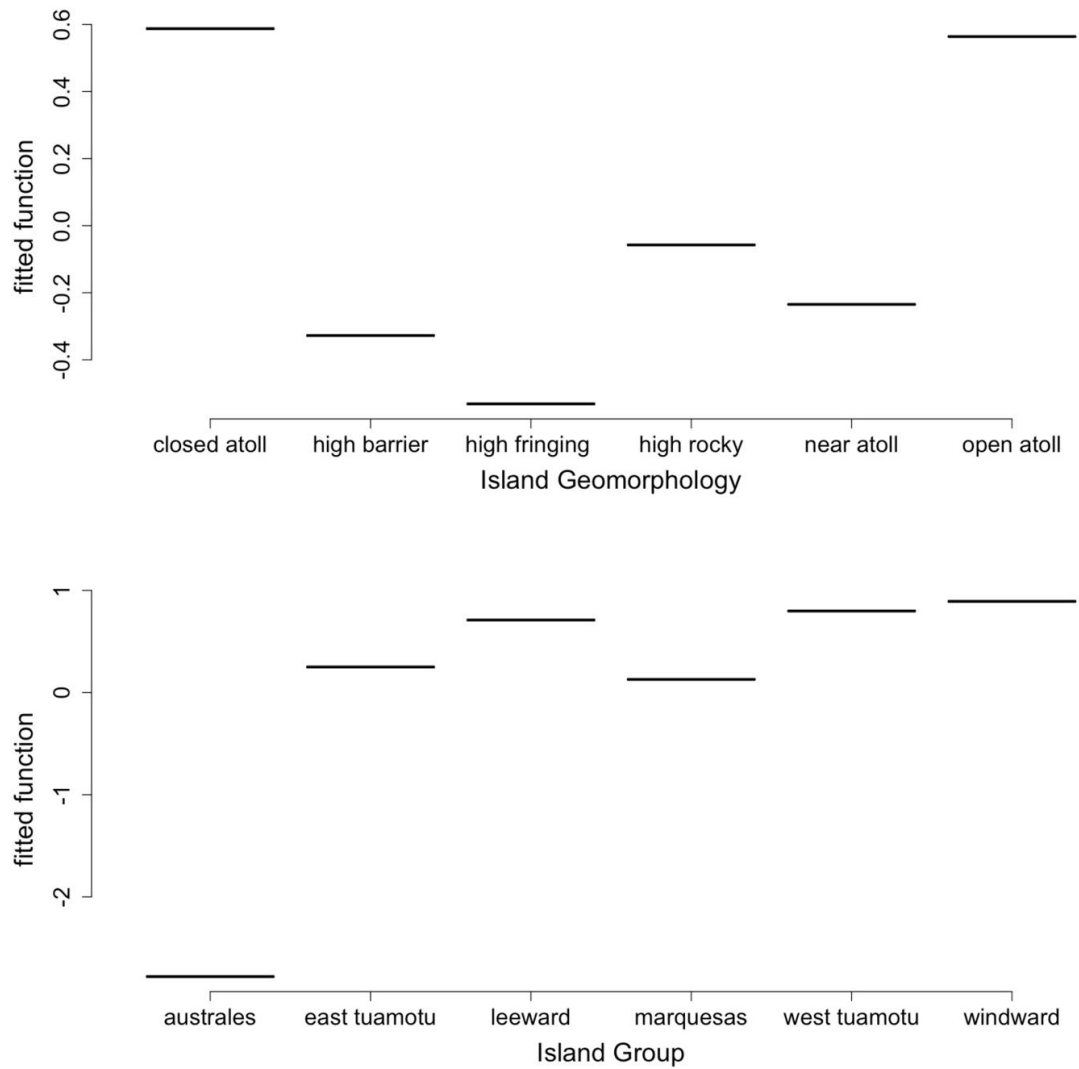
Appendix S5: Reconstructed catch data, in tons from French Polynesia (Bale et al., 2009; Pauly et al., 2020; R. White et al., 2020). A) Total catch of elasmobranchs and other catches B) Taxa-specific elasmobranch catches.



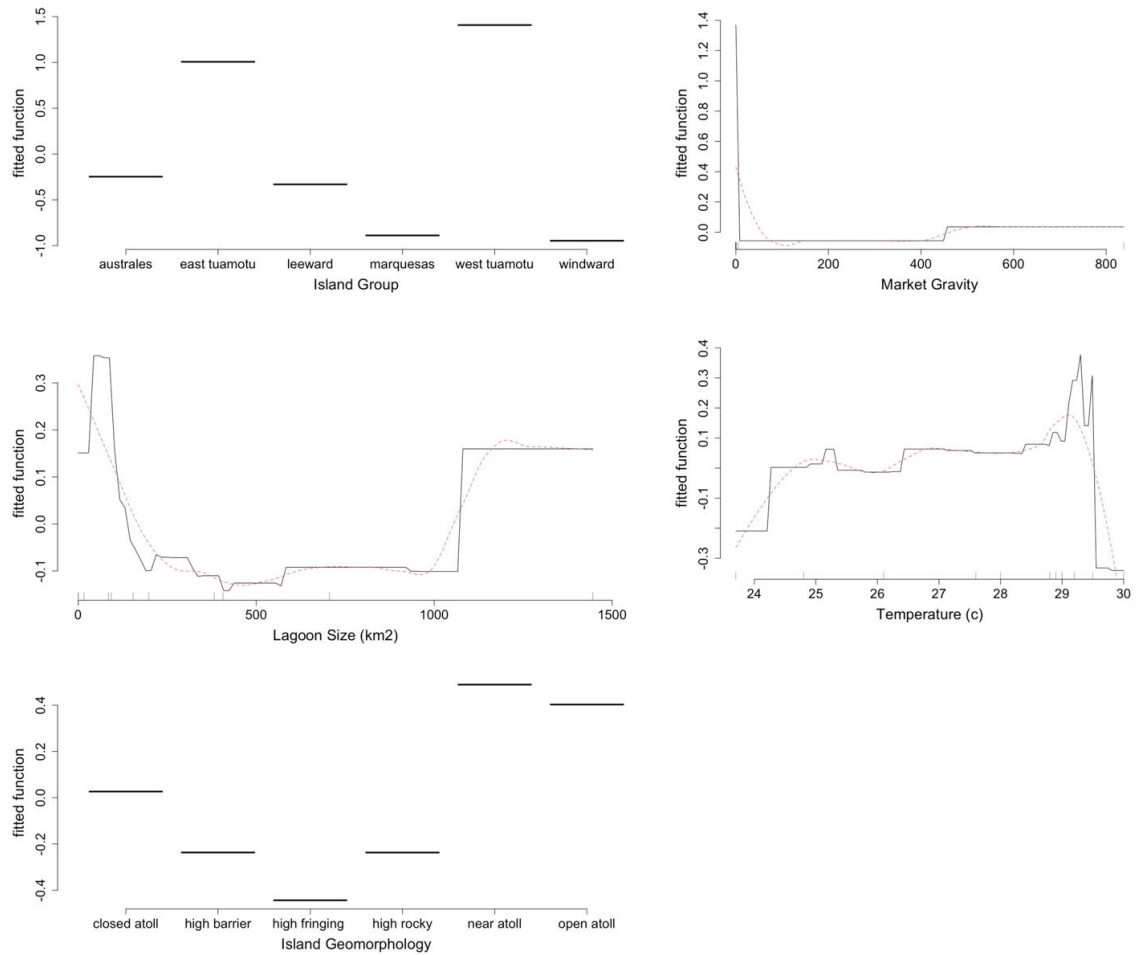
Appendix S6: Partial dependency plots generated by single run of final boosted regression tree model, showing the relationship between final model predictor variables and total shark MaxN.



Appendix S7: Partial dependency plots generated by single run of final boosted regression tree model, showing the relationship between final model predictor variables and reef mean MaxN of all sharks.



Appendix S8: Partial dependency plots generated by single run of final boosted regression tree model, showing the relationship between final model predictor variables and blacktip reef shark MaxN.



Appendix S9: Partial dependency plots generated by single run of final boosted regression tree model, showing the relationship between final model predictor variables and grey reef shark MaxN.

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CHAPTER III

VARIATION IN PREDATORY FISH ABUNDANCES ACROSS HUMAN AND ENVIRONMENTAL GRADIENTS ON REMOTE CORAL REEF IN THE SOUTH PACIFIC

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ABSTRACT

Despite their importance, coral reefs are threatened by many anthropogenic factors including overfishing. Understanding how fish assemblages vary across environmental conditions and human pressures may provide restoration targets, and elucidate drivers of natural variability in assemblages, and responses to localized fishing. I used baited remote underwater video stations (BRUVS) to assess relative abundance of predatory teleosts (Lutjanidae, Scombridae, Megalopidae, Carangidae, Sphyraenidae, Serranidae and Lethrinidae) on 19 reefs across 11 different islands/atolls in French Polynesia which represent gradients of anthropogenic and environmental factors. Boosted Regression Tree (BRT) models for the relative abundance of all predatory teleosts revealed net primary productivity as the largest model contributor (relative influence *ca.* 37%), with more productive reefs having higher abundances. Island geomorphology (relative influence *ca.* 15.5%), human population density (14.3%), relative abundance of sharks (10.7%), and sea surface temperature (10.7%) also influenced abundances. Interestingly, higher abundances of teleosts were found on reefs with higher abundances of sharks after accounting for other factors. BRT models run at the individual family level for Lutjanidae and Carangidae revealed that net primary productivity was the most significant effect, while island geomorphology was the most influential factor for Serranidae. My results suggest that shifts in net primary productivity will likely have major consequences for the abundances of reef-associated teleost predators, these taxa may be highly sensitive to fishing pressures from even low human population densities. Further work is needed to resolve the mechanisms through which this might occur.

1. INTRODUCTION

Coral reefs are biodiversity hotspots, supporting upwards of 30% of all marine species (Fisher et al. 2015). They provide numerous ecosystem services on local and global levels including food production, generation of livelihoods, coastal protection, carbon sequestration, and biotechnology (e.g. Ferrario et al. 2014; Hughes et al. 2017; Moberg & Folke 1999; Woodhead et al. 2019). Estimates of the value of annual ecosystem goods and services provided by reefs globally range from *ca.* US \$36,000 ha⁻¹ to over US \$2,000,000 ha⁻¹ (Costanza et al. 2014). For example, an estimated six million fishers rely on coral reefs (Teh et al. 2013), and fish make up the vast majority of animal protein in the diets of peoples in Pacific Island nations and territories, making fish and the coral reefs that support them a mainstay of nutrition and food security (Bell et al. 2009).

Coral reef ecosystems are under considerable threat across almost the entirety of their range due to anthropogenic factors including ocean acidification, climate change, pollution, bleaching, habitat destruction, predator outbreaks, and pervasive overfishing (Bellwood et al. 2004; Hughes 1994; Ruppert et al. 2013; Ruttenberg et al. 2011). Even remote reefs with no or few human inhabitants are experiencing threats from global stressors and occasionally local acute ones (Bruno & Selig 2007; Cinner et al. 2016; Hughes et al. 2018). However, this makes the preservation of biodiversity and species interactions a high priority to safeguard the resilience of these imperiled systems. Such an approach would be facilitated by a better understanding how fish abundances and diversity vary across environmental conditions and human pressures.

While there is much yet still to be understood about the consequences, both ecologically and economically, of the degradation of coral reef ecosystems, losing reefs would mean the decline or loss of many of these ecosystem services (e.g. Eddy et al. 2021; Woodhead et al. 2021; Worm et al. 2006).

Of particular interest are how relatively large-bodied teleost predators respond to human and environmental factors due to their potential to play important roles in population, community, and ecosystem dynamics on reefs (e.g. Dulvy et al. 2004, Bascompte et al. 2005, Lédée et al. 2015). These species are also often some of the first targeted by fishers (e.g. Jennings & Polunin 1996, Pauly et al. 1998, Pauly & Palomares 2001, Stallings 2009) and, therefore, may be susceptible to even low-intensity fishing. Also, these species may be competitors, intraguild prey, or prey for sharks which are threatened on many reefs worldwide (e.g. MacNeil et al. 2020, Roff et al. 2016). Therefore, it is possible that predatory teleost populations may be influenced by changes in reef shark abundance (e.g. Barely 2017, Lester et al. 2021a, Heithaus et al. 2022), but the direction and nature these changes is poorly resolved (e.g. Desbiens et al. 2021, Heithaus et al. 2022). Therefore, a better understanding of how even relatively low levels of human pressure and changes in environmental or biological factors might affect populations of predatory teleosts on reefs is of management concern.

French Polynesia is an ideal system to investigate how relative abundances of predatory fishes vary across environmental and anthropogenic gradients. French Polynesia's large exclusive economic zone (EEZ) encompasses five archipelagos in the South Pacific

which contain over 2% of the world's living reef area (Spalding et al., 2001). French Polynesia's EEZ is also the world's largest shark sanctuary, with prohibitions on shark fishing, trade, and export. Fish protein is a nutritional staple, constituting ~65% of the animal protein people consume, with 72% of fish being obtained from subsistence fishing. Fishing pressure, however, is not homogenous across the country (Bell et al. 2009).

Here, I used baited remote underwater video stations (BRUVS) to assess the relative abundance of predatory teleost species across French Polynesian forereefs, with a focus on the higher trophic level teleost predators that are more likely to be impacted by local fishing pressures. We aim to assess how predatory teleost abundance varies in relation to relative abundance of sharks as well as environmental and anthropogenic gradients in French Polynesia.

2. MATERIALS AND METHODS

2.1 Site Description

French Polynesia is an overseas collectivity of France in the south-central Pacific, between 7° - 27° S and 134° - 155° W (Figure 1). It has a total land area of only 4,167 km², but its exclusive economic zone extends over 5,030,000 km². French Polynesia is tropical with a warm rainy season (Nov – Apr) and a relatively drier cooler season (May – Oct), though there is latitudinal variation in climate. The country is made up of five

archipelagos: the Marquesas Islands, the Tuamotu Archipelago, the Society Islands, the Gambier Islands, and the Austral Islands. I categorized the islands into six groups based on geography: Marquesas, Leeward Society Islands, Windward Society Islands, West Tuamotus, East Tuamotus with the Gambier Islands, and the Austral Islands (Figure 1B). For more detailed site description see Chapter II.

2.2 Field Methods

Surveys using BRUVS were conducted on 19 reefs across 11 different islands/atolls in French Polynesia. I defined a reef as an area of approximately 4 km² with continuous coral reef habitat.

All sites were classified based on their geomorphology: open atoll, closed atoll, near atoll, high barrier, high fringing, and high rocky. Atolls were subdivided into open atolls and closed atolls. While closed atolls lack navigable passes, smaller shallow water passes, allow the movement of water and animals between the forereef and lagoon. High Islands were broken down into several categories. Near atolls feature 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). Because habitats and environmental conditions in the Marquesas differ markedly from elsewhere in French Polynesia, this site excluded from the BRT modeling.

BRUVS consisted of a GoPro camera (GoPro Hero4 Silver or GoPro Hero+ action camera) mounted to an aluminum frame with an *ca.* 1.5 m pole that held *ca.* 1 kg of oily fish bait (yellowfin tuna *Thunnus albacares*, small inshore fish, fish heads and scraps—typically tuna-, or sardines *Clupeidae spp.*) in a container in front of the camera. The camera and bait were positioned to face down current, which was determined using dye tabs. BRUVS were deployed in daylight hours on the forereef at 9 - 35 m depth. No two BRUVSs were deployed within 500 m of another within a sampling day to limit autocorrelation. Each BRUVS set had a minimum soak time of 60 min, with deployments up to 90 min. Each reef had a minimum of 42 sets deployed (mean = 56, max = 70).

At an individual reef, most sets were deployed over a single period of fewer than 10 days (max 37 days), and all sampling took place in 2016 or 2017. For each deployment, sea surface temperature °C (SST) was taken using a YSI Pro 2030, bottom depth (m) recorded, and water visibility visually estimated to the nearest meter up to 15 meters.

2.3 Video Data Extractions

Each video was watched and annotated to 60 min by an expert annotator using the Fingerprint Annotator (v1.1.44.0). All recorded observations were double checked by an independent expert annotator to ensure accurate identifications. Annotators watched for all members of target families (Lutjanidae, Scombridae, Megalopidae, Carangidae, Sphyraenidae, Serranidae and Lethrinidae) and identified them to the lowest possible taxonomic level. These families were selected as they contain large piscivorous fishes most often considered teleostean mesopredators (e.g. Desbiens et al. 2021).

MaxN, the maximum number of individuals of each target species seen in a single frame for each video, is the standard for reporting relative abundance for BRUVS data because it avoids re-counting the same individual that might enter and exit the field of view multiple times (Cappo et al., 2004; MacNeil et al., 2020). For each video, MaxN was calculated for each species in a family, these were then summed together to calculate MaxN for each target family. Teleosts that could not be identified to family level (less than 5% of observations) were excluded from analysis. Individuals who could not be identified to species but could be identified at the family level accounted for less than 10% of observations. Since these unknowns could potentially be individuals identified to species elsewhere in the video, MaxN for family unknowns was calculated separately. To avoid re-counting individuals MaxN for each target family was determined using the whichever MaxN sum, the sum of unknowns or the sum of those identified down to species, was the largest. MaxN for each family was then summed to determine Total MaxN for each video.

Shark MaxN was extracted in the same manner see Chapter 2 for further details.

2.4 Other Environmental and Anthropogenic Data

Net primary productivity (NPP) was determined using satellite-based observations obtained from an open-access database (*Ocean Productivity, Oregon State, 2021*) using the Vertically Generalized Production Model (Behrenfeld & Falkowski, 1997).

Productivity values for each site were calculated based on the nearest neighbor pelagic

cell for each reef location, averaged over the two sampling years (2016 and 2017) (Gove et al. 2013). SST taken during each deployment were averaged to obtain SST per reef. Human population size for each site was acquired using publicly available census data from 2017 (*Census Report 2017*, ISPF). Population size was divided by emerged land area to determine population density for each site. Population density was selected as the metric for human pressure because it outperformed other metrics of human impacts (market gravity and human population size) in preliminary BRT analysis.

2.5 Analyses

Data were analyzed using Boosted Regression Trees (BRTs). Rather than trying to find a single best regression tree, BRTs use boosting to create an ensemble from many hundreds or thousands of trees (Elith et al., 2008). BRTs account for interactions between predictors, can handle complex non-linear relationships and are insensitive to collinearity among variables (Abeare, 2009; Elith et al., 2008; Jouffray et al., 2019).

Predictor variables were island geomorphology, island group, average net primary productivity, human population density, SST, water visibility, and lagoon size and depth (m). Season, bait type, and time BRUVSs were without bait (rare instances where bait cage was broken and/or bait removed by animals), were also included in models to account for variation in sampling.

Models were run in R (version 4.0.2) and fitted using the R package *gbm.auto* (Dedman et al., 2017) which automates the model parameter (hyperparameter) selection, analysis,

model evaluation, and plotting processes for BRT modeling. Optimal hyperparameters for tree complexity, bag fraction, and learning rate, were determined 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). I used the combination of model parameters that yielded the smallest model deviance, and best correlation score between training data, and tested data for each model. Based on visual inspection of the distribution of response variable data, the Poisson distribution was used for all models presented here. The effects of simplifying these models were then tested, as recommended by Elith et al. (2008), using *gbm.simplify* from the ‘dismo’ package, which removes predictors one by one then tests if the model's training data correlation score improves without them, compared to the previous best model. Simplified models are discarded if they did not improve on the full models. For discussion purposes I focus only on variables with a relative influence above that expected by chance (100/number of variables, i.e. 8.33% in my models) (Müller et al., 2013). I constructed BRT models 1) for the sum of all high trophic level predator teleost families Lutjanidae, Scombridae, Megalopidae, Carangidae, Sphyraenidae, Serranidae, and Lethrinidae, and 2) separately for each of the families Lutjanidae (snappers), Serranidae (groupers), and Carangidae (jacks). All values are means $\pm$ SD unless otherwise noted.

3. RESULTS

Of the 1072 total BRUVS used in this study, only *ca.* 1% (n=11) had no observed teleost from one of the target taxa. Mean MaxN for overall teleosts was 22.58 ± 28.86 . Of the seven family groups, Lutjanidae (snappers), Serranidae (groupers), and Carangidae

(jacks) were the most frequently observed (Table 2, Table 3). Overall mean MaxN varied more than 20-fold across the sampled islands. It was highest on Nuka Hiva in the Marquesas (mean MaxN = 76.5 ± 43.4), which was almost twice that of the next highest value found at Rangiora in the Western Tuamotus (mean MaxN = 39.3 ± 28.0). The lowest MaxN was at Rurutu in the Austral islands (mean MaxN = 3.5 ± 2.3) (Figure 2a). The single reef with the highest relative abundance of teleosts was Nuka Hiva 2 (mean MaxN = 84.7 ± 34.6). Outside of the Marquesas, Rangiora 1 had the highest total teleost MaxN (mean 51.3 ± 32.0), while Rurutu 1 (mean 3.2 ± 2.5) had the lowest (Figure 3).

Spatial patterns of relative abundance varied across families. Lutjanidae were most abundant on Nuka Hiva (mean MaxN = 60.5 ± 42.0) followed by Takaroa (23.5 ± 14.4) and least abundant off Tahiti (0.4 ± 0.7) (Figure 2b). Serranidae were most abundant on Nuka Hiva (7.6 ± 10.5) followed by Tetiaroa (6.2 ± 2.2), and lowest on Rurutu (1.8 ± 1.5) (Figure 2c). Carangidae were most abundant on Rangiora (11.5 ± 20.8) and least abundant on Tubuai (0.2 ± 0.5) (Figure 2d).

3.1 Total Teleost Abundance

BRT models for teleost abundance were not zero-inflated, and the simplified model did not perform better than the full model. The final model accounted for ~58% of the variation seen among sets for total teleost abundance (Table 4). NPP was the most influential variable, with a relative influence of 37% (Figure 4). Teleost abundance increased with NPP above about $150 \text{ mg C m}^{-2} \text{ day}^{-1}$ (Figure 5a). Island geomorphology (RI = 15.5%), the next most influential factor, explained less than half the variance of

NPP. Open atolls had the highest relative abundance of predatory teleosts (mean MaxN=31.7±22.4) which was over 10x that on high islands with fringing reefs (3.5±2.3), which had the lowest mean MaxN (Figure 5b). Closed atolls (13.3±14.3) and near atolls (10.2±8.6) followed open atolls in terms of relative abundance of teleost predators, while high islands with barrier reefs had the second lowest abundance with an average MaxN of 5.3 ±6.1. At a coarser scale, total MaxN was four times higher on atolls overall (29.1±22.4) than all high islands (7.2±7.3).

Human population density explained 14.3% of the variation in my model. There was a sharp decrease in overall MaxN on reefs as the human population density increased to 50 people/km², but further increases in population density had a much smaller effect (Figure 5c).

Shark MaxN (10.7% of model variance) had a generally positive relationship with teleost MaxN (Figure 5d). SST accounted for just over 10% of the variance of my model and had a non-linear relationship with MaxN: the highest abundances were found at the warmest temperatures (Figure 5e).

3.2 Lutjanidae Relative Abundance

Models for Lutjanidae (snapper) abundance were not zero-inflated, and the simplified model did not perform better than the full model. The final model accounted for over 60% of the variation seen among sets (Table 4). NPP was the most influential factor (relative influence *ca.* 31%). Lutjanid abundances increased with NPP above about 150 mg C m⁻² day⁻¹ (Figure 6a). Human population density accounted for nearly 19% of

model variance, with a sharp decline in lutjanid abundance as human density increased up to 50 people/km², and smaller declines thereafter (Figure 6b).

Island geomorphology (RI = 16.1%) and island group (RI = 8.8%) were also more influential to the final model than the random variable. Open atolls (mean MaxN = 20.1 ± 16.3) had much higher MaxN than other island geomorphology categories. High islands with barrier reefs had the lowest MaxN (0.7 ± 1.3) (Figure 6c). The West Tuamotus had the highest relative abundances of any island group for Lutjanidae (mean MaxN = 20.1 ± 16.3) that were nearly ten times higher than the East Tuamotus, the island group with the next highest MaxN (2.2 ± 3.0) (Figure 6c). These are followed by the Windward Society Islands (mean MaxN = 1.8 ± 7.7), Leeward Society Islands (1.4 ± 1.9), and Austral islands (0.9 ± 1.1) (Figure 6d).

3.3 Carangidae Relative Abundance

BRT models of Carangidae (jack) abundance were not zero-inflated, and simplified model did not perform better than the full model. The final model accounted for over 40% of the variation seen among sets (table 4), with NPP being the most influential factor by far (RI = 55%; Figure 4). This was followed by Shark MaxN (RI = 25%), and depth (RI = 14%). NPP had a positive relationship with Carangidae MaxN after about 160 mg C m⁻² day⁻¹ (Figure 7a). Shark MaxN had a positive relationship with Carangidae abundance (Figure 7b), while depth had a non-linear relationship with MaxN: Carangidae abundances peaked at ~10-15 m (Figure 7c).

3.4 Serranidae relative abundance

BRT models for Serranidae (grouper) abundance were not zero-inflated, and simplified model did not perform better than the full model. The final model accounted for around 29% of the variation seen among sets (Table 4, Figure 4), with island geomorphology accounting for nearly 35% of the explained variance. This was followed by depth (12.7%), shark MaxN (11.5%), and time without bait (10.6%). Serranidae MaxN on open atolls (6.2 ± 2.2) was three times higher than on high islands with fringing reefs (mean MaxN = 1.8 ± 1.5), where they were least abundant (Figure 8a). Closed atolls and near atolls also had relatively high mean MaxN for groupers (5.0 ± 2.0 , and 4.2 ± 1.8 respectively). The abundance of Serranidae increased with water depth up to about 15m before decreasing then remaining similar for depths above 22 m. While there was a generally positive relationship between shark MaxN and Serranidae abundance, the relationship was non-linear, with a dip in Serranidae abundance between a shark MaxN of ~8, and then a spike in abundance around 10 (Figure 8c). A nonlinear relationship also occurred for time without bait, where Serranidae MaxN showed a positive relationship up to about 20 min before decreasing (Figure 8d).

4. DISCUSSION

Despite overall teleost abundances being relatively high, they varied greatly throughout French Polynesia. Indeed, there was a more than 20-fold difference in MaxN across sampled islands. Examining only islands included in BRT models, predatory teleosts were more abundant in the Western Tuamotus and less abundant moving southward towards the Society Islands, particularly in East Tuamotus and Austral Islands. However,

this pattern varied by family, particularly among groupers, which showed less variation in abundance between sites, and were most abundant off Tetiaroa, in the Society Islands (Figure 2). I found that these patterns of abundance are driven by environmental and anthropogenic factors, primarily net primary productivity.

Overall predatory teleost populations in French Polynesia seem to have comparable or greater abundances compared to other similar sites in the Indo-Pacific region (e.g. Skinner et al. 2020, Lester et al. 2021a, 2021b). For instance, median MaxN of the three most abundant families in French Polynesia - Carangidae (1), Lutjanidae (2), and Serranidae (4) - were similar to the medians reported for these families in the North Male Atoll in the Maldives (Skinner et al. 2020), and the median for the total abundance of predatory teleosts is slightly larger than reported for mesopredatory fish found on reefs off North West Australia (Lester et al. 2021a).

Within French Polynesia, net primary productivity was the primary predictor of predatory teleost abundances. This is consistent with other studies of reef fish abundance in the Indo-Pacific which have demonstrated a strong relationship to productivity, particularly in regional-scale studies where more localized effects of fishing are less pronounced (e.g. Gove et al. 2016, Harborne et al. 2018, Heenan et al. 2006, Williams et al. 2015). Sites investigated in French Polynesia had NPP ranging from 87 - 206 mg C m⁻² day⁻¹. Sites with NPP above 160 mg C m⁻² day⁻¹ showed a marked increase in total predatory teleost abundance. This pattern near mg C m⁻² day⁻¹ occurred in snappers and jacks individually as well and is similar to the pattern found for fish biomass in Micronesia

(Harborne et al. 2018). These results support the growing body of literature demonstrating the importance of ocean productivity in regulating the carrying capacity of reef systems even for non-planktivorous fish, and that this relationship is non-linear (e.g. Harborne et al. 2018, Cinner 2016, Williams et al. 2015, Nadon et al. 2012).

Net primary productivity may underpin the relationship between predatory teleost abundance and island geomorphology, the second most influential factor in my total abundance model. Predatory teleosts were on average 4x more abundant on atolls than on high islands with coral reefs. Productivity tends to be higher on atolls than comparable high islands, because atolls have a more pronounced island mass effect - the phenomena where by primary production is increased around oceanic islands - likely as the result of the export of nutrients from enclosed lagoons (Vollbrecht et al., 2021, Gove et al., 2016). This argument is supported by the fact that Nuka Hiva, a high island and not an atoll, was the site with the highest overall abundance of predatory teleosts, as well as the highest productivity. However some caution should be exercised in comparing Nuka Hiva to sites elsewhere in French Polynesia because of its lack of coral reefs and other large habitat differences (hence it was not included in my BRT analysis). Furthermore, access to diverse habitat types also may help explain higher abundances at atolls. For example, lagoon habitats of atolls act as nurseries and refugia for many teleosts (e.g. Skinner et al. 2020, Green et al. 2015, Tupper 2007) which can increase abundance of fish on adjacent coral reefs (e.g. Green et al. 2015, Mumby et al. 2004). Similarly, reef passes that typify open atolls often act as sites for spawning aggregations (e.g., Breckwoldt et al. 2022, Mitcheson et al. 2020, Mourier et al. 2019, Taylor et al. 2015).

Human population density was the third most influential factor for predatory teleost abundance overall and second most important in the snapper model. In both models, there was a sharp decrease in overall MaxN on reefs, as the human population density increased to 50 people km⁻². However, further increases in population density had much less effect. This is not surprising given that fish consumption on remote islands/atolls in French Polynesia is nearly double that of urban areas, and the vast majority of consumed fish is obtained via subsistence fishing rather than purchased commercially (Bell et al. 2009). Additionally, total reconstructed catch estimates from French Polynesia indicate that subsistence and artisanal fishing catches make up a large percentage of total catch and have even outstripped industrial catches some years in the past decade (Bale et al. 2009, Coulter et al. 2020, Pauly et al. 2020, White et al. 2020). It follows then that localized impacts, particularly on more resident species like snapper, begin to accrue at relatively low human population densities, such that larger human populations have comparatively small additional effects.

It is notable that while human impact was a large contributor in models for predatory teleost relative abundance, it did not influence reef shark abundances across the same locations (Chapter II). This likely is due to the success of the shark sanctuary implemented in 2006 and the resulting low fishing pressure on sharks (Ward-Paige & Worm, 2017). Interestingly, shark abundance was positively correlated with teleost relative abundance, particularly groupers and jacks. The relationship between shark abundances and predatory teleosts on coral reefs has been hotly debated and appears to

vary among locations and across teleost taxa (see Chapman et al. 2022, Heithaus et al. 2022 for reviews). For example, in Northwest Australia, smaller teleost predators were more abundant where sharks were less abundant (Ruppert et al 2013). Increasing shark abundance was associated with higher large teleost abundance (>50 cm), and lower abundance of smaller mesopredatory teleosts (Barley et al. 2017). However, on the Great Barrier Reef, Australia there was no obvious relationship between shark abundances and teleost biomass (Desbins et al 2021). Instead, environmental factors were primarily responsible for structuring fish communities. The functional links between reef shark and teleost abundances remain largely unclear and may be driven by intraguild competition and a suite of indirect interactions through multiple pathways (e.g. Roff et al. 2016, Lester et al. 2021, Heithaus et al 2022). The diets of many of the target teleost species in this study overlap with reef sharks (e.g. Frisch et al. 2015, Roff et al. 2016), and some reef shark species may not frequently feed on the predatory teleosts above a certain size (e.g. Barley et al. 2017). My results suggest that in French Polynesia, sharks do not negatively affect predatory teleost abundances through either competitive or predator-prey interactions. Instead, they may facilitate larger populations through indirect interactions. Alternatively, the positive relationship between teleost predators and reef sharks may be due to both groups responding to unmeasured variables in a similar way. For example, both may be responding to higher densities of smaller prey fish or local disturbance history. However, if populations of smaller prey fish are linked to NPP I would expect to see the covariation in shark and predatory abundances relative to prey availability to be reflected in the overall effect size of NPP. Further work that explicitly

includes data on prey, including smaller teleost taxa, would help to further explore the functional links between shark abundances and those of large teleost predators on reefs.

Coral reefs ecosystems face a myriad of chronic and acute stressors ranging from overfishing across multiple trophic levels, to climate change. All these stressors have the potential to disrupt fish communities and the associated resources required by human and biological communities. I found that shifts in primary productivity could have major consequences for the abundances of reef-associated teleost predators. Furthermore, these taxa, especially snappers, appear to be highly sensitive to fishing pressures from even relatively low human population densities. I also found that teleost populations were greater in the presence of larger shark populations, suggesting that actions to protect and even restore shark populations may have positive impacts on fish communities, including taxa that are relied upon by people for food.

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Table 1: Characteristics of sample sites.

Site Name	# of Reefs Sampled	Island Geomorphology	Island Group	Population Density (person km ⁻²)	Season Sampled	Lagoon Size (km ²)
Apataki	2	open atoll	West Tuamotu	21.05	Wet	706
Mangareva	2	near atoll	East Tuamotu	49.43	Dry	407
Maupiti	2	near atoll	Leeward Society	117.73	Wet	44
Moorea	2	high barrier	Windward Society	134.86	Wet	382
Nuka Hiva	2	high rocky	Marquesas	9.20	Wet	0
Rangiroa	2	open atoll	West Tuamotu	34.29	Wet	1446
Rurutu	2	high fringing	Austral Islands	78.00	Wet	0
Tahiti	1	high barrier	Windward Society	181.30	Wet	154
Takaroa	2	open atoll	West Tuamotu	33.7	Dry	93
Tetiaroa	1	closed atoll	Windward Society	40.00	Wet	16
Tubuai	1	high barrier	Austral Islands	49.27	Dry	85

Table 2: Target Teleost species observed on BRUVS.

Family Group	# of Reefs Present	% sets Present	Mean MaxN	SD MaxN
Lutjanidae (snappers)	19	75.28%	13.58	24.29
Scombridae (Mackerel, Tuna & Bonita)	3	3.45%	0.04	0.22
Megalopidae (Tarpon)	2	0.19%	0.002	0.043
Carangidae (Jacks)	19	66.23%	3.21	9.02
Sphyrnaeidae (Barracuda)	12	4.38%	0.24	3.60
Serranidae (Groupers)	19	97.20%	4.51	3.95
Lethrinidae (Emperors)	19	44.12%	0.99	1.98
Total Target Teleosts	19	98.97%	22.58	28.86

Table 3: The top five most abundant species of teleost for each family as measured by mean MaxN

Common Name	Family	Genus	Species	Mean MaxN	SD
Bluefin trevally	Carangidae	Caranx	melampygus	1.11	2.99
Unknown Jack/Trevally	Carangidae	Carangidae	spp.	1.10	5.05
Doublespotted queenfish	Carangidae	Scomeroides	lysan	1.08	6.23
Giant trevally	Carangidae	Caranx	ignobilis	0.14	0.65
Bigeye trevally	Carangidae	Caranx	sexfasciatus	0.08	2.30
Long-nosed emperor	Lethrinidae	Lethrinus	olivaceus	0.41	0.71
Unknown Emperor	Lethrinidae	Lethrinus	spp.	0.34	1.38
Yellow-spotted emperor	Lethrinidae	Lethrinus	erythracanthus	0.26	1.08
Yellow lipemperor	Lethrinidae	Lethrinus	xanthochilus	0.06	0.55
Yellow-striped emperor	Lethrinidae	Lethrinus	ornatus	0.01	0.09
Paddletail	Lutjanidae	Lutjanus	gibbus	6.09	12.18
Blue stripe seaperch	Lutjanidae	Lutjanus	kasmira	4.44	18.26
Red bass	Lutjanidae	Lutjanus	bohar	1.11	1.75
Small-toothed jobfish	Lutjanidae	Aphareus	furca	1.07	1.59
Onespot seaperch	Lutjanidae	Lutjanus	monostigma	0.39	1.47
Indo-Pacific Tarpon	Megalopidae	Megalops	cyprinoides	0.00	0.04
Dogtooth Tuna	Scombridae	Gymnosarda	unicolor	0.04	0.22
Peacock rockcod	Serranidae	Cephalopholis	argus	2.06	3.32
Flagtail rockcod	Serranidae	Cephalopholis	urodeta	1.27	1.12
Black-tipped rockcod	Serranidae	Epinephelus	fasciatus	0.38	1.07
Coronation trout	Serranidae	Variola	louti	0.19	0.53
Camouflage rockcod	Serranidae	Epinephelus	polyphekadion	0.18	0.47
Unknown Barracuda	Sphyracidae	Sphyracidae	spp.	0.13	1.96
Blacktail barracuda	Sphyracidae	Sphyracidae	qenie	0.09	3.02
Great barracuda	Sphyracidae	Sphyracidae	barracuda	0.01	0.11
Bigeye barracuda	Sphyracidae	Sphyracidae	fosteri	0.01	0.17
Unknown Teleost	Unknown Teleost	Unknown Teleost	Unknown Teleost	1.20	6.57

Table 4: Boosted regression tree parameters and final model statistics. CV= Cross Validated.

Model Response Variable	Tree Complexity	Learning Rate	Bag Fraction	Zero Inflated?	% Deviance Explained	Training Correlation	CV % Deviance Explained	CV Correlation
Total Teleost MaxN	5	0.005	0.75	NO	63.28	0.729	57.57	0.673
Lutjanidae MaxN	5	0.005	0.75	NO	67.63	0.727	60.37	0.677
Carangidae MaxN	5	0.005	0.5	NO	54.76	0.637	40.01	0.517
Serranidae MaxN	5	0.005	0.75	NO	39.7	0.646	29.77	0.538

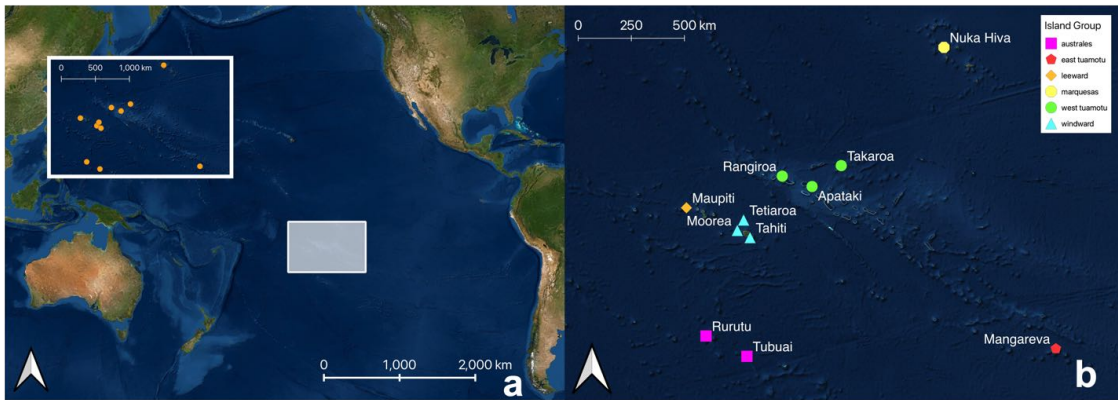


Figure 1: Sample sites in French Polynesia (a). The 11 sites containing 19 sampled reefs, were grouped into six island groups (b).

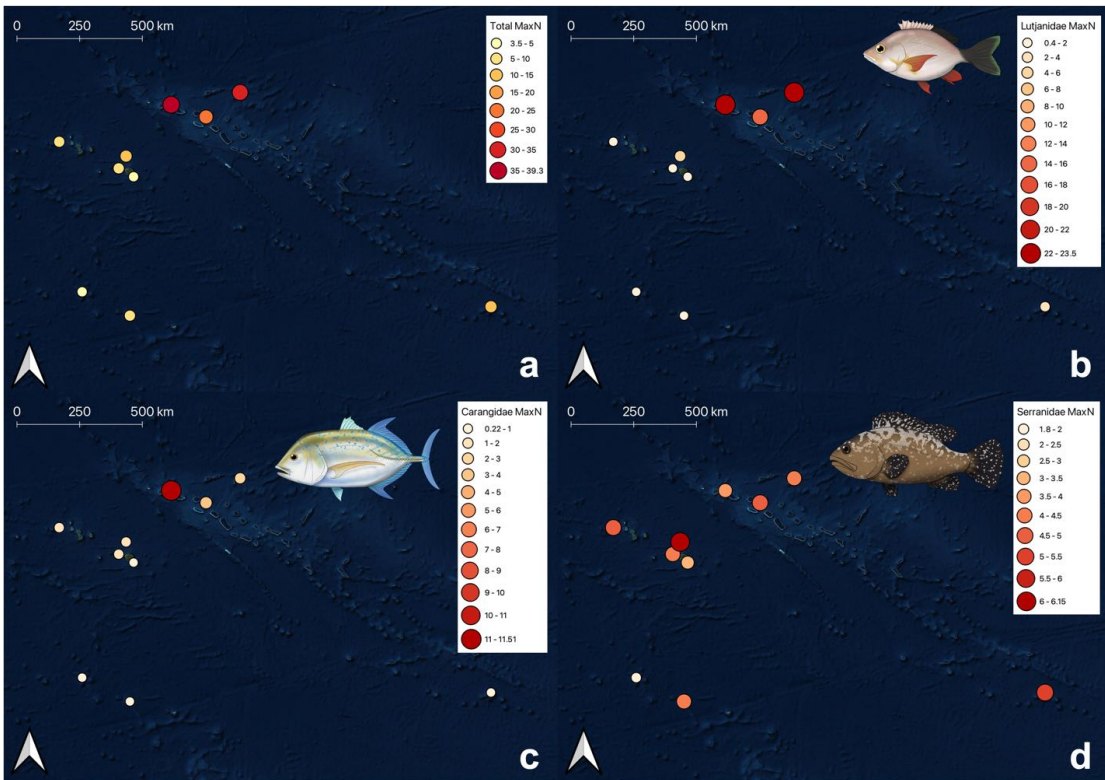


Figure 2: Relative abundances of predatory teleosts in French Polynesia. Mean MaxN by site for (a) all target teleosts, (b) Lutjanidae, (c) Serranidae, and (d) Carangidae. Nuka Hiva in the Marquesas not included.

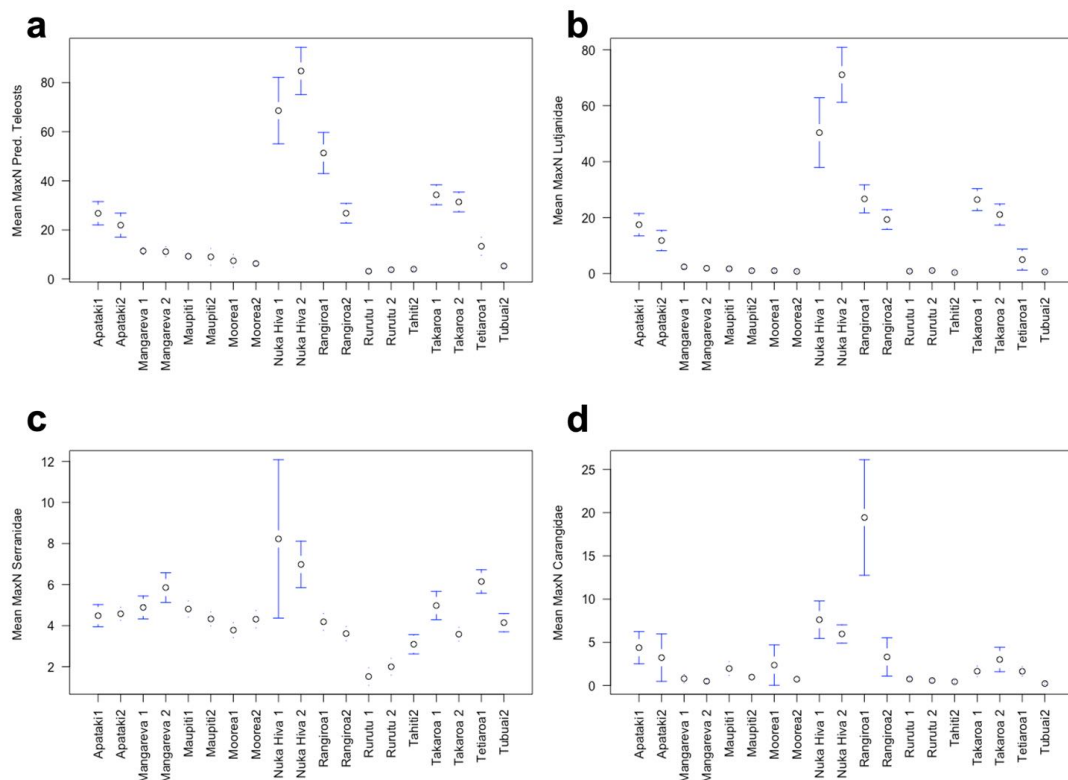


Figure 3: Mean plots of MaxN by reef for (a) all target teleosts, (b) Lutjanidae, (c) Serranidae, and (d) Carangidae.

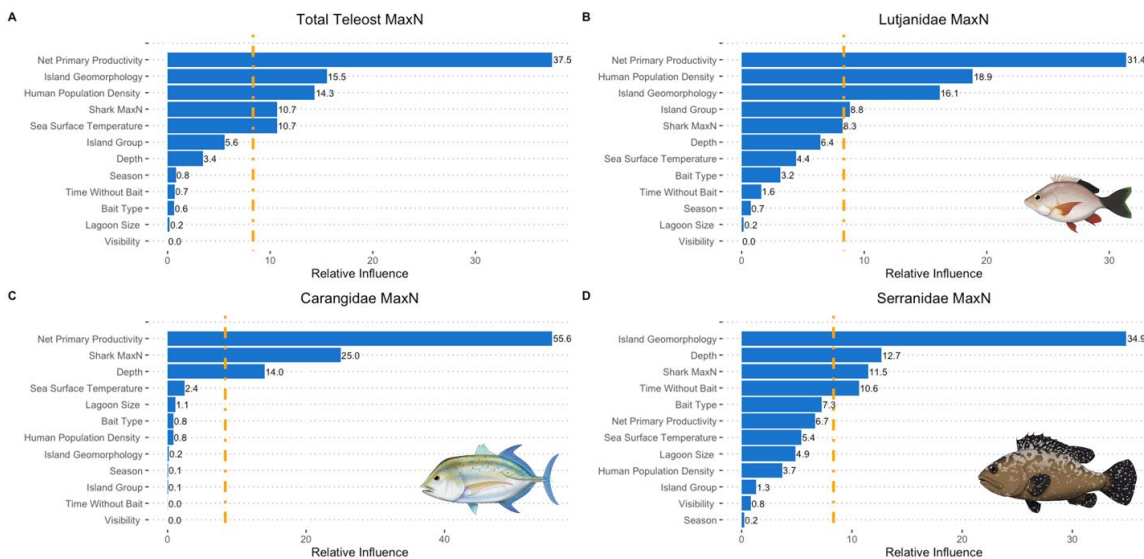


Figure 4: Mean relative influence of all predictor variables in boosted regression tree models on (a) total teleost MaxN, (b) Lutjanidae MaxN, (c) Serranidae MaxN, and (d) Carangidae MaxN. Variables with relative influence over that indicated by the orange line have influence above that expected by chance (100/number of variables).

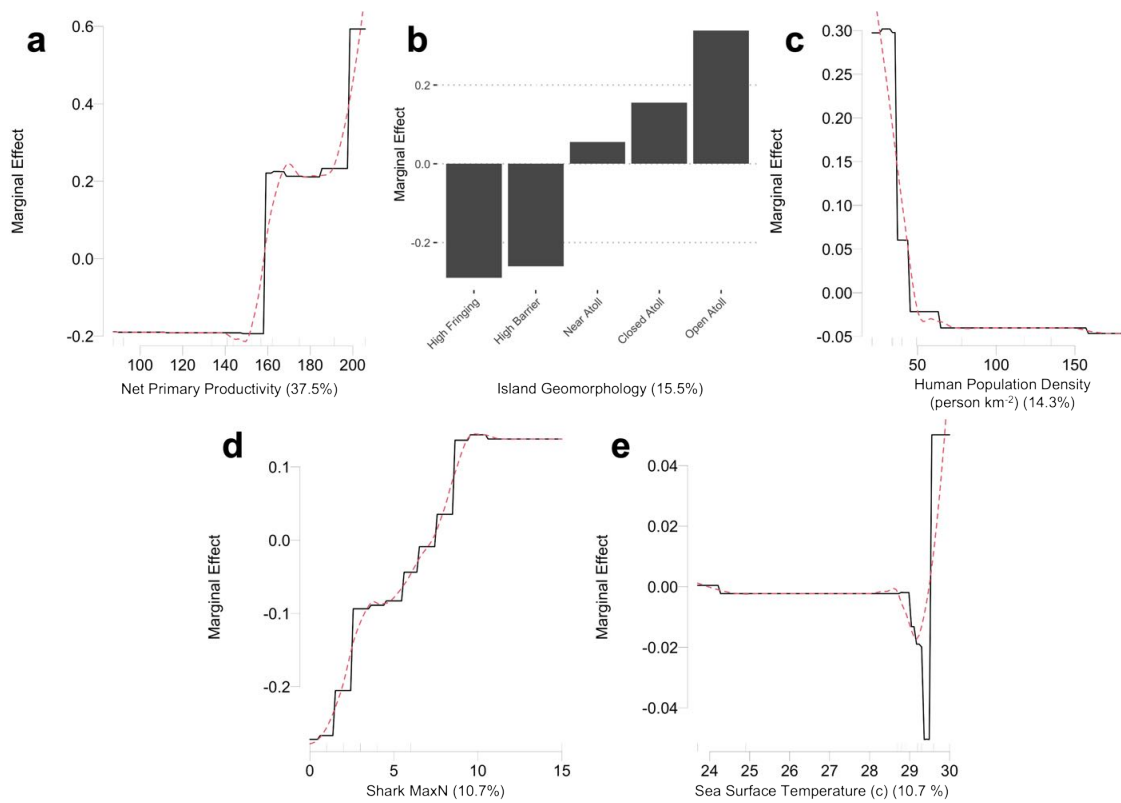


Figure 5: Partial dependence plots showing relationships of environmental variables to teleost relative abundance as measured by mean MaxN. Relative influence of each variable is indicated as a percent. Red line is smoothed. X-axis rug ticks in panels a,c,d & e, indicate the decile distribution of the predictor variable data.

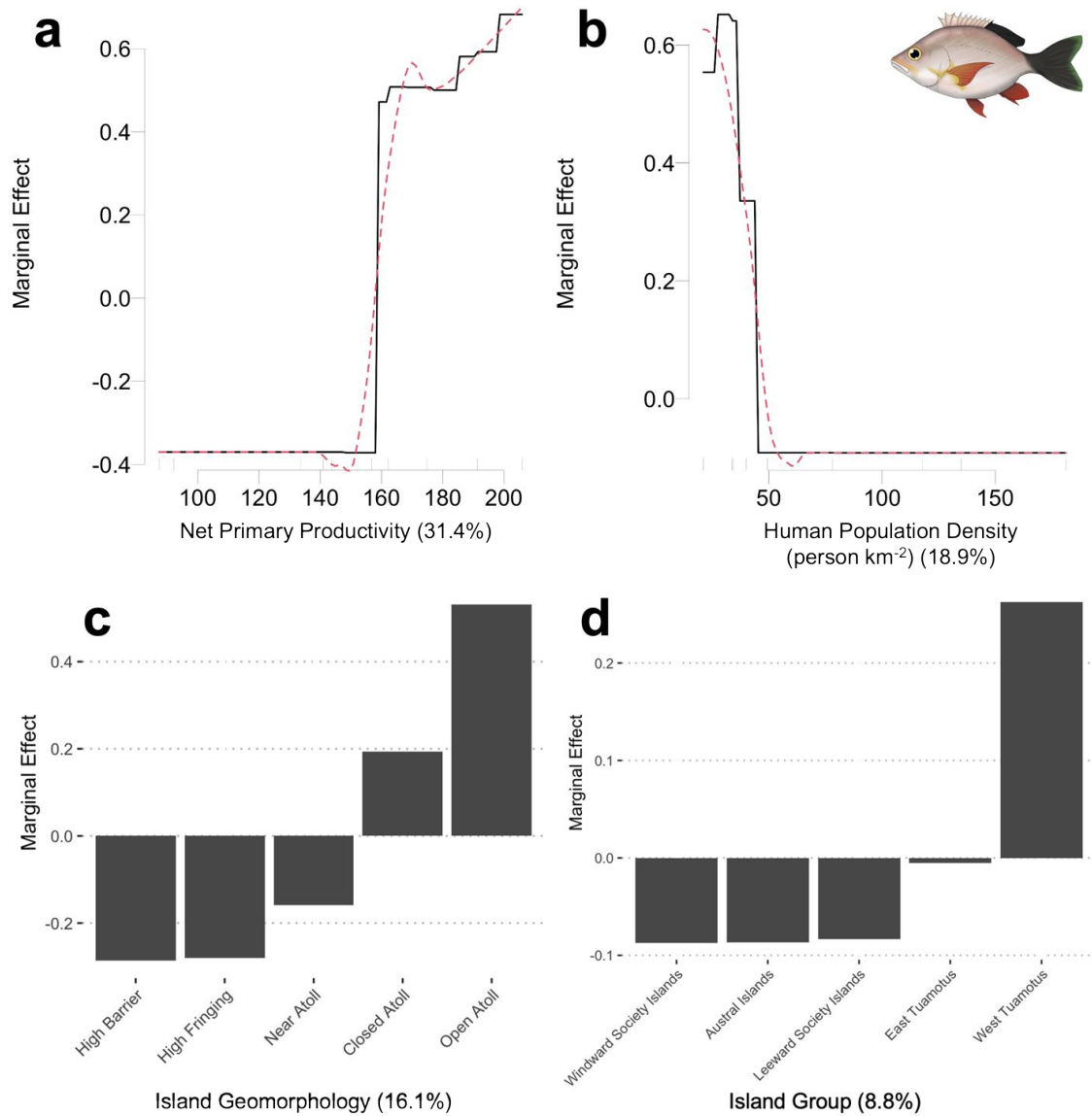


Figure 6: Partial dependence plots showing relationships of environmental variables to Lutjanidae relative abundance as measured by mean MaxN. Relative influence of each variable is indicated as a percent. Red line is smoothed. X-axis rug ticks in panels A and B indicate the decile distribution of the predictor variable data.

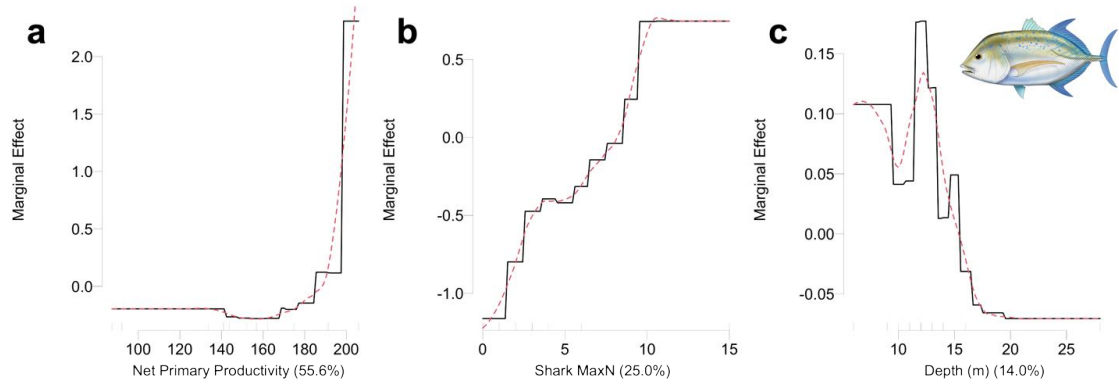


Figure 7: Partial dependence plots showing relationships of environmental variables to Carangidae relative abundance as measured by mean MaxN. Relative influence of each variable is indicated as a percent. Red line is smoothed. X-axis rug ticks indicate the decile distribution of the predictor variable data.

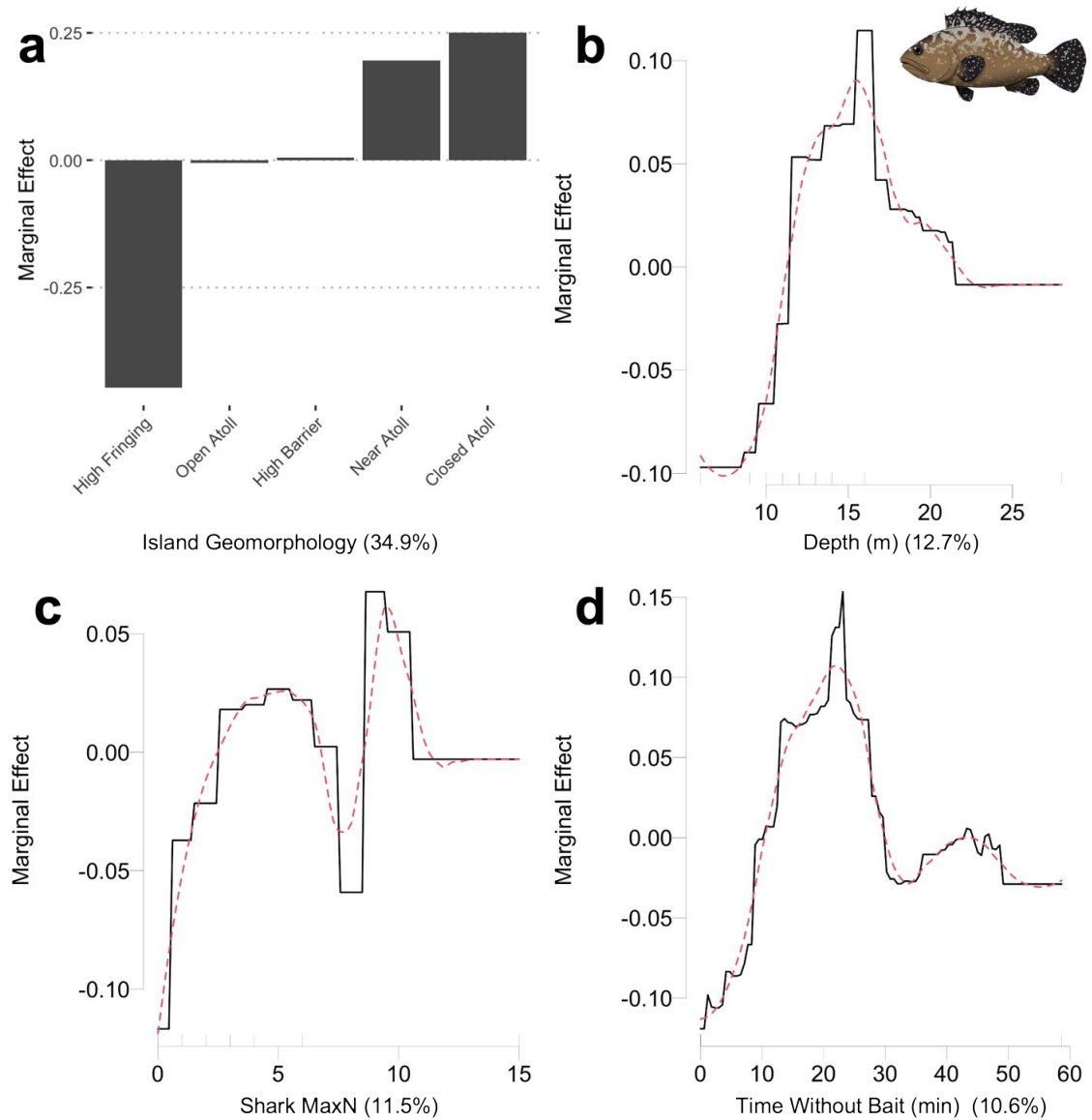


Figure 8: Partial dependence plots showing relationships of environmental variables to Serranidae relative abundance as measured by mean MaxN. Relative influence of each variable is indicated as a percent. Red line is smoothed. X-axis rug ticks in panels A and B indicate the decile distribution of the predictor variable data.

SUPPLEMENTAL MATERIAL

Table S1: List of species observed from target families

Common Name	Family	Genus	Species
Almaco jack	Carangidae	Seriola	rivoliana
Bigeye trevally	Carangidae	Caranx	sexfasciatus
Black jack	Carangidae	Caranx	lugubris
Blue trevally	Carangidae	Carangoides	ferdau
Bluefin trevally	Carangidae	Caranx	melampygus
Brassy Trevally	Carangidae	Caranx	papuensis
Doublespotted queenfish	Carangidae	Scomeroides	lysan
Giant trevally	Carangidae	Caranx	ignobilis
Golden trevally	Carangidae	Gnathanodon	speciosus
Island trevally	Carangidae	Carangoides	orthogrammus
Rainbow Runner	Carangidae	Elagatis	bipinnulata
Unknown Jack/Trevally	Carangidae	Carangidae	spp.
White Trevally	Carangidae	Pseudocarnax	dentex
Yellowtail Scad	Carangidae	Atule	mate
Long-nosed emperor	Lethrinidae	Lethrinus	olivaceus
Orange-striped emperor	Lethrinidae	Lethrinus	obsoletus
Pink-eared emperor	Lethrinidae	Lethrinus	lentjan
Unknown Emperor	Lethrinidae	Lethrinus	spp.
Variegated emperor	Lethrinidae	Lethrinus	variegatus
Yellow lipemperor	Lethrinidae	Lethrinus	xanthochilus
Yellow-spotted emperor	Lethrinidae	Lethrinus	erythracanthus
Yellow-striped emperor	Lethrinidae	Lethrinus	ornatus
Yellowtail emperor	Lethrinidae	Lethrinus	atkinsoni
Blue stripe seaperch	Lutjanidae	Lutjanus	kasmira
Brown stripe seaperch	Lutjanidae	Lutjanus	vitta
Crimson seaperch	Lutjanidae	Lutjanus	erythropterus
Green jobfish	Lutjanidae	Aprion	virescens
Maori seaperch	Lutjanidae	Lutjanus	rivulatus
Onespot seaperch	Lutjanidae	Lutjanus	monostigma
Paddletail	Lutjanidae	Lutjanus	gibbus
Red bass	Lutjanidae	Lutjanus	bohar
Red emperor	Lutjanidae	Lutjanus	sebae
Small-toothed jobfish	Lutjanidae	Aphareus	furca
Yellow-margined seaperch	Lutjanidae	Lutjanus	fulvus
Indo-Pacific Tarpon	Megalopidae	Megalops	cyprinoides
Dogtooth Tuna	Scombridae	Gymnosarda	unicolor
Black-tipped rockcod	Serranidae	Epinephelus	fasciatus

Blacksaddle rockcod	Serranidae	Epinephelus	howlandi
Blue maori	Serranidae	Epinephelus	cyanopodus
Blue-lined rockcod	Serranidae	Cephalopholis	formosa
Brown-barred rockcod	Serranidae	Cephalopholis	boenak
Camouflage rockcod	Serranidae	Epinephelus	polyphekadion
Blue spot trout	Serranidae	Plectropomus	laevis
Coral trout	Serranidae	Plectropomus	leopardus
Coronation trout	Serranidae	Variola	louti
Flagtail rockcod	Serranidae	Cephalopholis	urodeta
Four-saddle rockcod	Serranidae	Epinephelus	spilotoceps
Greasy rockcod	Serranidae	Epinephelus	tauvinia
Hexagon rockcod	Serranidae	Epinephelus	hexagonatus
Maori cod	Serranidae	Epinephelus	undulatostratus
Marquesan grouper	Serranidae	Epinephelus	irroratus
One-blotch grouper	Serranidae	Epinephelus	melanostigma
Peacock rockcod	Serranidae	Cephalopholis	argus
Six spot rockcod	Serranidae	Cephalopholis	sexmaculata
Snubnose rockcod	Serranidae	Epinephelus	macrospilos

CHAPTER IV

ELASMOBRANCH SPECIES RICHNESS AND ASSEMBLAGE COMPOSITION IN THE WORLD'S LARGEST SHARK SANCTUARY

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ABSTRACT

Indo-Pacific coral reefs host diverse assemblages of elasmobranchs from small-bodied mesopredators to apex predators, ranging from reef residents to occasional visitors. Reef sharks and rays as a group are threatened by human activities and are facing widespread population declines, primarily due to fishing. Human factors may affect not only elasmobranch abundance, but also their assemblage composition. Thus, to better protect and conserve shark and ray populations we need to more explicitly understand the factors associated with differences in abundance and assemblage structure at local and regional scales. Here I used baited remote underwater video stations (BRUVS) to examine the species richness and assemblage composition of elasmobranchs across French Polynesia, the world's largest shark sanctuary. Boosted regression tree (BRT) models revealed that island group, latitude, and island geomorphology were the most influential factors affecting elasmobranch species richness. Though assemblages at most islands were dominated by blacktip reef (*Carcharhinus melanopterus*) and grey reef sharks (*Carcharhinus amblyrhynchos*), and rays were generally rare, I found that there was significant variation in elasmobranch assemblage composition throughout French Polynesia. Species assemblages and associations, particularly at smaller scales, may be driven by species interactions, both positive and negative, that warrant further investigation.

1. INTRODUCTION

Indo-Pacific coral reefs host a diverse array of sharks and rays which occupy diverse ecological roles from small-bodied to apex predators and include both reef residents and transient species (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. Ferretti et al. 2010, Robbins et al. 2006, Roff et al. 2018). Global Fingerprint, a survey conducted on coral reefs around the globe, 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 expectation (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. Additionally, management and socioeconomic factors also influence assemblage composition, with heavily impacted reefs showing a shift from shark dominated assemblages to ray dominated ones (Simpfendorfer et al. in press).

While these studies provide an important global perspective, to better manage elasmobranch populations it is important to understand the factors driving the relative abundance of elasmobranch species across multiple spatial and temporal scales. French Polynesia is the world's largest shark sanctuary, with prohibitions on shark fishing, trade, and export being put in place in 2006. French Polynesia supports robust shark populations that are minimally impacted by anthropogenic factors (Chapter II, MacNeil et al. 2020) and are primarily by environmental factors including island geomorphology,

temperature and net primary productivity (Chapter II). However, it is unclear if similar patterns are true of species richness, and how species assemblages might vary across environmental gradients. Here I expand upon the work done in (Chapter II). I use baited remote underwater video stations (BRUVS) to survey the species richness and assemblage composition of elasmobranchs across environmental and anthropogenic gradients in an Indo-Pacific coral reef system with low human impacts and no direct fishing pressure on sharks.

2. MATERIALS & METHODS

2.1 Site Description

French Polynesia, in the south-central Pacific (Figure 1), has an exclusive economic zone covering *ca.* 5,030,000 km². It consists of five archipelagos: the Marquesas Islands, the Tuamotu Archipelago, the Society Islands, the Gambier Islands, and the Austral Islands (Figure 1). For this study, the islands were divided into six groups based on geography: Marquesas, Leeward Society Islands, Windward Society Islands, West Tuamotus, East Tuamotus (including the Gambier Islands), and Austral Islands. A more detailed site description can be found in Chapter II.

2.2 Field Methods

Baited remote underwater video stations (BRUVS) were used to survey 35 reefs, defined as an area of *ca.* 4 km² with continuous coral reef habitat, across 17 different

islands/atolls (hereafter “islands”). Islands were categorized according to their geomorphology as: open atoll, closed atoll, near atoll, high barrier, high fringing, and high rocky (Table 1). Open atolls have boat-navigable passages. Closed atolls lack such passages, though 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).

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 BRUVS were positioned so the camera faced down-current. Deployment of BRUVS occurred during daylight hours on forereefs at depths 9 - 35 m. Each BRUVS set had a minimum soak time of 60 min, with deployments up to 90 min. No two BRUVSs were deployed within 500 meters of one another within a sampling day to prevent autocorrelation, and each reef had a minimum of 42 sets (Mean = 58; Max = 70).

All sampling took place in either 2016 or 2017. Sampling at individual reef locations usually took place over a single period of < 10 days (max. 37 days). During deployment

of each set the bottom depth was recorded, sea surface temperature (SST) taken using a YSI Pro 2030 model, (<https://www.ysi.com/>) and water visibility was visually estimated to the nearest meter up to 15 m.

2.3 Video Data Extractions

Using the Fingerprint Annotator (v1.1.44.0) (<https://www.vulcan.com/>), each video was viewed to 90 min or the end of the video with a minimum length of 60 min. Videos were reviewed by at least two annotators, and all observations 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 MaxN, the maximum number of individuals of each target species seen in a single frame for each video. MaxN avoids double counting the same individual that might enter and exit the field of view multiple times and is thus 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”) accounted for less than 5% of observations and 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, 2021*) using the Vertically Generalized Production Model (Behrenfeld & Falkowski, 1997) were used to determine Net Primary Productivity (NPP). Each reef's NPP values were averaged over the two sampling years (2016-2017) from the nearest neighbor pelagic cell for each location. SST was taken during each deployment 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 analysis. Consistent with Cinner & Marie (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 BRUV sets.

2.5 Assessing Co-occurrence and Species Habitat associations with Chi-Squared Testing

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, I standardized sets to 60 min soak times. Based on preliminary analysis, and due to infrequency of sightings, the two 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, *Mobula alfredi*; Chilean devil ray, *Mobula tarapacana*).

I considered p-values significant at an alpha of 0.05, and Pearson's residuals were used to determine where species had positive and negative associations.

Species' associations with specific islands and island groups were examined using Chi-square tests on the sum of MaxN for abundance and species richness. I 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 Assess Similarity of Species Assemblages with Cluster Analysis

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 with Boosted Regression Trees (BRT)

Boosted Regression Trees 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 interactions between predictor variables (Abeare, 2009; Elith et al., 2008; 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 time 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. I 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). I 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. I 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.

3. RESULTS

A total of 16 species of elasmobranchs, including 10 shark and 6 ray species, were recorded on the 2,017 BRUVS analyzed. Sharks were more abundant than rays at all islands, and at least one shark was seen at every reef. Rays, however, were absent from 16 of 35 (45.7%) reefs and 4 islands. There was one island (Uapou) where more ray species were observed than shark species, despite the fact that sharks were overall more abundant (Figure 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, at Nuka Hiva, Uapou and Tikehau. The average number of elasmobranch species seen on each BRUV was 1.67 (± 0.99), with up to 5 species being sighted on a single video. The number of elasmobranch species sighted at each reef ranged from 2 to 11, with just under six elasmobranch species seen on average at each reef (5.91 ± 2.16).

Of shark species with ranges in French Polynesia (Siu et al. 2017), only one species of reef shark (galapagos shark; *Carcharhinus galapagensis*), and one transient species that occupies primarily nearshore habitats (bull shark, *Carcharhinus leucas*) did not appear at my BRUVS. The rest of the shark species 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 on my BRUVS. The only species not observed, the deep-water stingray (*Plesiobatis davies*) and pelagic stingray (*Pteroplatytrygon violacea*), are both species that are not expected to occur in forereef habitats.

Blacktip reef sharks (*Carcharhinus melanopterus*) and grey reef sharks (*Carcharhinus amblyrhynchos*) were the most abundant and frequently sighted species (Table 2) and were seen at all islands and on 34 of the 35 sampled reefs. Great hammerheads (*Sphyrna mokarran*) were the least abundant species and were only seen in the West Tuamotus. No species was seen at less than two separate islands though four other species – the Chilean devil ray (*Mobula tarapacana*), oceanic manta (*Mobula birostris*), blotched fantail ray (*Taeniurops meyeri*), and silvertip shark (*Carcharhinus albimarginatus*) – were seen at only two islands. Of these species, three were only seen within a single island group. The blotched fantail ray 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 (Figure 3).

3.1 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 (Figure 4). Island group was the most influential factor, with a relative influence of 32% (Figure 4). 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 nine elasmobranch species overall. The

East Tuamotus (mean species per reef = 4.6 ± 1.5) had eight species overall, while the least speciose island 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 (Figure 5B).

Island geomorphology had a relative influence of *ca.* 20%, 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 (mean species per reef = 6.3 ± 1.5). These were followed by closed atolls (5.60 ± 0.89), high islands with barrier reefs (mean species per reef = 5.0 ± 1.6), and near atolls (mean species per reef = 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.

3.2 Species assemblages

Hierarchical cluster analysis examining species assemblages separated reefs into five significant clusters (Figure 6). All nodes within each cluster had p-values less than or equal to 0.05, indicating that all nodes within clusters were significantly different to 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, though this pattern did not hold for other island groups. Rurutu and Tubuai in the Austral islands were separated, for example, with species 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 two sites had very different species richness overall, with seven different species seen at Takaroa and only four at Tubuai and are around 1,100 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 (Figure 3).

With the exception of Maupiti – with 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. Uapou, the other island in the Marquesas, formed a unique cluster that featured a very high proportion of rays (Figures 3, 6, 7).

Chi-squared analysis revealed spatial patterns of species relative abundance (Figure 7 & Figure S2). Rays, common blacktip sharks (*Carcharhinus limbatus*), silvertip sharks (*Carcharhinus albimarginatus*), 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 (Figure 7A & Figure S2) and Society Islands (Figure 7D, 7E, S5 & S6), but more often than expected in the Tuamotus (Figure 7B, 7C, 7F, S3, S4, S5). 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 (Figure 7). 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 seven islands (Figure S2-S7). Sicklefins and grey reef sharks appear to have largely inverse distributions. Sicklefins were seen less than expected in the Tuamotus and more than expected in the Windward Society Islands (Figure 7). At the island level, sicklefin and grey reef sharks showed negative associations at all but one island, though not all of these associations were strong (Figures S2- S7).

3.4 Species co-occurrence

Pairwise chi-squared comparisons of species presence on individual videos revealed that several species co-occurred significantly more than expected (Figure 8). 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 and grey reef sharks. However, sicklefin and grey reef sharks showed a strong disassociation,

occurring together on individual videos far less than would be expected (Figure 8). Common blacktip sharks, mobulid rays, and stingrays had strong positive associations (Figure 8).

4. DISCUSSION

As with relative abundances of sharks (Chapter 2), 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 in Australia (Espinoza et al. 2014), and New Caledonia (Juhel et al. 2017). 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 (*Sphyrna lewini*), and great hammerhead sharks (*Sphyrna mokarran*), as well as silvertip sharks (*Carcharhinus albimarginatus*), relative to both the Great Barrier Reef and New Caledonia (Espinoza et al. 2014, Juhel et al. 2017). However, similar to many other nations in the Indo-Pacific (e.g. Juhel et al. 2017, Simpendorfer et al, 2023 in press), I found that elasmobranch assemblages in French Polynesia were dominated by sharks, with a general paucity of rays.

The Marquesas were an exception to the 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). The 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 Equator and Mexico (e.g., Jaine et al. 2012, Armstrong et al. 2016, Armstrong et al. 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. This, in addition to its productive waters, may account for the presence of scalloped hammerheads and silvertip sharks that may 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. Bessundo et al. 2011), and Revillagigedo National Park (e.g. Aldana-Moreno et al. 2019) are similar to the Marquesas in many respects, being remote islands with rocky reefs and productive waters.

The two most common species seen in French Polynesia, blacktip reef sharks (*Carcharhinus melanopterus*) and grey reef sharks (*Carcharhinus amblyrhynchos*), 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 visa-versa. These results align with other studies that have found there is niche partitioning between these two 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, Lédée, et al., 2018; Papastamatiou et al., 2018). When observed together though, 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 (*Triaenodon obesus*) 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 byproduct mutualism, where foraging success of each species is enhanced in the presence of the other due to selfish foraging decisions made by each. 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. 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 mutualism. It is possible that such specific foraging consequences could drive other patterns of species co-occurrence and abundance in French Polynesia, as abundance of shark predators has been found to have a positive relationship with that of teleost predators (Chapter 3).

Sicklefin lemon sharks (*Negaprion acutidens*) were the largest-bodied shark commonly observed on my BRUVS. 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 & Potter 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 habits,

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), though lagoons and backreef areas are important nursery habitats for sicklefin lemon sharks (e.g. Mourier et al., 2013; Mourier & Planes, 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 found to be a significant driver of both grey reef shark abundances and blacktip reef shark abundances in French Polynesia (Chapter 2) though 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 (Chapter 2), it was less important in driving patterns of species richness. Instead, island group and latitude were the variables that explained the most variation in my BRT models.

Latitude is a well-known driver of shark species richness globally, with shark species richness tending to peak around 30-40° (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 I found fewer species also had lower abundance. However, this is not the case for all islands. The Marquesas, which contained the northernmost islands, had middling-to-low overall abundance compared to the rest of French Polynesia (Figure 2), but were the most speciose islands.

Island group had the largest effect on species richness within my study and was likely a result of islands within a group being spatially clustered and often have similar bathymetry and disturbance histories that are not accounted for elsewhere in my models. While species assemblages from the same island group were often clustered together, 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 dominated by whitetip reef sharks. It is notable that reefs of the same island always were found within the same broad clusters, though not always as nearest neighbors, indicating 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. Closer examination of habitat differences of reefs on the same island such as distance to reef pass, location of leeward/windward sides of the island, differences in bathymetry, or coral cover may provide further insight into the drivers of elasmobranch species assemblages and local levels.

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 (Chapter 2). Some species (e. g. grey reef sharks), however, may be more sensitive to human influences, but still persist even at the highest levels of market gravity in French Polynesia (Chapter 2). 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. The lack of human impacts also contrasts with global patterns where anthropogenic factors often drive elasmobranch diversity (e.g. Simpendorfer et al. 2023 in press), 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 I find that French Polynesia overall is characterized by high abundances and species richness of elasmobranchs, sharks in particular. Though assemblages at most islands were dominated by blacktip reef sharks and grey reef sharks, and demonstrated a paucity of rays, here I find that there was significant variation in elasmobranch assemblages. While some of this variation appears to be driven by habitat features, spatial dynamics and history, as models found that island geomorphology, latitude, and island group to be the primary drivers of species richness. I also find that species assemblages and associations at smaller scales may be driven by species interactions, both positive and negative, that warrant further investigation. Future studies on the effects of microscale habitat variation on shark assemblages may shed further light on the dynamics of elasmobranch assemblage composition on coral reefs.

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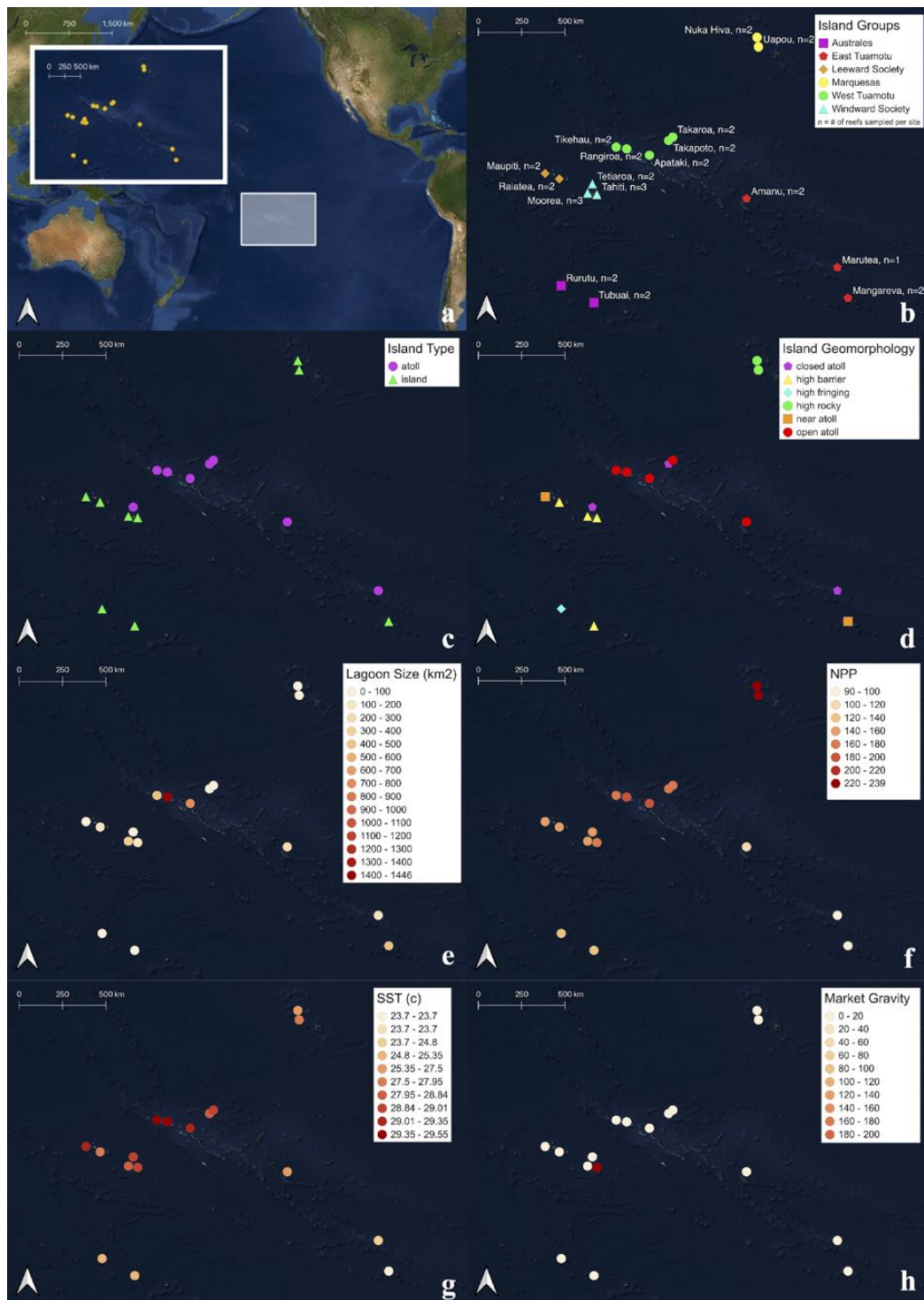
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Table 1: Characteristics of sample islands.

Site Name	# of Reefs Sampled	Island Geomorphology	Island Group	Market Gravity	Season Sampled	Lagoon Size (km ²)
Amanu	2	open atoll	East Tuamotu	0.0041	Dry	240
Apataki	2	open atoll	West Tuamotu	0.0182	Wet	706
Mangareva	2	near atoll	East Tuamotu	0.0005	Dry	407
Marutea	1	closed atoll	East Tuamotu	0.0003	Dry	112
Maupiti	2	near atoll	Leeward Society	0.0330	Wet	44
Moorea	3	high barrier	Windward Society	6.6582	Wet	382
Nuka Hiva	2	high rocky	Marquesas	0.0015	Wet	0
Raiatea	2	high barrier	Leeward Society	0.0690	Dry	198
Rangiroa	2	open atoll	West Tuamotu	0.0199	Wet	1446
Rurutu	2	high fringing	Austral Islands	0.0077	Wet	0
Tahiti	3	high barrier	Windward Society	303.9799	Wet	154
Takapoto	2	closed atoll	West Tuamotu	0.0095	Dry	85
Takaroa	2	open atoll	West Tuamotu	0.0086	Dry	93
Tetiaroa	2	closed atoll	Windward Society	0.7265	Wet	16
Tikehau	2	open atoll	West Tuamotu	0.0239	Wet	461
Tubuai	2	high barrier	Austral Islands	0.0060	Dry	85
Uapou	2	high rocky	Marquesas	0.0016	Wet	0
Amanu	2	open atoll	East Tuamotu	0.0041	Dry	240
Apataki	2	open atoll	West Tuamotu	0.0182	Wet	706

Table 2: Elasmobranch species observed on BRUVS. LC =Least concern, NT =Near Threatened, VU =Vulnerable, EN =Endangered, CR =Critically Endangered, NA =Not Applicable. Primary habitats determined by habitat description Ebert et al. (2021), and being consistent with the definition of reef sharks and rays as found in defined 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
Mobula spp.	Unknown Mobula	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



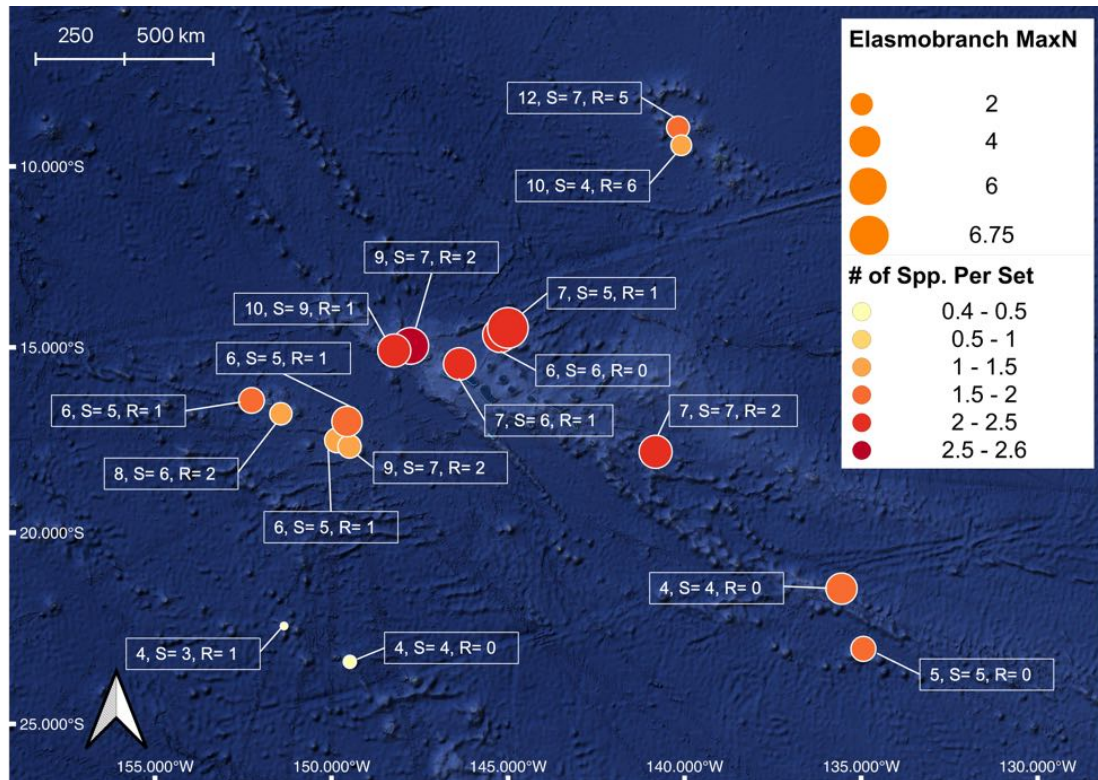


Figure 2: The relative abundance and number of elasmobranch species observed at sampling islands in French Polynesia. Mean MaxN of elasmobranchs at each island is represented by the size of the point, while the point's color represents the mean number of species observed per set. The number of species observed in total at each island is indicated via the label and then broken down into total number of shark species (S= n) and ray species (R=n)

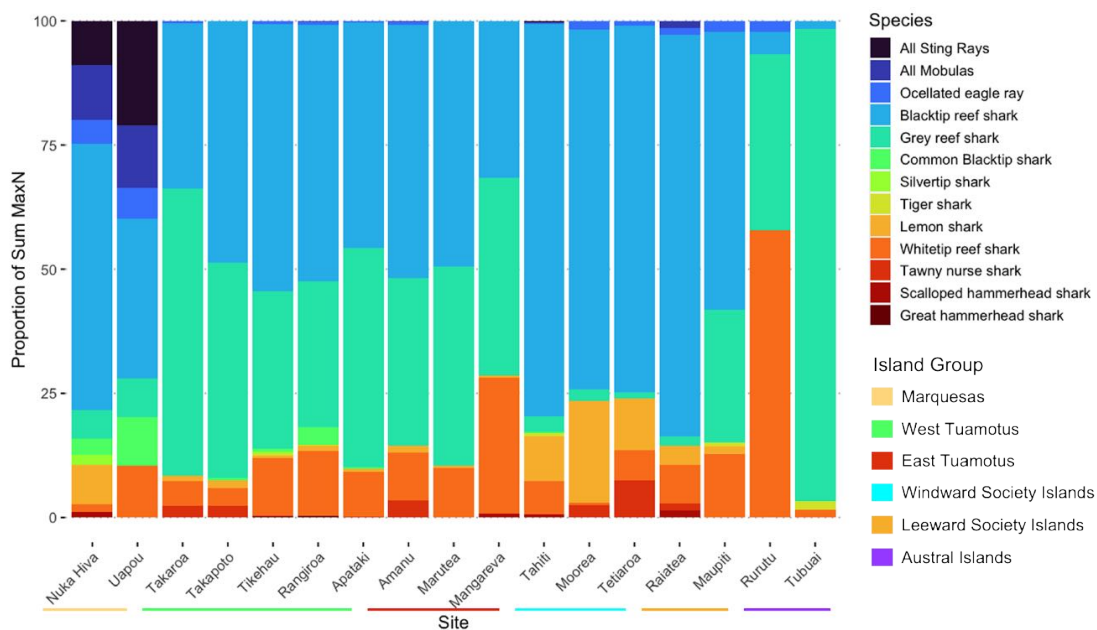


Figure 3: The proportion of relative abundance made up by elasmobranch species observed at islands in French Polynesia. Island groups are denoted by colored lines under each site.

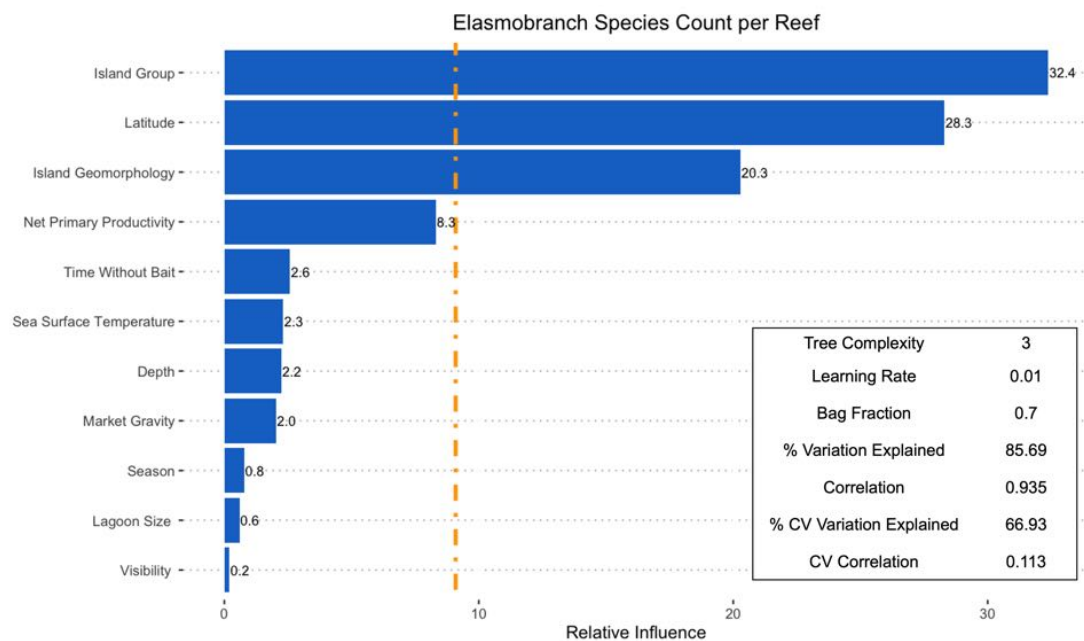


Figure 4: Relative influence of all predictor variables in boosted regression tree models of total number of elasmobranch species seen per reef. Variables with relative influence over that indicated by the orange line have influence above that expected by chance (100/number of variables). Box inside each plot show model parameters and performance statistics. CV= Cross Validated.

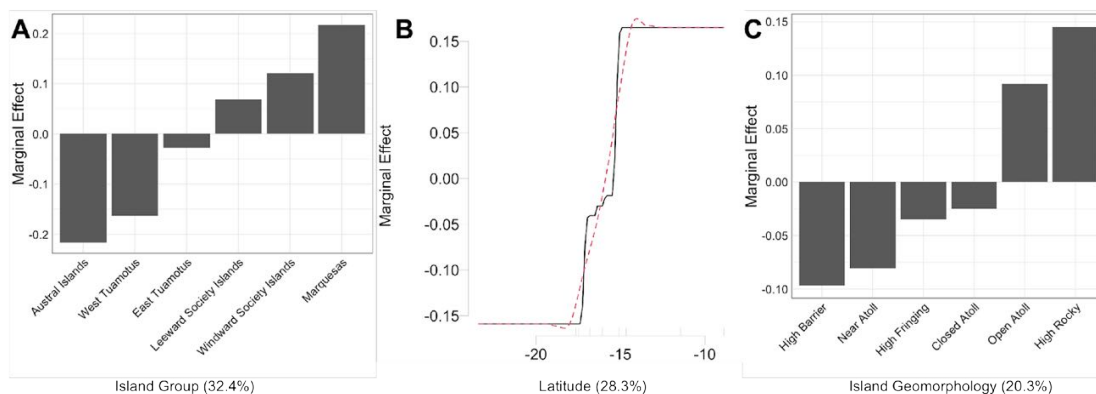


Figure 5: Partial dependence plots showing relationships of environmental variables to total number of elasmobranch species seen per reef. Relative influence of each variable is indicated as a percent. Tick marks indicate the distribution of the predictors.

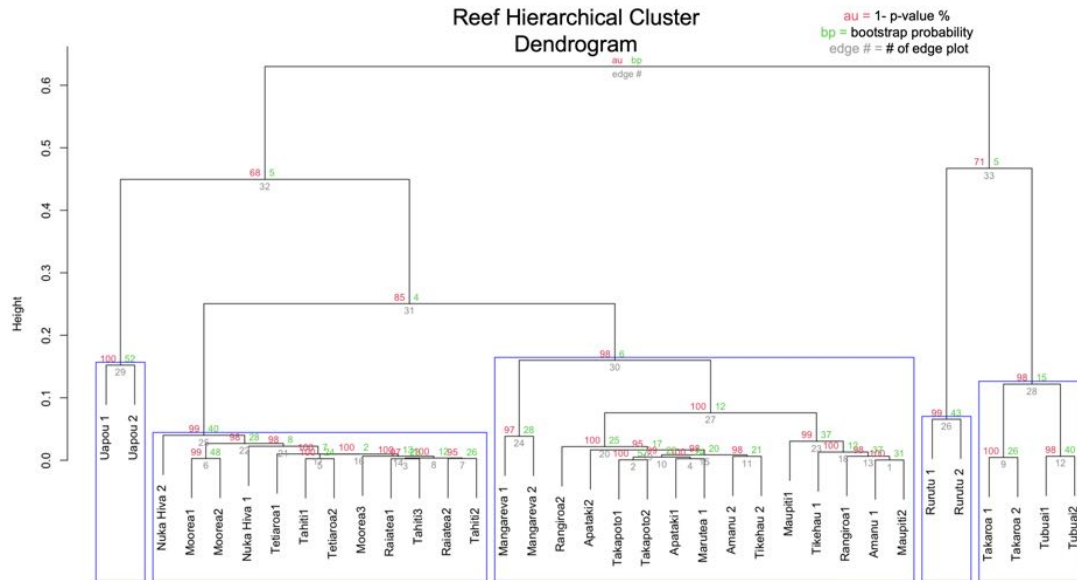


Figure 6: Hierarchical cluster dendrogram examining species assemblages as determined by mean MaxN each reef. The significance of each split is assessed by an approximately unbiased (AU) p-value and represented as 1 minus the p-value, noted on the upper left of each node in red. On the left in green 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 ($\alpha = 0.05$) is boxed in blue. Additional information about curve fitting for clusters can be seen in supplemental Figure S7, the plot number for this can be found below each node in gray.

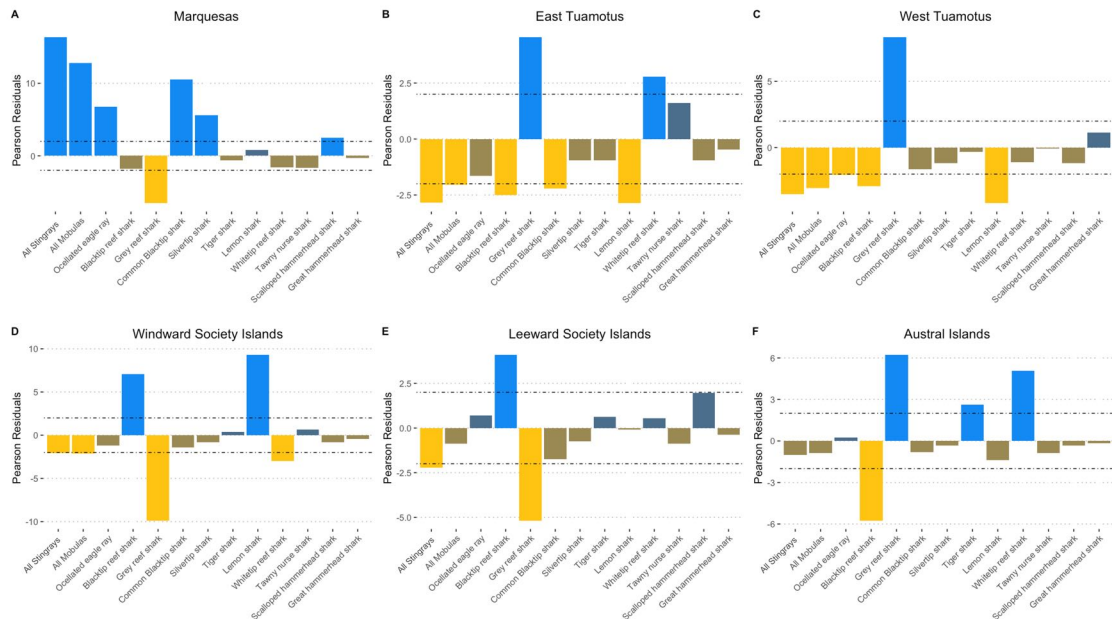


Figure 7: Plots show Pearson's residuals from chi-squared test comparing species mean MaxN at different island groups. Species with Pearson's >2 indicates a significant positive association (shown in bright blue), and is observed in that island more than expected, conversely species with a Pearson's <-2 indicates a significant negative association (shown in bright yellow) and is observed in that island less than expected. Species that showed no significant association are in dull blue and yellow.

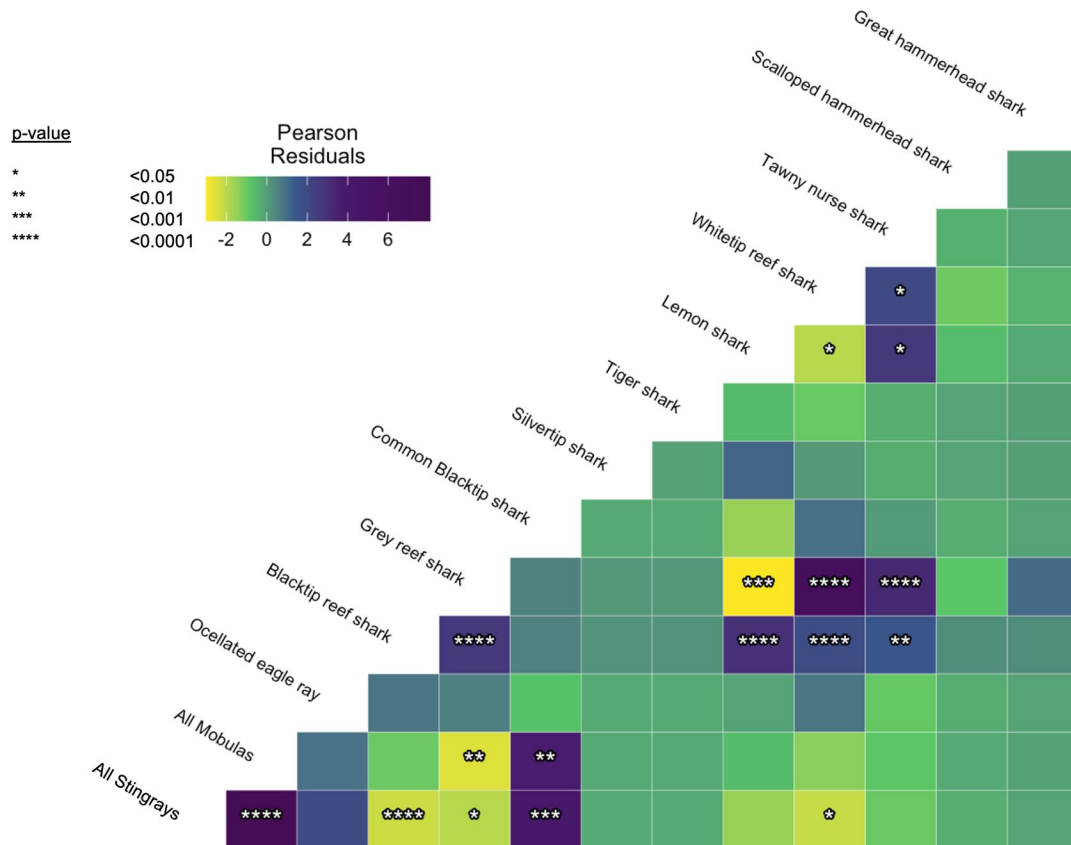


Figure 8: Heatmap of Pearson's residuals for pairwise chi-squared testing examining species co-occurrence on sets using presences/absence data. Species pairs with a significant association ($p\text{-value} < 0.05$) are indicated by a star and the number of stars indicates the level of significance.

Supplemental Materials:

Curve Fitting for Hierarchical Clustering of Reef

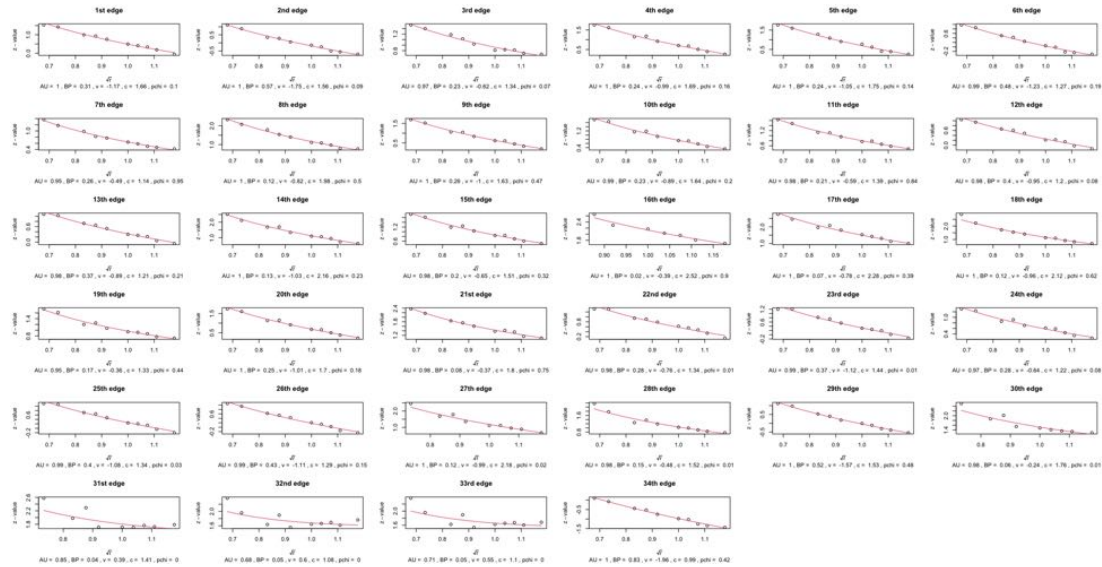


Figure S1: Diagnostic plots of the multiscale bootstrapping for each cluster in Figure 6.

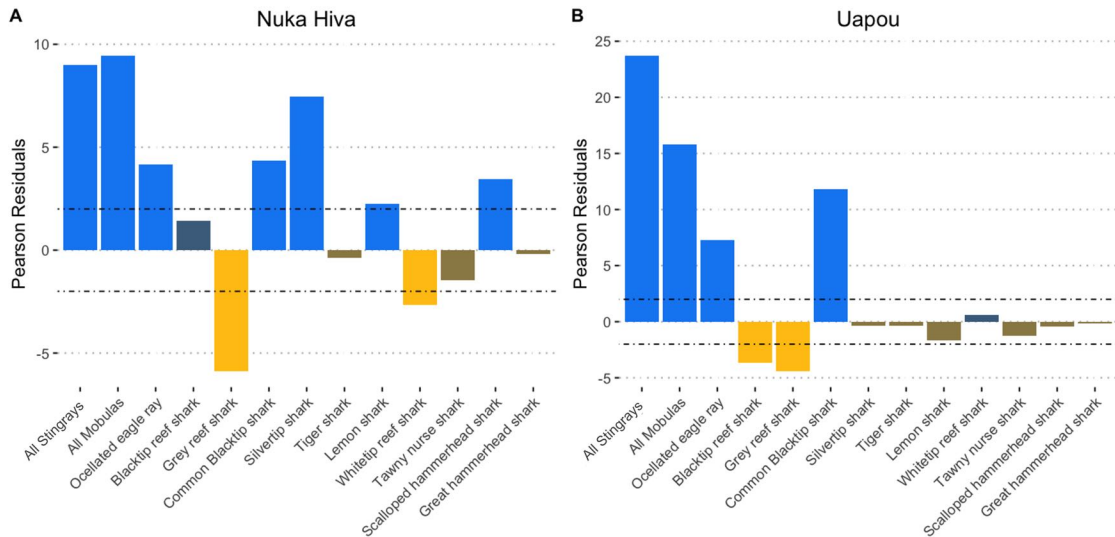


Figure S2: Plots show Pearson's residuals from chi-squared test comparing species mean MaxN at island A) Nuka Hiva and B) Uapou in the Marquesas. Species with Pearson's >2 indicates a significant positive association (shown in bright blue), and is observed in that island more than expected, conversely species with a Pearson's <-2 indicates a significant negative association (shown in bright yellow) and is observed in that island less than expected. Species that showed no significant association are in dull blue and yellow.

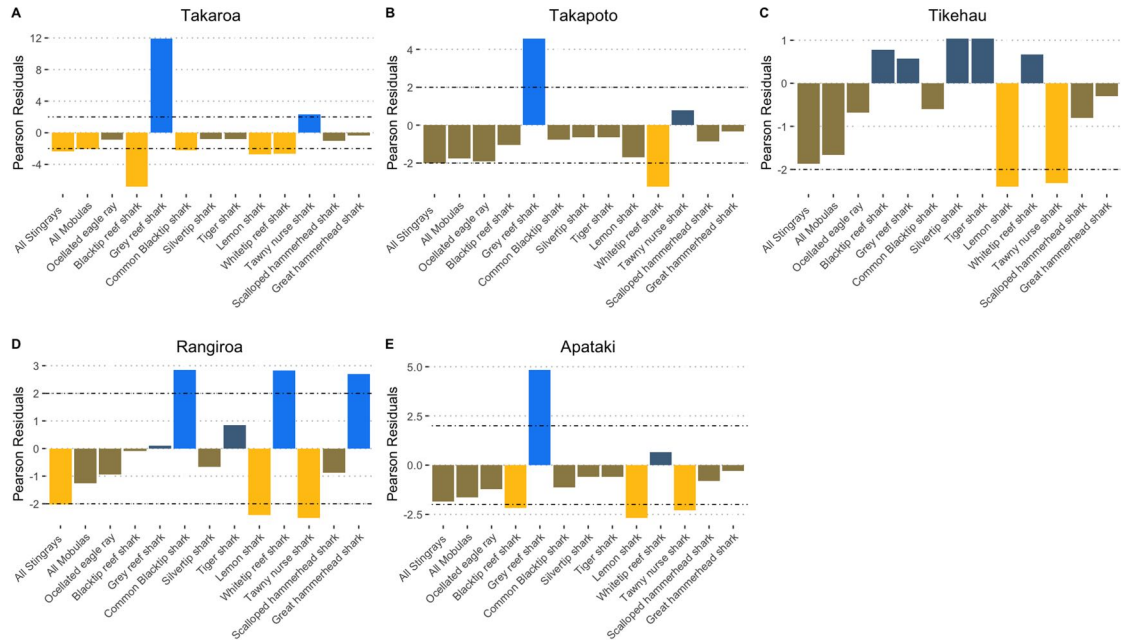


Figure S3: Plots show Pearson's residuals from chi-squared test comparing species mean MaxN at island A) Takaroa, B) Takapoto, C) Tikehau, D) Rangiroa, and E) Apataki in the West Tuamotus. Species with Pearson's >2 indicates a significant positive association (shown in bright blue), and is observed in that island more than expected, conversely species with a Pearson's <-2 indicates a significant negative association (shown in bright yellow) and is observed in that island less than expected. Species that showed no significant association are in dull blue and yellow.

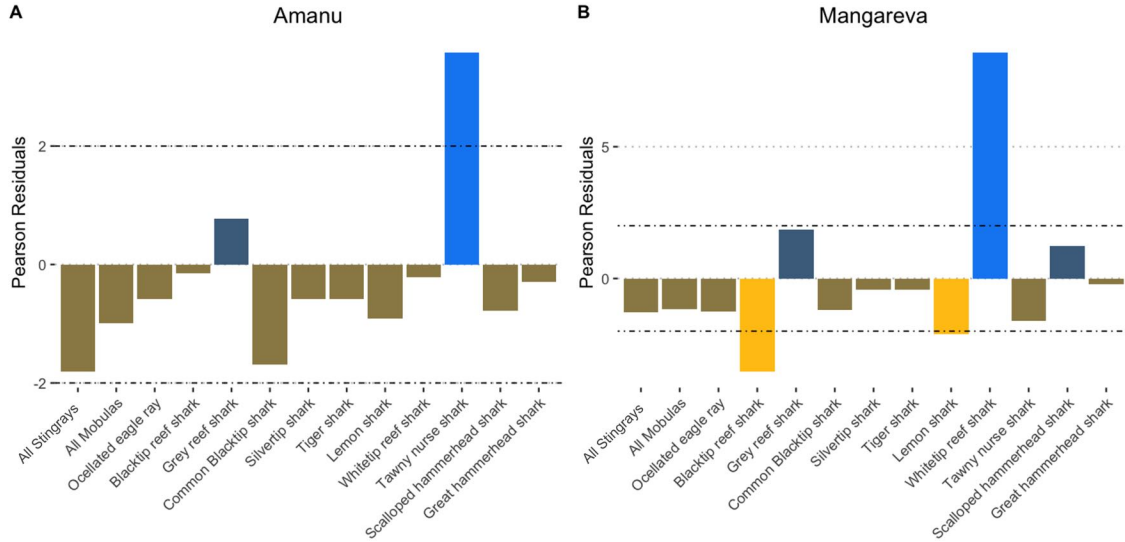


Figure S4: Plots show Pearson's residuals from chi-squared test comparing species mean MaxN at island A) Amanu and B) Mangareva in the East Tuamotus. Species with Pearson's >2 indicates a significant positive association (shown in bright blue), and is observed in that island more than expected, conversely species with a Pearson's <-2 indicates a significant negative association (shown in bright yellow) and is observed in that island less than expected. Species that showed no significant association are in dull blue and yellow.

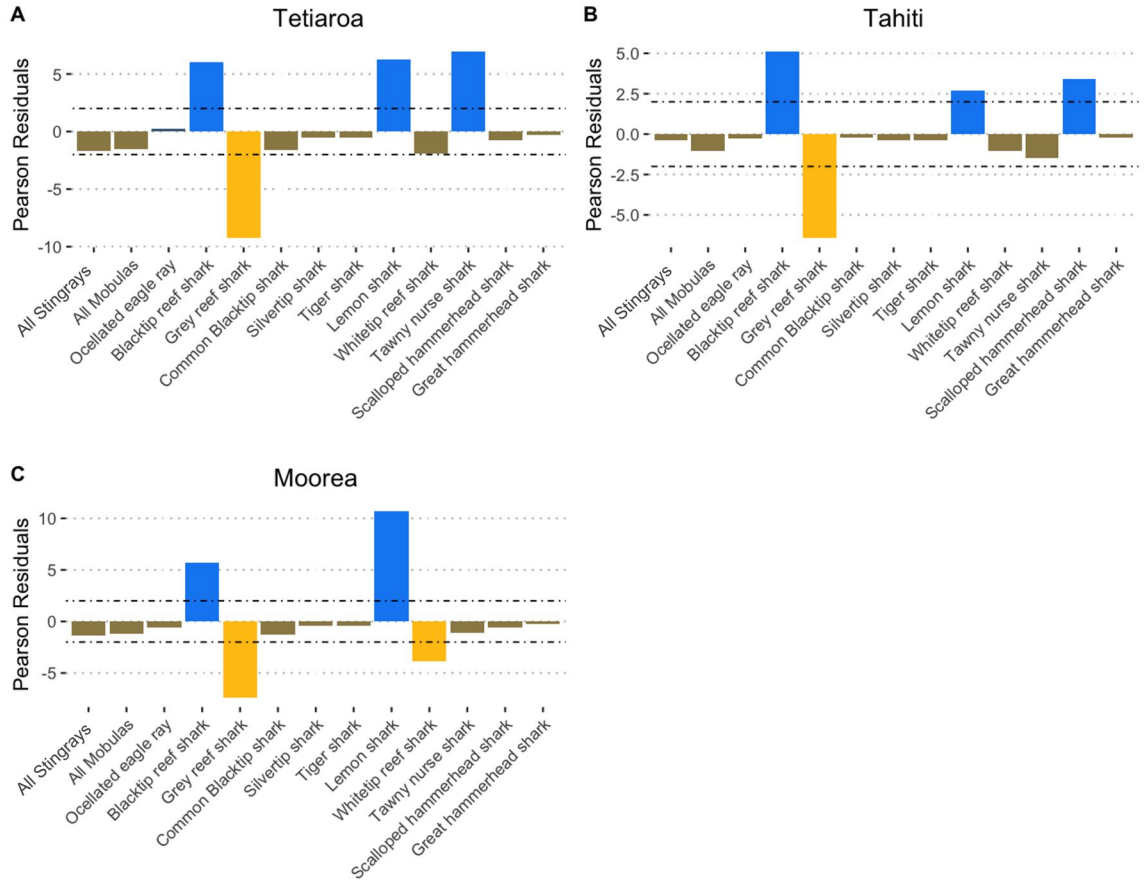


Figure S5: Plots show Pearson's residuals from chi-squared test comparing species mean MaxN at island A) Tetiaroa, B) Tahiti, and C) Moorea in the Windward Society Islands. Species with Pearson's >2 indicates a significant positive association (shown in bright blue), and is observed in that island more than expected, conversely species with a Pearson's <-2 indicates a significant negative association (shown in bright yellow) and is observed in that island less than expected. Species that showed no significant association are in dull blue and yellow.

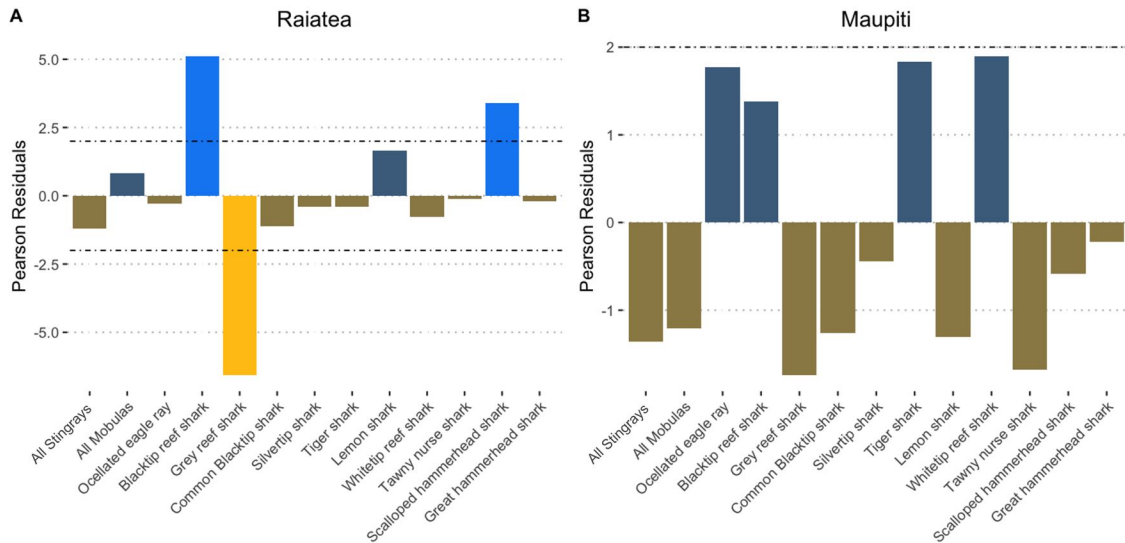


Figure S6: Plots show Pearson's residuals from chi-squared test comparing species mean MaxN at island A) Raiatea and B) Maupiti in the Leeward Society Islands. Species with Pearson's >2 indicates a significant positive association (shown in bright blue), and is observed in that island more than expected, conversely species with a Pearson's < -2 indicates a significant negative association (shown in bright yellow) and is observed in that island less than expected. Species that showed no significant association are in dull blue and yellow.

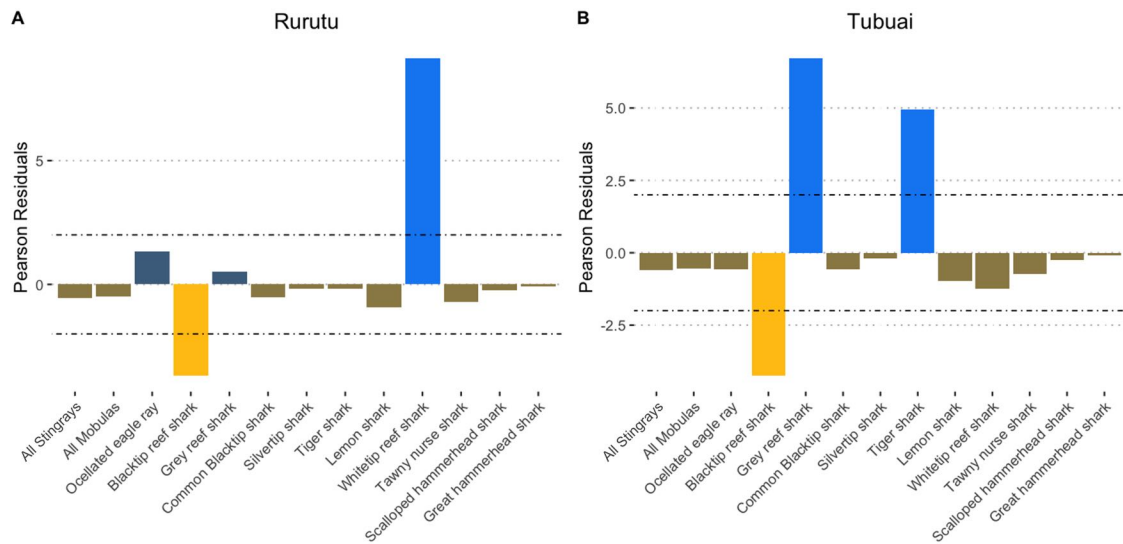


Figure S7: Plots show Pearson's residuals from chi-squared test comparing species mean MaxN at island A) Rurutu and B) Tubuai in the Austral islands. Species with Pearson's >2 indicates a significant positive association (shown in bright blue), and is observed in that island more than expected, conversely species with a Pearson's <-2 indicates a significant negative association (shown in bright yellow) and is observed in that island less than expected. Species that showed no significant association are in dull blue and yellow.

CHAPTER V

RELATIONSHIP BETWEEN REEF PREDATOR ABUNDANCE AND CORAL CONDITION IN THE WORLD'S LARGEST SHARK SANCTUARY

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Alastair Harborne, Jeremy J. Kiszka, Michelle Heupel, and Michael R. Heithaus

ABSTRACT

Understanding the factors influencing coral reef health is critical to effective management in the face of multiple stressors to these ecologically and economically important habitats. While the presence of sharks has often been cited as critical to the health of coral reefs, empirical support for this hypothesis is mixed. This lack of clarity could be due to the degraded state of most reef shark populations, functional redundancy with large piscivorous teleosts, and context dependence in the relative importance of sharks. To increase our understanding of reef predator ecology, I explored the relationship between reef health and relative abundances of sharks and large piscivorous teleosts at 24 reefs across 12 different islands/atolls of French Polynesia. Reefs represented a gradient of health, human impacts, and relative abundances of both sharks and large piscivores. Reefs with high abundances of both shark and teleost predators tended to be rated as “healthy” or “very healthy”, while reefs with low abundances of both shark and teleost predators were mostly rated as “degraded” or “fair” though a few were ranked as “healthy” or “very healthy”. Reefs with high shark abundance and low predatory teleost abundances tended to be in relatively poor states. Boosted Regression Tree (BRT) models of biomass of smaller teleosts explained ~65% of the variation seen among surveys and showed that biomass of piscivorous teleosts (29.4%), net primary productivity (NPP) (25.7%), and sea surface temperature (SST) (17.8%) had the highest relative influence. BRT models of percent cover of hard coral + crustose coralline algae explained around 42% of the variation found and showed that biomass of predatory teleosts (32.9%), shark MaxN (16.6%), and island group (13.5%) were the most influential factors. Positive effects of sharks occurred across relatively low abundances suggesting that positive

effects of sharks might accrue with modest rebuilding in areas where populations have declined dramatically. While further work is needed, it appears that large populations of both sharks and large piscivorous teleosts are associated with healthier reefs.

1. INTRODUCTION

The relative importance of sharks in structuring communities and ecosystem processes remains an area of active research (e.g. Heithaus et al. 2022). While sharks can play diverse roles in ecosystems as predators, competitors, facilitators of other species, and in nutrient transport, current studies suggest that the overall importance of sharks in ecosystems likely varies within and among species and ecosystem types (e.g. Heithaus et al. 2008, 2022, Ferretti et al. 2010, Heupel et al. 2014). In certain scenarios, sharks can exert considerable influence on ecosystem processes. For instance, in Shark Bay, Western Australia, tiger sharks (*Galeocerdo cuvier*) play a pivotal role in structuring seagrass systems, primarily through the primarily through risk effects (for reviews see Burkholder et al. 2013, Heithaus et al. 2022). Moreover, evidence suggests that white sharks (*Carcharodon carcharias*) off the coast of California, USA, may impede the recovery of kelp forests by suppressing sea otter (*Enhydra lutris*) populations or modifying their habitat use patterns (Moxley et al. 2019). These results, however, do not appear to apply ubiquitously, and there is considerable uncertainty in the relative importance of sharks in coral reef ecosystems (Heithaus et al. 2022, Roff et al., 2016; Ruppert et al., 2016).

The uncertainty surrounding the ecological importance of sharks on reefs stems from multiple factors. First, coral reefs tend to have complex and diffuse food webs that can reduce the strength of individual interactions (Rizzari et al. 2014, Frisch et al. 2016, Roff et al. 2016, Desbiens et al. 2021, Chapman et al. 2022). Thus, shark effects on reef health may be minimal or only occur in rare circumstances (e.g. Desbiens et al. 2021). Also, most shark species on coral reefs are large-bodied mesopredators (e.g. Heupel et al. 2014, Roff et al. 2016) and can fill trophic roles similar large-bodied teleost predators such as jacks, barracuda, groupers and large snappers (e.g. Frisch et al. 2016, Papastamatiou et al. 2015). Thus, it is possible they are functionally redundant with large predatory teleosts and reductions in shark populations may be offset by any remaining large teleosts, increases in predatory teleost populations, or diet shifts by these fishes. Another challenge lies in the widespread and considerable declines in reef shark populations (e.g.

MacNeil et al. 2020) that may have led to the erosion of their effects on reefs before studies of their importance commenced (e.g. Desbiens et al. 2021, Heithaus et al. 2022, Roff et al. 2016). Despite these challenges, evidence for shark induced trophic cascades on coral reef systems is mixed, with some studies supporting the presence of cascades mediated by teleost population density changes (e.g. Barely et al. 2017, Ruppert et al. 2013) while others provide evidence that shark effects may be weak (e.g. Madin et al. 2020, Roff et al. 2016, Desbiens et al. 2021). Therefore, the importance of sharks in structuring coral reef systems is likely context dependent (Lester et al. 2021). Given the considerable threat to both coral reef systems (Bellwood et al. 2004, Hughes 1994, Ruppert et al. 2013, Ruttenberg et al. 2011) and to shark populations globally (e.g. Ferretti et al. 2010, Robbins et al. 2006, Roff et al. 2018) a better understanding of the functional roles of reef predators, including sharks, is important for conservation. One approach for investigating the ecological importance of sharks and large piscivorous teleosts is to assess their relationships with reef health (e.g. coral cover, populations of smaller fishes) across gradients in their abundances.

Effects of large teleost predators and sharks on coral reef health will occur through changes in the behaviors or population sizes of primary consumers that feed on algae that can overgrow corals, or on corallivorous consumers (e.g. Mumby et al 2007). Therefore, shark and/or teleost predator abundance would be predicted to have negative associations with small consumer abundances if they are influencing coral communities through direct predation mechanisms. A lack of this relationship, however, does not preclude top-down effects of large predators which might modify the spatial extent and strength of small consumer effects on algae and corals through non-lethal pathways (e.g. Rasher et. al 2017, Lester et al. 2021). For example, Rasher et al. (2017) found that on Fijian reefs, hunting behaviors of sharks, reef topography, and tidal movement created predictable “hot-spots” of predation risk that are avoided by herbivores, and thus shape reef landscapes.

French Polynesia is the world’s largest shark sanctuary, with prohibitions on shark fishing, trade, and export being put in place in 2006. These protections have been largely successful (Ward-Paige & Worm 2017, MacNeil et al. 2020), and large shark and predatory teleost populations occur in many locations (Chapters 2, Chapter 3, MacNeil et al. 2020). There is, however, marked variation in the relative abundance of both of these groups across islands and atolls (Chapters 2, 3) Thus, French Polynesia is an excellent location to better understand the relationship between the abundances of sharks and large piscivorous teleosts and the health of coral reefs.

The goal of this study was to gain insights into the potential relative effects of large piscivorous teleosts and sharks on coral reef ecosystems. Specifically, I investigate how the abundances of small teleost consumers and coral condition varied in response to the abundances of large predatory teleosts, sharks, and a variety of environmental and human factors.

2. MATERIALS AND METHODS

2.1 Site Description

French Polynesia in the south-central Pacific contains over 2% of the world's living coral reef (Spalding et al. 2001). This overseas collectivity of France lies between, 7° - 27° S and 134° - 155° and has an exclusive economic zone covering *ca.* 5,030,000 km². It consists of five archipelagos: the Marquesas Islands, the Tuamotu Archipelago, the Society Islands, the Gambier Islands, and the Austral Islands. The relative abundances of reef sharks and predatory teleosts vary considerably across the islands of French Polynesia (Chapters 2 & 3). In general, the West Tuamotus had the highest abundance of sharks and teleost predators, followed by the East Tuamotus (including the Gambier Islands). The Society Islands were the next most abundant overall, however teleost predators were more abundant on the Leeward Society Islands than on the Windward Society islands, while the reverse was true of sharks, which were relatively more abundant on the Windward Society Islands than the Leeward Society Islands. The Austral

Islands had the lowest relative abundance of both predatory teleosts and sharks compared to the other island groups.

2.2 Field Methods

Sampling occurred at 24 reefs across 12 different island/atolls (hereafter ‘islands’). Reefs are defined as an area of approximately 4 km² with continuous coral reef habitat. Islands were categorized according to their geomorphology as: open atoll, closed atoll, near atoll, high barrier, and high fringing (Table 1). Atolls were defined as open or closed based on the presence of boat navigable passes between forereef and lagoon. Open atolls have such passages while closed atolls lack them, though smaller shallow water passes still allow limited movement of water and animals. High islands that occupy a very small area of the lagoon inside their annular reef were classified as near atolls (sometimes called “pseudo-atolls”) (Davis 1928, Goldberg 2016). Other high islands were classified by their reef types: barrier reefs with lagoons and fringing reefs with no lagoon (Table 1).

2.3 Underwater Visual Censuses

Underwater Visual Censuses (UVCs) were performed by teams of two people snorkeling along 50 x 2m transects and replicated 4-5 times at each reef (Table 1). Surveys were conducted at a depth of 9 m (SD±0.30). To reduce missing observations of cryptic or skittish animals, two fish-counting passes were done, the first to count highly mobile fishes, and the second to count smaller, less mobile fishes. All animals were classified to

the lowest possible taxonomic level, with 99.93% of observations being identified down to species, and all observations being identified down to at least genus level. Length was estimated to the nearest centimeter. This was converted to weight estimates using the formula $W = aL^b$ where W is weight in grams, L is length in centimeters and a & b are constants determined by species specific length-weight relationships (Kulbicki et al. 2005). This weight is then converted to biomass by dividing by the total survey area (100m).

Often considered mesopredators (e.g. Desbiens et al. 2021, Chapter 3), members of the families Lutjanidae, Scombridae, Megalopidae, Carangidae, Sphyraenidae, Serranidae, and Lethrinidae (here after ‘predatory teleosts’) were grouped to obtain a biomass for predatory teleosts. All other teleosts were grouped to obtain biomass for smaller-bodied teleosts (hereafter ‘prey’ teleosts). Elasmobranchs were not included in these calculations.

Benthic surveys were conducted after the initial pass of fish surveys to avoid influencing fish counts. The point intercept method was done every half meter of the 50 m transect, and substrate type (i.e. sand, rubble, pavement, algae, hard coral, soft coral, and invert) was recorded. Algae types were further broken down into crustose coralline algae (CCA), turf, and fleshy macroalgae. Relief was assessed for each transect using the 0-5 scale outlined by Wilson et al. (2007), where zero indicates no vertical relief, and a five indicates an exceptionally complex benthos with numerous caves and overhangs.

2.4 Baited Remote Underwater Video Stations

BRUVS were used to survey all reefs. BRUVS consisted of a GoPro Hero4 Silver or GoPro Hero+ action camera (<https://www.gopro.com>) mounted to an aluminum frame. Extending in front of this camera was an attached bait arm (*ca.* 1.5 m in length) with a container holding *ca.* 1 kg of oily fish bait (yellowfin tuna *Thunnus albacares*, small inshore fish, fish heads and scraps- typically tuna-, or sardines *Clupeidae spp.*). BRUVS were positioned so the camera faced down current, the direction of which was determined using dye tabs. BRUVS were deployed on the forereef at depths of 9 - 35 m during daylight hours. To prevent autocorrelation, no two BRUVS were deployed within 500 meters of one another within a sampling day. A minimum of 48 sets (Mean = 58; Max = 70) were deployed on each reef, and each BRUV had a minimum soak time of 60 min.

During deployment of each set, bottom depth was recorded, and sea surface temperature (SST) taken using a YSI Pro 2030 model. Sampling at individual reef locations usually took place over a single period of < 10 days (max. 37 days) during the years 2016 & 2017.

2.5 Video Data Extractions

To determine relative abundances of sharks each BRUVS video was viewed and annotated to 60 minutes by two annotators, using the Fingerprint Annotator software

(v1.1.44.0) (<https://www.vulcan.com/>). All observations were checked by an expert reviewer to confirm identifications and resolve inconsistencies.

Relative abundance of sharks was measured using MaxN, the maximum number of individuals of each target species seen in a single frame for each video. MaxN is the standard for reporting relative abundance for BRUVS data as it avoids double counting the same individual that might enter and exit the field of view multiple times (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. Individuals that could not be identified to species accounted for less than 3% of observations and were only included in MaxN calculations if there were no other sharks seen during that set ($< 0.5\%$ of sets). The MaxN of sets was then averaged to obtain MaxN values for each reef.

2.6 Other Environmental and Anthropogenic Data

Net Primary Productivity (NPP) was determined using open access satellite-based observations (*Ocean Productivity Oregon State, 2021*) employing the Vertically Generalized Production Model (Behrenfeld & Falkowski, 1997). The value for each reef was taken from the nearest neighbor pelagic cell then averaged over the two sampling years (2016-2017) (Gove et al., 2013). SST were taken during each BRUVS deployment then averaged to obtain an average SST per reef. Human population density of each island was selected as the metric for human pressure because it outperformed other metrics (i.e. marked gravity and human population size) in preliminary analysis. Human

population density was calculated by dividing the human population size for each island (*Census Report 2017*, ISPF) by that island's emerged land area.

2.7 Coral Health Index

To assess general health of each reef I use a modified two-dimensional coral health index as described in Kaufman et al. (2011). This coral health index combines two parameters, percent cover of hard corals + crustose coralline algae and fish biomass as a fraction of 500 g/m², which are averaged to produce a score which ranges from 0 to 1, which is then graded into five categories: very degraded, degraded, fair, healthy, and very healthy.

2.8 Boosted Regression Trees (BRT)

To examine the relationship between reef health and predator abundance I used Boosted Regression Trees (BRTs). BRTs are a machine learning technique that can account for high proportions of variability despite complex multivariate relationships. Rather than trying to find a single best regression tree, BRTs use boosting to create an ensemble from many hundreds or thousands of trees (Elith et al. 2008). In this way BRTs can handle complex non-linear relationships, are not sensitive to collinearity among variables, and account for interactions between predictor variables (Abeare 2009, Elith et al. 2008, Jouffray et al. 2019).

As response variables, I used 1) the benthic component of the coral health index - the percent cover of hard coral and CCA - and 2) the biomass of prey fish. Explanatory variables included island geomorphology, island group, NPP, SST, relief, human population density and lagoon size. With benthos as the response variable, I also used the abundances of sharks (as measured by mean MaxN), the biomass of predatory teleosts, and biomass of prey teleosts as explanatory variables. To reduce any stochasticity introduced by encountering large fish schools, and to account for any bias introduced by UVC sampling, biomass of both predatory teleosts and prey teleosts was averaged across each reef. When modeling prey fish biomass as the response variable, both prey fish biomass and predatory fish biomasses were log transformed to better fit a Gaussian distribution. Mean shark MaxN and percent cover of hard coral and crustose coralline algae were also used as explanatory variables in these models.

All models were fitted using the R package *gbm.auto* (Dedman et al. 2017) in R version 4.0.2 (R core team, 2022). The model parameter (hyperparameter) selection, analysis, model evaluation, and plotting processes for BRT modeling are all automated by this package. I selected the gaussian distribution for my models based on visual inspection. To determine optimal hyperparameters I tested across a series of values for tree complexity (1, 2, 3, 4, & 5), bag fraction (0.5, 0.55, 0.60, 0.65, 0.7, 0.75), and learning rate (0.0005, 0.001, 0.005, 0.01). The combination of model parameters that yielded the smallest model deviance, and best correlation score between training data and tested data was selected for final models. All models were checked for zero-inflation, and no evidence for any zero-inflation was found. For discussion purposes, I focus only on

variables with relative influence above that expected by chance, $100/\text{number of variables}$ (Müller et al. 2013). All values are reported as means $\pm$ SD.

3. RESULTS

Of the 24 sampled reefs, seven were rated “very healthy” according to the two-dimensional Coral Health Index, five were rated “healthy”, six “fair” and six as “degraded.” None were ranked as “very degraded” (Table 1). Cover of crustose coralline algae (CCA) and hard corals together averaged 52.7% ($\pm$ 18.5) and ranged from a mean of 25.4% - 77.2% (Figure 1). CCA and hard corals dominated the benthos, with algae (turf & fleshy macroalgae) being the next-most common substrate, with a combined mean cover of 22.3% ($\pm$ 17.7), followed by rubble (10.9% $\pm$ 13.8) and pavement (9.7% $\pm$ 12.6).

Mean teleost biomass on reefs ranged from 62.4 g/m² to 2535.8 g/m². Large piscivorous teleosts had a mean biomass of 119.6 ($\pm$ 225.1 g/m²) with reef means ranging from 4.99 g/m² - 804.34 g/m². Prey teleosts had a mean biomass of 343.91 $\pm$ 549.47 g/m² with mean values for individual reefs ranging from 56.23 g/m² to 1731.47 g/m² (Table 1, Figure 2). There was a positive relationship between biomass of predatory teleosts and shark MaxN (Figure 4, 7A, 10). Mean shark MaxN on reefs ranged from 0.25 to 5.81 (Table1), with a mean of 2.82 $\pm$ 1.61.

Reefs with high abundances of both shark and teleost predators tended to be rated as “healthy” or “very healthy” (Figure 3). None of the sampled reefs had high abundance of predatory teleosts and low abundance of sharks, however a few reefs had high shark abundances with low teleost biomass, these reefs were ranked as “fair” or “degraded”. Reefs with low abundance of both shark and teleost predators were mostly rated as “degraded” or “fair” though a few were ranked as “healthy” or “very healthy”.

The BRT model exploring prey teleost biomass ($\log \text{ g/m}^2$) accounted for a large amount of the variation ($\sim 65\%$) seen among surveys (Figure 8). Biomass of predatory teleosts was the most influential factor with a relative influence of 29.4% (Figure 8), and a positive relationship (Figure 9A, Figure 5). NPP was the second most influential factor with a relative influence of 25.7% (Figure 8). PDPs indicated a generally negative relationship between net primary productivity and prey teleost biomass (Figure 9B). Average SST had a relative influence of 17.6%, and partial influence plots indicated that prey fish biomass drops sharply above 28°C . The relative influence of shark MaxN (1.7%) fell below that expected by chance (10%).

The BRT model exploring percent cover of hard coral and crustose coralline algae accounted for $\sim 42\%$ of the variation seen between surveys (Figure 6). Biomass of predatory teleosts was the most influential variable, with a relative influence of 32.9% (Figure 6). Large piscivorous predatory teleosts had little effect on coral cover at low densities, but at *ca.* 150 g.m^2 these effects rapidly increased and were high and positive across increasing fish densities. As a result, coral cover varied greatly at low predatory

teleost densities before assuming a positive relationship above $\sim 215 \text{ g/m}^2$ (Figure 4, 7A, 10).

Shark MaxN was the second most influential factor with a relative influence of 16.6% (Figure 6). Coral cover increased with shark abundance up to a MaxN ~ 2 , at which point the effect decreased substantially, and even became negative between MaxNs of 2-3, before increasing but remaining relatively weak after a MaxN of 3 sharks (Fig 4, 7B, 10).

Island group had a relative influence of *ca.* 13.5%. Coral cover was highest in the Windward Society Islands (62.0 ± 9.1) followed by the Leeward Society Islands (57.6 ± 16.7), East Tuamotus (56.9 ± 22.0), West Tuamotus (49.1 ± 16.8), then Austral Islands (36.8 ± 19.1) (Figure 7C). While prey teleost biomass had a relative influence (9.5%) narrowly below what would be expected by chance (10%), it had a generally positive relationship with percent cover of hard corals + CCA (Figure 7D).

4. DISCUSSION

Across French Polynesia there was marked variation in reef health as measured by the two-dimensional Coral Health Index, as well as abundances of sharks, large piscivorous teleosts and smaller teleosts. This provided an opportunity to explore the relationship between two potentially functionally redundant predator groups and coral reef health. Overall, reefs that ranked high on the CHI tended to be found where relative abundance of both teleost predators and shark predators were high, however degraded reefs fell

across a wide combination shark abundances while only falling at lower abundances of predatory teleosts. There were no reefs with low numbers of sharks and high numbers of large teleost predators, and very few reefs where high numbers of shark predators and low numbers of large teleost predators were found. Thus, in French Polynesia higher predator abundances were associated with reef health, but sharks and large piscivorous teleosts may not be similarly important.

Despite incorporating environmental factors and anthropogenic impacts in models, the biomass of large piscivorous teleosts had the largest, and positive, effects on both the biomass of smaller teleosts and the combined cover of hard corals and CCA.

Furthermore, all reefs ranked as “degraded” by the CHI had predatory teleost biomass below 65 g/m², while all reefs above that number were ranked “very healthy” or “healthy,” with one exception. The strength of the relationship between the abundance of large piscivorous teleosts and benthic communities and smaller teleosts suggests that either high predatory teleost abundance led to healthier corals or that good coral condition on reefs support a higher carrying capacity of teleosts. The later hypothesis is supported by the fact that there was a positive relationship between large piscivorous teleost biomass and biomass of prey teleosts. As this suggests that direct top-down control of prey teleosts by larger predatory teleosts is not driving the relationship between predatory teleosts and coral condition. Furthermore, high abundances of large piscivorous teleosts only occurred at reefs where sharks were also abundant. However, there were areas with abundant shark populations and low biomass of large piscivorous teleosts, and these reefs were ranked mostly as “degraded”. The lack of clear and direct influence of

large predatory teleosts on prey teleosts here isn't particularly surprising, Desbiens et al. (2021) also found positive correlations between predatory teleost biomasses and their prey biomasses on the Great Barrier Reef. However, a fuller breakdown of both predatory and prey teleosts into functional groups could better elucidate these relationships, as many species interactions are context dependent. For instance, Mumby et al. (2006) demonstrated that the predation impact of the largest grouper on grazing was minimal as gape limitation prevented attack of large bodied parrotfish.

The relative abundance of sharks did not noticeably influence the biomass of small teleosts, but was an important factor, with a relative influence behind only predatory teleost biomass, in models of coral cover. This result is similar to that found by Desbiens et al. (2021), who found no evidence suggesting that sharks suppress fish populations on the Great Barrier Reef, Australia. In contrast, Barley et al. (2017a) found that higher shark abundances were associated with lower abundance of smaller mesopredatory teleosts (<50 cm), and higher large teleost abundance (>50 cm) in northwestern Australia.

While my results suggest that variation in shark abundances found across the islands and atolls of French Polynesia are unlikely to influence the biomass of smaller reef-associated teleosts, it does not preclude sharks indirectly affecting the wider community (e.g. Heithaus et al. 2008). Indeed, sharks may modify the spatiotemporal patterns and intensity of fish foraging, including by species that may forage on algae that competes with coral. Risk effects induced by reef sharks have been widely documented. For example, in Northwestern Australia, Lester et al. (2021) recorded increased vigilance and

anti-predator behavior by mesopredatory reef fish in response to predator presence. Similarly, on Fijian reefs predictable “hot-spots” of predation risk created by shark hunting behaviors, reef topography, and tidal movement were reported to be avoided by herbivorous fish and thus shape reef landscape (Rasher et al. 2017). Furthermore, Barley et al. (2017b) demonstrated that mesopredatory fish differed in locations with higher shark abundances. It is possible that this mechanism is occurring in French Polynesia as well. Indeed, the positive relationship between coral cover and increasing shark MaxN at relatively low shark densities, at least for French Polynesia, raises the possibility of indirect effects of sharks. My data, however, do not preclude the possibility that sharks are attracted to healthier reefs. This later hypothesis is not generally supported by both the presence of high shark relative abundances at degraded reefs and those with relatively low fish populations. It is notable here that the two most common species of shark seen on the BRUVS, blacktip reef sharks (*Carcharhinus melanopterus*) and grey reef sharks (*Carcharhinus amblyrhynchos*), may supplement their diets from locations other than the forereef. Blacktip reef sharks use lagoon habitats frequently even as adults (e.g. Mourier et al. 2013, Papastamatiou et al. 2009) and grey reef sharks have been shown to rely more on pelagic food webs in some locations (McCauley et al. 2012). This demonstrates that not all shark species are likely to have the same association strength with reef fish, even among reef resident shark species. Thus, the impacts of shark species on reef health may be species specific and investigating species-specific relationships, rather than treating sharks as an aggregate group may yield better insight into the relationships of sharks and reef health.

Importantly, French Polynesia supports high abundances of sharks relative to other locations in the Indo-Pacific and other regions in the world (Chapter 2, MacNeil et al. 2020). Therefore, even sites with a relative abundance that is “low” reefs in French Polynesia still have larger shark populations than found on more heavily fished reefs elsewhere. For instance, in Fiji, Gotze & Fullwood (2013) found a mean MaxN of sharks of 0.8 on and 0.3 in fished areas. While in Indonesia Jaiteh et al. (2016) found a mean MaxN of 0.8 and 0.6 on un-fished reefs and 0.3 on fished reefs. These averages on fished reefs from other regions are comparable to the lowest mean MaxN found on any reef in French Polynesia ~0.3, and much lower than the average mean MaxN of found overall (2.82). Therefore, if the relative importance of shark presence to ecosystem health is realized at relatively low shark densities, as suggested by the relationship found between sharks and reef health, then this analysis may have been less likely to document shark effects. That I did observe apparent shark effects at relatively low abundances, suggests that shark restoration efforts may not need to restore shark populations to completely “natural” or shark population densities, for sharks to have a positive influence on coral reef health. Because island geomorphology has a strong influence on the carrying capacity of reef systems for sharks (Chapter 2), with atolls supporting much higher shark abundances than high islands, the actual thresholds and relationships of shark abundance to coral cover may be more clearly understood if atolls and high islands were separated in analysis.

Human population density at a given island did not significantly influence coral health or small teleost biomass. Indeed, many “degraded” reefs were found on remote islands with

low population size such as Apataki and Tikehau. This suggests that general reef health is not driven by direct local human impacts, but by other factors. These factors may be global scale chronic factors that impact reefs worldwide such as ocean acidification and warming waters. For example, bleaching events have been documented in Moorea in the Windward Society Islands in 1991, 1994 2002, and 2007 (e.g Pratchett et al. 2013) and in 1997 in Rangiora in the West Tuatmotus (Roff et al. 2014). Similarly, a crown of thorns outbreak was documented in the Society Islands starting around 2002 (e.g. Kayal et al 2012). Bleaching events, and other similarities in disturbance history, are likely why island group was an influential factor in the model for percent cover of hard corals and crustose coralline algae. Similarly, both NPP and SST were important factors in the model of prey teleost abundance.

5. CONCLUSIONS

I found that, in the world's largest shark sanctuary, the health of coral reefs, as measured by the two-dimensional coral health index, was largely influenced by the presence of both large piscivorous teleosts and sharks. These effects, however, were not similar or linear. The presence of predatory teleosts appeared to be more important and to have positive effects across a wide range of biomasses present on a reef while the effects of sharks on reef health occurred primarily at relatively low abundances. Taken together this suggests that these predator taxa do not appear to be fully redundant functionally although studies in areas with high large piscivorous teleost abundance and low shark abundance would help clarify the relative influences of the two groups.

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TABLES & FIGURES

Table 1: Characteristics of sampled reefs. Biomasses are reported in g/m².

Reef Name	# of UVCs	Island Geomorphology	Island Group	Human Population Density	Season Sampled	Mean Relief	Mean Shark MaxN	Mean Predatory Teleost Biomass	Mean Prey Teleost Biomass	Mean Hard Coral + CCA % Cover	Coral Health Index Grade
Amanu 1	5	open atoll	East Tuamotus	10.88	Dry	2.00	2.72	94.78	849.96	0.43	Very Healthy
Amanu 2	5	open atoll	East Tuamotus	10.88	Dry	2.20	4.05	804.34	1731.47	0.76	Very Healthy
Apataki 1	5	open atoll	West Tuamotus	21.05	Wet	2.00	4.29	13.06	67.19	0.55	Degraded
Apataki 2	5	open atoll	West Tuamotus	21.05	Wet	2.00	2.70	62.97	71.45	0.33	Degraded
Mangareva 1	5	near atoll	East Tuamotus	49.43	Dry	3.00	2.40	114.01	537.15	0.25	Healthy
Mangareva 2	5	near atoll	East Tuamotus	49.43	Dry	3.00	1.00	113.03	840.96	0.66	Very Healthy
Marutea 1	5	closed atoll	East Tuamotus	8.67	Dry	3.60	3.11	230.58	380.03	0.75	Very Healthy
Maupiti 1	5	near atoll	Leeward Society	117.73	Wet	3.20	1.73	42.35	152.48	0.49	Fair
Maupiti 2	5	near atoll	Leeward Society	117.73	Wet	3.00	1.95	14.15	149.33	0.49	Fair
Raiatea 1	4	high barrier	Leeward Society	47.48	Dry	1.00	1.35	16.98	202.66	0.54	Fair
Raiatea 2	5	high barrier	Leeward Society	47.48	Dry	1.00	1.44	8.99	356.87	0.77	Healthy
Rangiroa 1	5	open atoll	West Tuamotus	34.29	Wet	2.00	3.19	158.97	186.83	0.45	Fair
Rangiroa 2	5	open atoll	West Tuamotus	34.29	Wet	4.20	5.81	195.63	261.41	0.50	Healthy
Tahiti 1	5	high barrier	Windward Society	181.30	Wet	3.00	2.12	17.76	104.25	0.62	Fair
Tahiti 2	5	high barrier	Windward Society	181.30	Wet	3.20	1.17	14.54	107.19	0.63	Fair
Tahiti 3	5	high barrier	Windward Society	181.30	Wet	3.00	1.62	4.99	71.18	0.61	Degraded
Takapoto 1	5	closed atoll	West Tuamotus	33.40	Dry	2.75	3.34	210.70	393.91	0.46	Very Healthy
Takapoto 2	5	closed atoll	West Tuamotus	33.40	Dry	1.67	4.63	214.46	237.23	0.66	Healthy
Takaroa 1	5	open atoll	West Tuamotus	33.70	Dry	2.00	4.40	256.52	298.79	0.72	Very Healthy
Takaroa 2	5	open atoll	West Tuamotus	33.70	Dry	1.20	6.49	166.92	542.72	0.41	Very Healthy
Tikehau 1	5	open atoll	West Tuamotus	28.00	Wet	1.75	2.44	31.56	65.81	0.39	Degraded
Tikehau 2	5	open atoll	West Tuamotus	28.00	Wet	2.20	4.54	6.13	56.23	0.44	Degraded
Tubuai 1	5	high barrier	Austral Islands	49.27	Dry	1.20	0.53	22.32	160.44	0.30	Degraded
Tubuai 2	5	high barrier	Austral Islands	49.27	Dry	1.00	0.25	45.02	426.91	0.44	Healthy

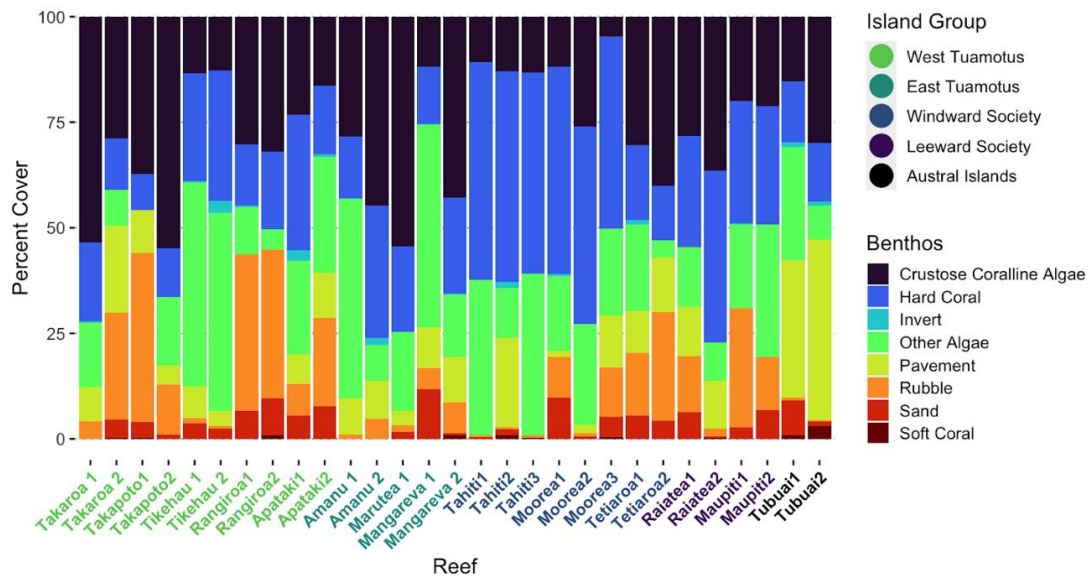


Figure 1: The mean percent cover of benthos seen on underwater visual surveys observed at surveyed islands in French Polynesia. Island groups are denoted by color of reef names on x-axis.

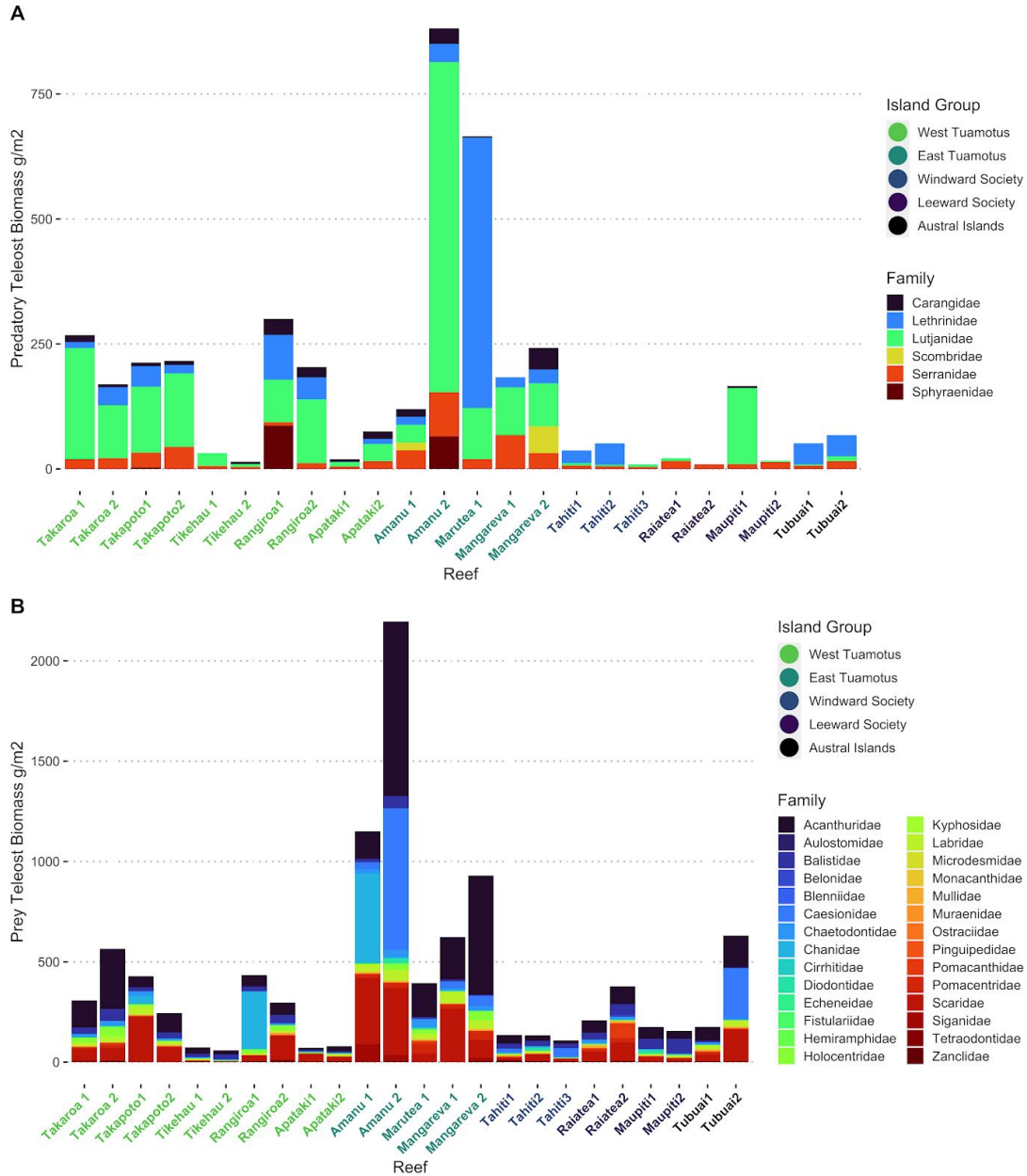


Figure 2: Average biomass of A) predatory and B) prey teleosts seen at each sampled reef. Family composition is indicated by bar colors and island groups are denoted by color of reef names on x-axis.

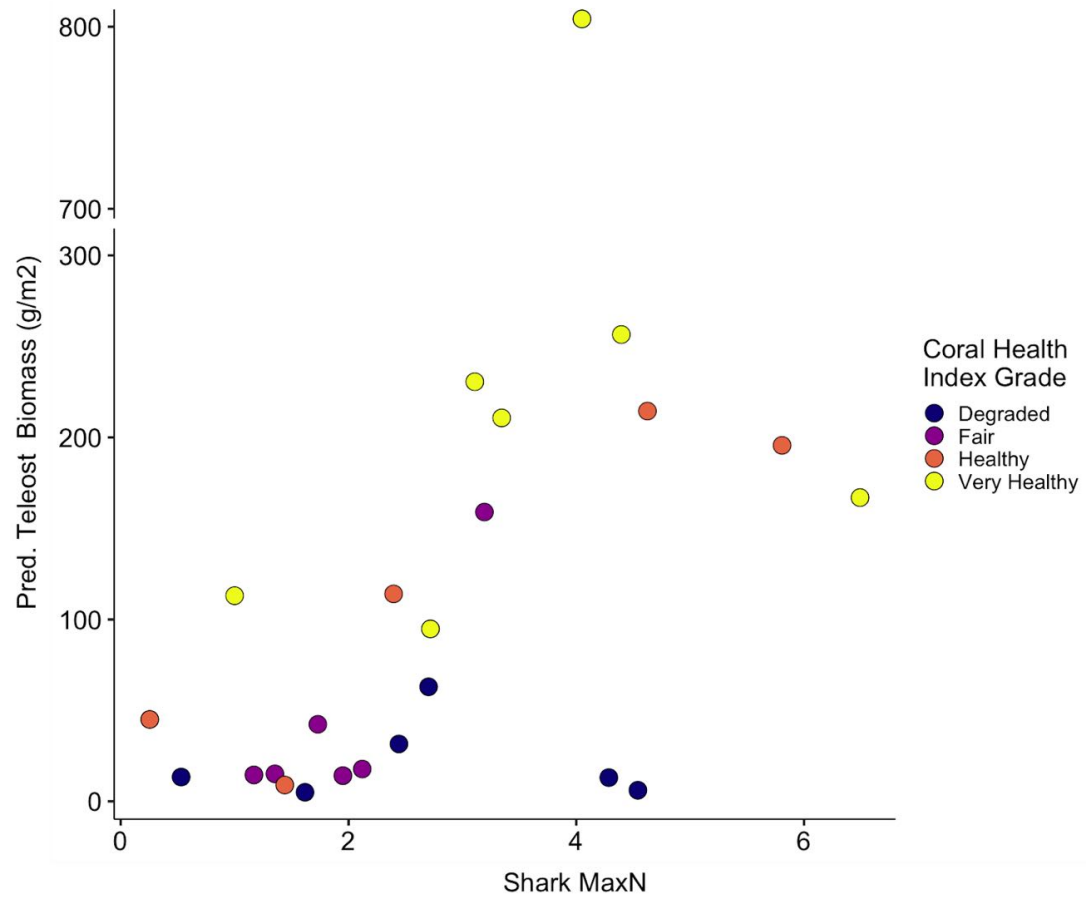


Figure 3: Average biomass of teleosts vs shark MaxN seen at each sampled reef. The color of each point indicates that reef's coral health index grade.

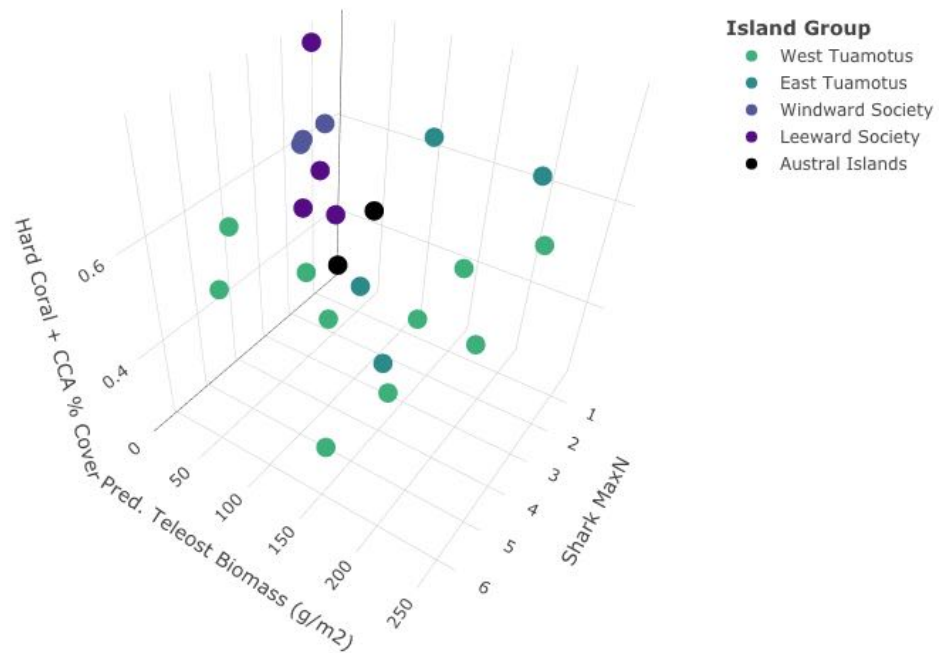


Figure 4: Three-dimensional scatter plot comparing shark MaxN, percent cover of hard corals and crustose coralline algae, and biomass (g/m²) of predatory teleosts averaged for each reef. Each point colored according to the island group where the reef is found. The reef Amanu 2 excluded for clarity see full plot in supplemental materials (Figure S1).

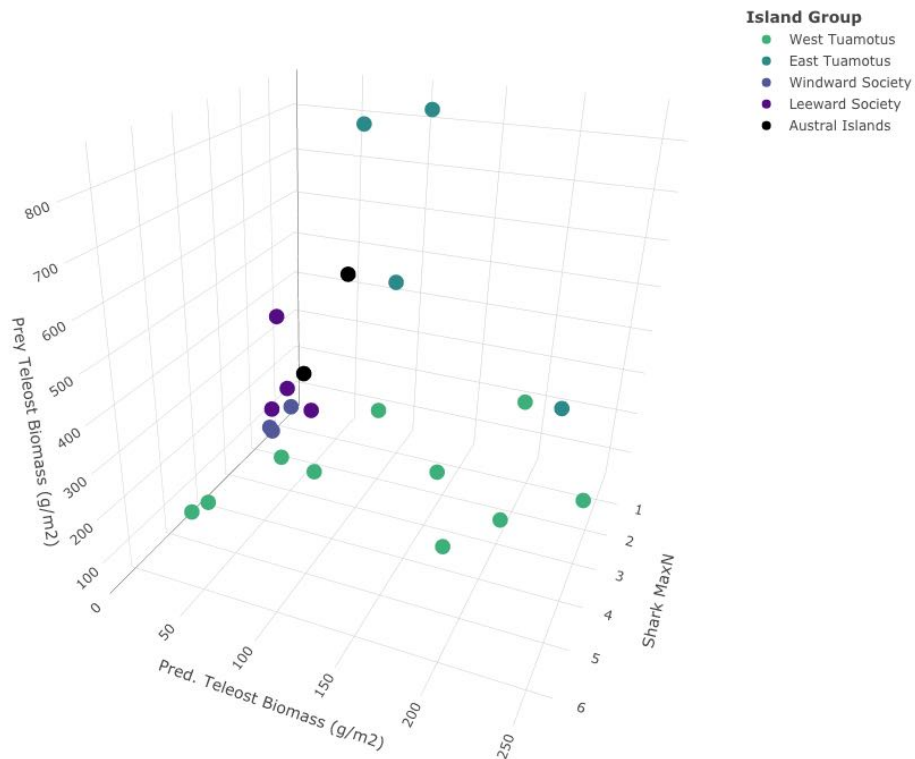


Figure 5: Three-dimensional scatter plot comparing shark MaxN, prey teleost biomass (g/m²), and biomass (g/m²) of predatory teleosts averaged for each reef. Each point colored according to the island group where the reef is found. The reef Amanu 2 excluded for clarity see full plot in supplemental materials (Figure S2).

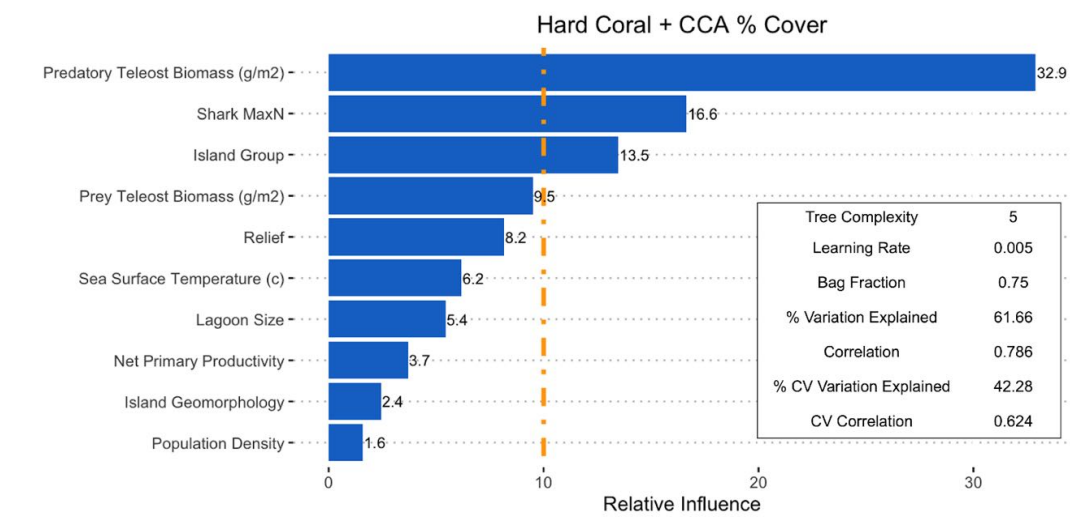


Figure 6: Relative influence of all predictor variables in boosted regression tree models of percent cover of hard corals and crustose coralline algae seen in benthic surveys. Variables with relative influence over that indicated by the orange line have influence above that expected by chance (100/number of variables). Box inside each plot show model parameters and performance statistics. CV= Cross Validated.

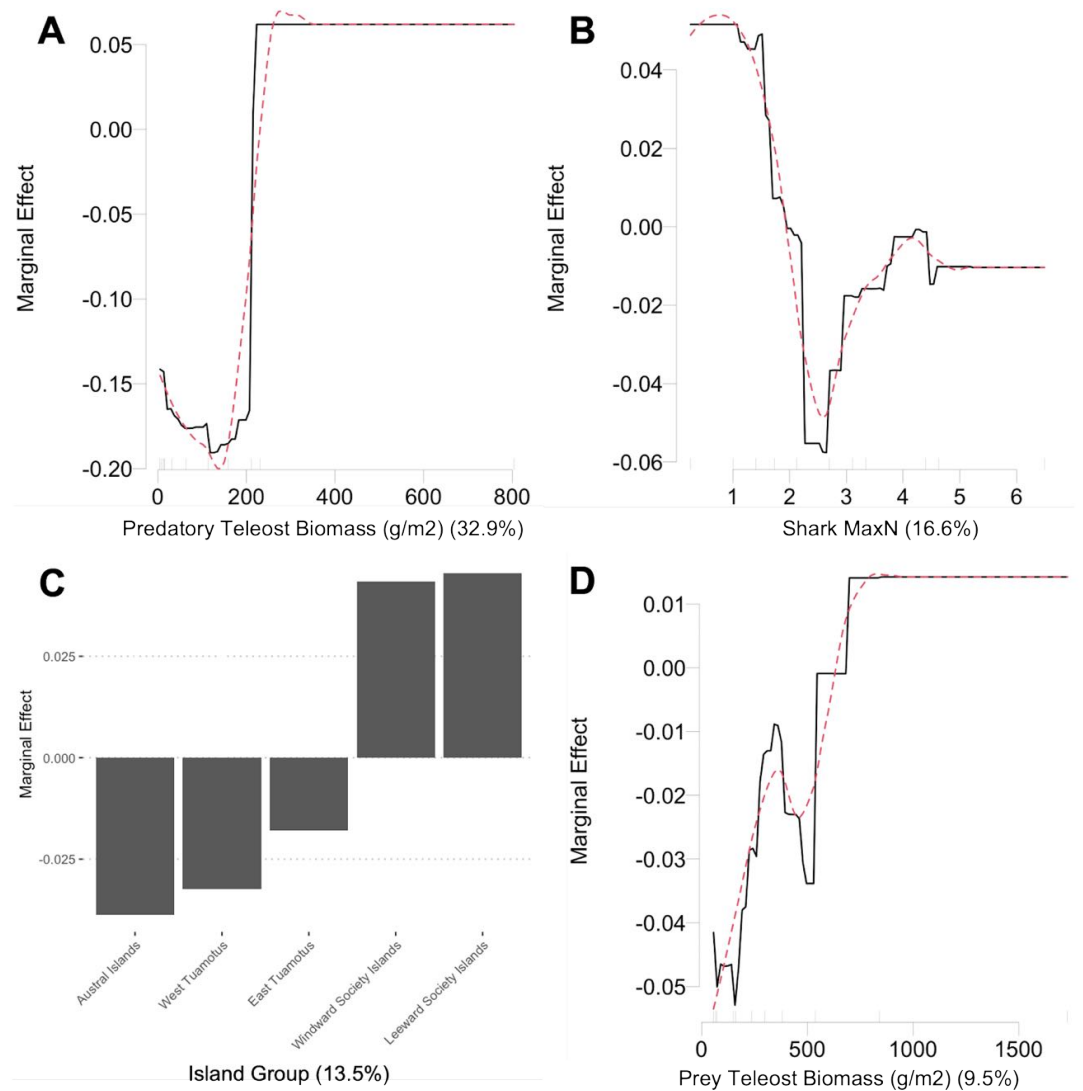


Figure 7: Partial dependence plots showing relationships of environmental variables to percent cover of Hard Corals and Crustose Coralline Algae. Relative influence of each variable is indicated as a percent. Red line is smoothed. X-axis rug ticks in panels A, B, & D indicate the decile distribution of the predictor variable data.

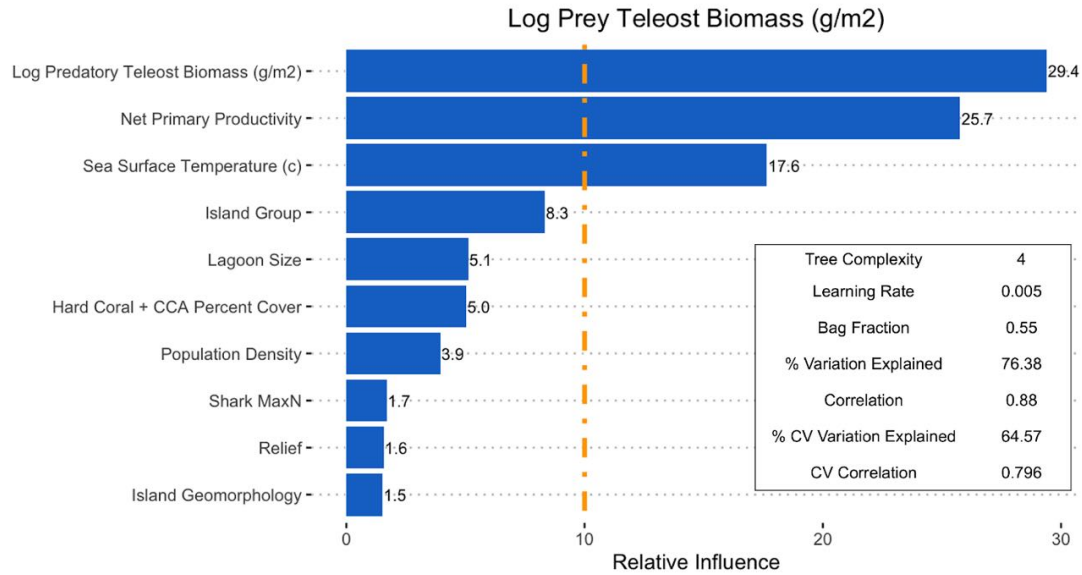


Figure 8: Relative influence of all predictor variables in boosted regression tree models of log of prey teleost biomass as seen in UVCs. Variables with relative influence over that indicated by the orange line have influence above that expected by chance (100/number of variables). Box inside each plot show model parameters and performance statistics. CV= Cross Validated.

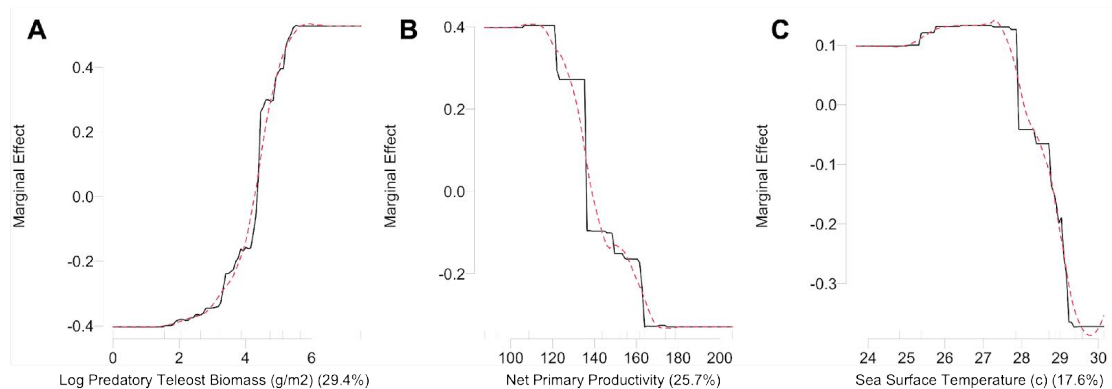


Figure 9: Partial dependence plots showing relationships of environmental variables to log of prey teleost biomass. Relative influence of each variable is indicated as a percent. Red line is smoothed. X-axis rug ticks indicate the decile distribution of the predictor variable data.

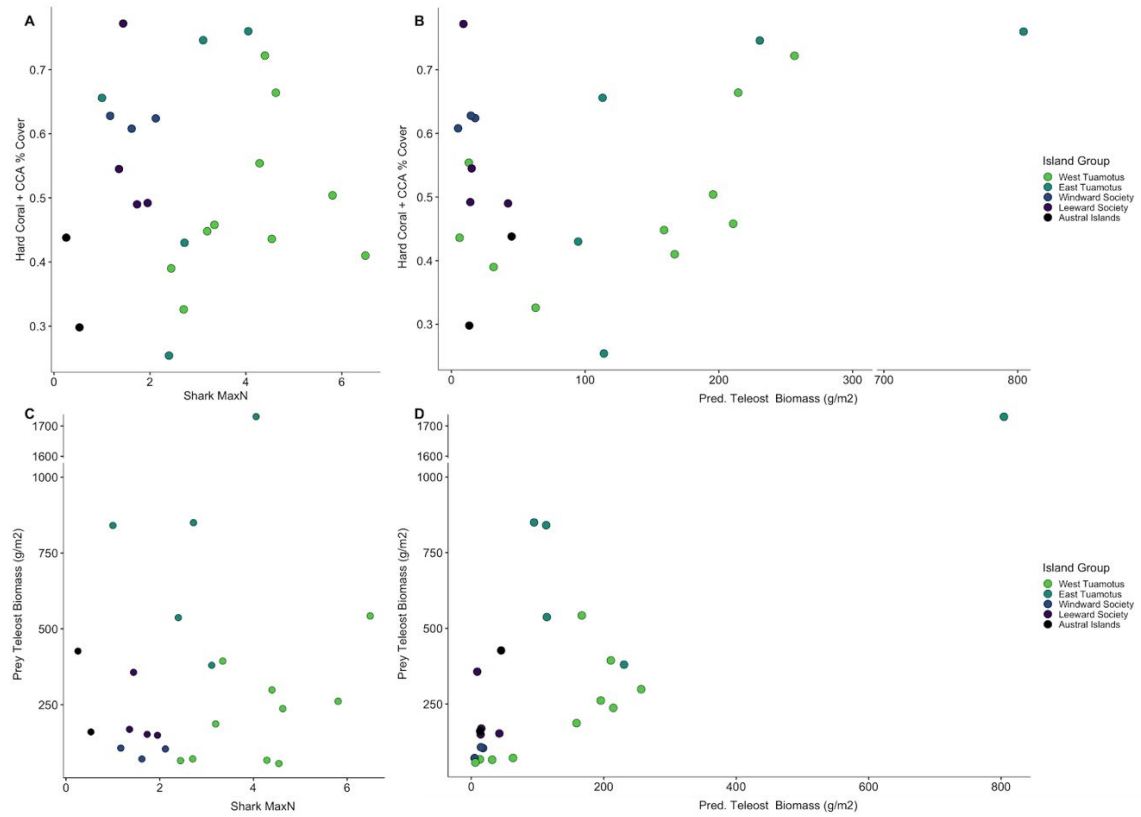


Figure 10: Scatter plots showing the relationship between percent cover of hard coral and crustose coralline algae and A) shark MaxN and B) predatory teleost biomass, as well as Prey teleost biomass and C) shark MaxN and D) predatory teleost biomass. Each point colored according to the island group where the reef is found.

SUPPLEMENTAL MATERIAL

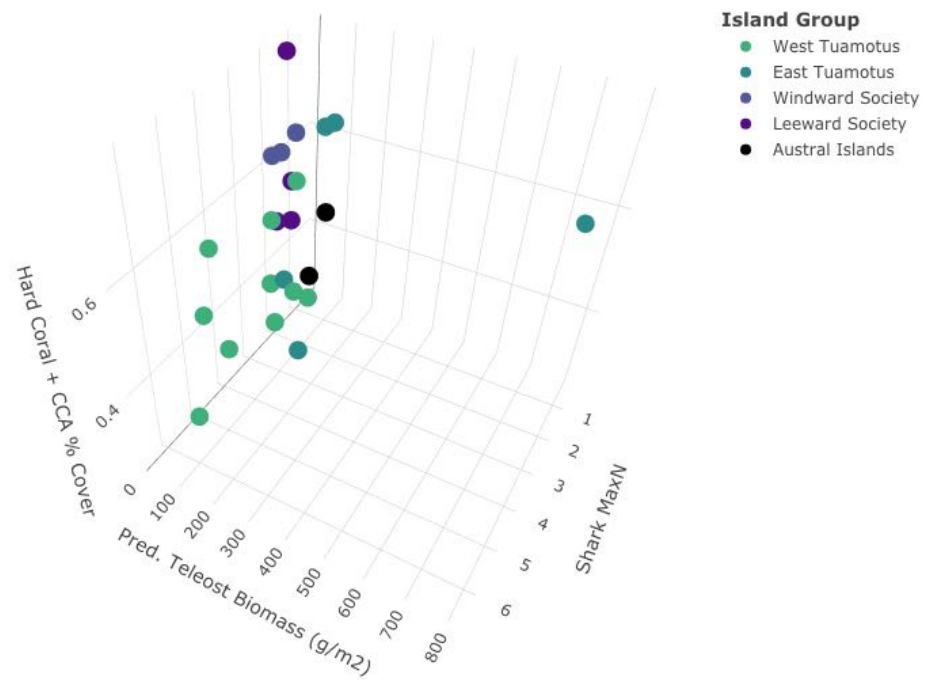


Figure S1: Three-dimensional scatter plot comparing shark MaxN, percent cover of hard corals and crustose coralline algae, and biomass (g/m²) of predatory teleosts averaged for each reef. Each point colored according to the island group where the reef is found.

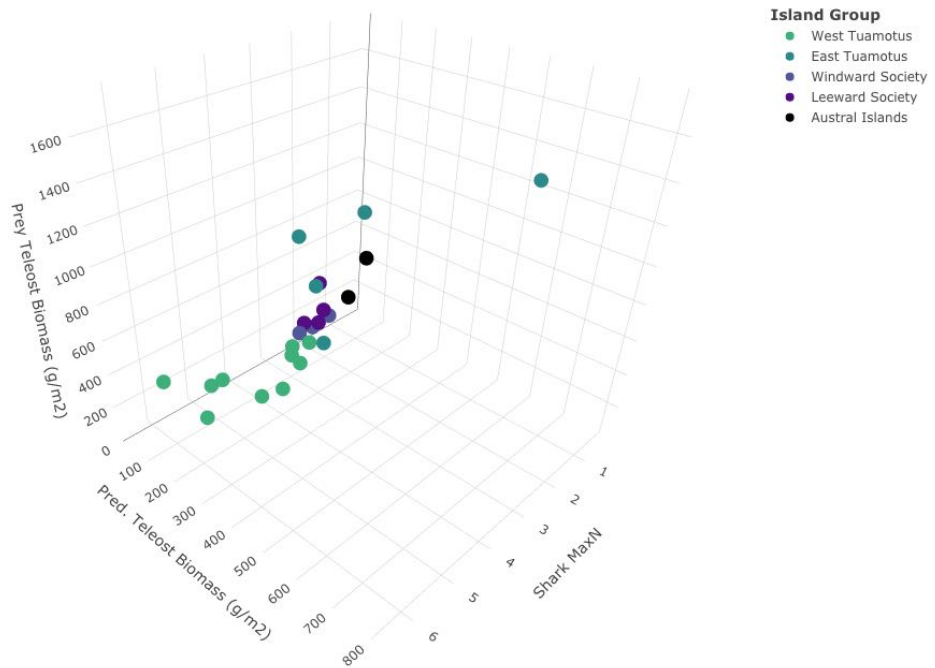


Figure S2: Three-dimensional scatter plot comparing shark MaxN, biomass g/m² of prey teleosts, and biomass (g/m²) of predatory teleosts averaged for each reef. Each point is colored according to the island group where the reef is found.

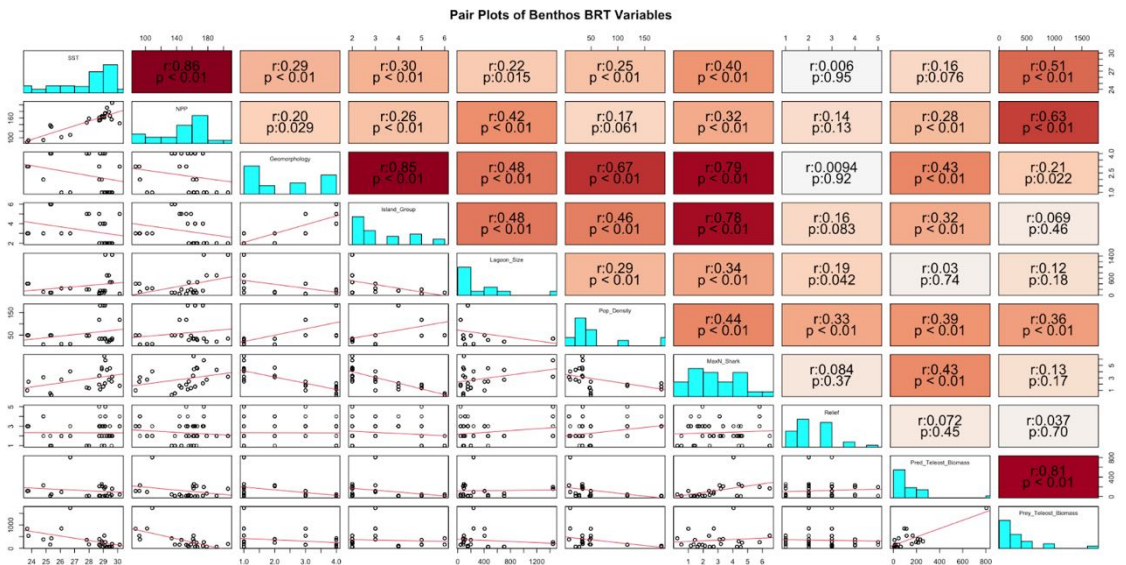


Figure S3: Pair plots for explanatory variables from BRT model of Hard Coral + CCA percent cover.

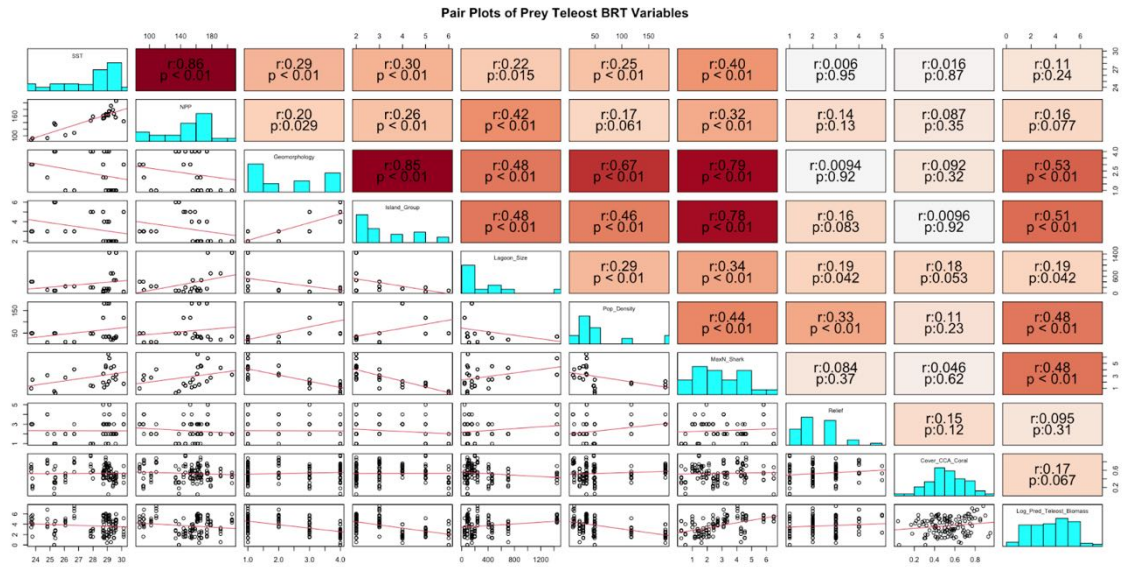


Figure S4: Pair plots for explanatory variables from BRT model of Log Prey Teleost Biomass.

CHAPTER VI

GENERAL CONCLUSIONS

Populations of sharks and other large marine predators have been undergoing dramatic global declines, driven primarily by overexploitation (Ferretti et al., 2010; Myers & Worm, 2003; Dulvy et al. 2021, Pacoureau et al., 2021). While we know sharks are potentially important marine predators, our knowledge of the ecological consequences of their declines is limited by our lack of understanding of the exact roles that sharks play in structuring ecosystems (Heupel et al. 2014, 2019; Desbiens et al. 2021; Chapman et al. 2022; Heithaus et al. 2008, 2022; Sandin et al. 2022). Furthermore, we do not have appropriate targets for restoring populations due to a lack of understanding of what ecological conditions influence the abundance of sharks in the absence of human impacts.

Here, I used French Polynesia as a model system to investigate drivers of the abundance and the potential ecological importance of sharks and large-bodied teleosts in coral reefs where human impacts on sharks are minimal. In Chapter 2, I found that French Polynesia supports reef shark relative abundances that are among the highest for Indo-Pacific nations sampled using similar methods (e.g., Goetze et al., 2018; MacNeil et al. 2020; Juhel et al., 2018). Within French Polynesia, human pressure, as measured by market gravity, was not a driver of shark relative abundance. Instead, relative abundance of sharks varied significantly with island geomorphology, with shark abundances being nearly three times lower on average at high islands than at atolls. While open atolls had abundances nearly 20% higher than closed atolls. Island group, temperature and net primary productivity had smaller effects. Although species-specific patterns varied slightly from those of all sharks combined, results suggest that environmental factors,

particularly island geomorphology, should be taken into account when setting shark abundance recovery targets. Because geomorphological characteristics of islands explained considerable variation in shark relative abundances, incorporating different targets for atolls and high islands could improve restoration efforts without expensive monitoring or measurements of habitat features.

In Chapter 3, I found that the relative abundance of predatory teleosts (Lutjanidae, Scombridae, Megalopidae, Carangidae, Sphyraenidae, Serranidae and Lethrinidae) was most influenced by net primary productivity, with more productive reefs having higher abundances. Island geomorphology, human population density, relative abundance of sharks, and sea surface temperature also influenced abundances. Interestingly, higher abundances of teleosts were found on reefs with higher abundances of sharks after accounting for other factors. For Lutjanids and Carangids, net primary productivity was the most significant effect, while island geomorphology was the most influential factor for Serranids. My results suggest that shifts in primary productivity likely would cause shifts in the abundances of reef-associated teleost predators. Furthermore, these taxa, especially snappers, appear to be highly sensitive to fishing pressures from even relatively low human population densities. I also found that teleost populations were greater in the presence of larger shark populations, suggesting that actions to protect and even restore shark populations may have positive impacts on fish communities, including taxa that are relied upon by people for food.

In Chapter 4, I found relatively high species richness of elasmobranchs on forereefs, but rays were rare in most locations. Though assemblages at most islands were dominated by blacktip reef sharks and gray reef sharks, there was significant variation in elasmobranch assemblages. This variation appears to be driven in part by habitat features, spatial dynamics and history because island geomorphology, latitude, and island group were the most influential factors in models of species richness. However, species assemblages and associations at smaller scales may be driven by species interactions, both positive and negative. Future studies on the effects of microscale habitat variation on shark assemblages may shed further light on the dynamics of elasmobranch assemblage composition on coral reefs.

In Chapter 5, I found that reefs with high abundances of both shark and teleost predators tended to be rated as “healthy” or “very healthy”, while reefs with low abundance of both shark and teleost predators were mostly rated as “degraded” or “fair” though a few were ranked as “healthy” or “very healthy”. This, along with BRT model results suggests that predator abundance has a strong relationship with coral reef health. These effects, however, were not linear, or similar for predatory teleosts and sharks. The presence of predatory teleosts appeared to be more important and to creating positive effects across a wide range of biomasses present on a reef while the effects of sharks on reef health occurred primarily at relatively low abundances. Taken together this suggests that these predator taxa are not fully redundant functionally although studies in areas with high large piscivorous teleost abundance and low shark abundance would help clarify the relative influences of the two groups.

Overall, this dissertation provides insights on how shark and predatory teleost relative abundance and assemblage composition varies in relation to environmental and anthropogenic gradients in a coral reef system with relatively light human pressures as well as providing an important step towards elucidating the relative importance of these predators in coral reef ecosystems. This information is critical as we seek to conserve and restore imperiled marine predator populations. Future work examining how abundance, species richness, and assemblage composition of these predators varies in response to the effects of microscale habitat variation could provide further insight into dynamics of predator assemblages on coral reefs in the world's largest shark sanctuary.

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