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Effects of habitat, fishing, and fisheries management on reef fish populations in Palau

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Abstract

Palau has a rich tradition of fisheries management and stewardship of its waters, and as in many island nations, small-scale coral reef fisheries are a vital part of the local culture, economy, and food security. However, reef fisheries in Palau are data-poor and there is increasing concern that reef fish stocks are declining. To evaluate the current and future status of these resources, information is needed on the abundance, biomass, and size structure of reef fish resource species. To this aim, the Palau International Coral Reef Center (PICRC) conducted a nation-wide study to investigate the status of commercially important reef fish stocks in 2017. Fishery-independent surveys were conducted by diver operated stereo-video (stereo-DOV) at 94 sites across the archipelago. Results showed that fish biomass varied from 0.13 to 293 g m^{-2}. Habitat was the most significant predictor of fish biomass, with the highest biomass found at western fore-reef sites and the lowest at inner reef sites. Region also affected fish biomass, with significantly higher biomass found in the Northern Reefs compared to those around Babeldaob (the largest island in Palau). In channel habitats, marine protected area (MPA) proximity, fishing pressure from Koror (Palau's main population center) and local fishing pressure significantly influenced fish biomass. In western fore-reef habitats, fish biomass was significantly affected by region, with differences observed between the Northern Reefs and Babeldaob, and between the Southern Reefs and Babeldaob. Fishing pressure from Koror had a significant effect on fish biomass in inner reef habitats, with a weak negative relationship observed. Using length frequencies from the stereo-DOV surveys we also estimated spawning potential ratio (SPR) for seven species and found the majority had SPR values between 20% and 40%. Overall, the low fish biomass and SPRs suggests that many of Palau's principal fisheries species have been overexploited. This is the first study to evaluate the status of resource reef fish stocks across the main islands of Palau and provides a baseline to assess changes in fish populations over time.

Keywords: coral reef fisheries, data-limited stock assessment, seafood security, Palau, overfishing

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Highlights:

- Reef fish biomass was low (<25 g m^{-2}) at 83% of sites across Palau
- Highest biomass was found in the fore-reef west habitat and Northern Reefs region
- SPR was 20 - 40% for the majority of assessed species

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1. Introduction

Palau has a rich tradition of stewardship of its waters and small-scale coral reef fisheries are a vital part of the local culture, economy, and food security (Johannes, 1981, 1998; Richmond et al., 2007). Seafood is the main source of protein for the local population, with the majority of landed reef fish consumed locally by residents (FAO, 2015; Dacks et al., 2020). Subsistence fishing is still a major activity in Palau. However over time fishing also became important for the local economy, and currently around half of landed reef fish are sold commercially to residents, tourists or exported (Prince et al., 2015; Dacks et al., 2020). Since the 1970s, there have been increasing concerns among fishers that reef fish stocks have declined due to overfishing and unsustainable practices and more recent studies have shown that Palau's fisheries are fully exploited (Johannes, 1981, 1991; Newton et al., 2007). In order to combat this, Palau has implemented measures to help protect its marine resources through the Marine Protection Act 1994 (amended in 2015, Marine Protection Amendment 2015). The Act includes regulations on minimum mesh sizes for nets, a ban on fishing using any kind of underwater breathing apparatus and a permanent fishing ban for *Bolbometopon muricatum* and *Cheilinus undulatus*. There are also seasonal fishing bans for five species of grouper (Serranidae), including a minimum size limit during the open season, and two species of rabbitfish (Siganidae). In 2020 a bill was passed, banning the export of any living resource in the reef, territorial sea and internal waters of Palau (Senate Bill No. 10-63, HD3, CD1). In addition, Palau has developed an extensive network of small marine protected areas (MPAs) as part of the 2003 Protected Areas Network (PAN) Act and the 2006 Micronesia Challenge (Friedlander et al., 2017; Birkeland, 2017). The MPAs range in size from 0.03 km^2 to 56.6 km^2, with an average size of 6.26 km^2. Each MPA has its own fisheries management regulations, but most are no-take, no-entry zones, with some allowing harvest during specific times or occasions. Almost 50% of PAN sites have a "poor" enforcement rating, with illegal extraction in no-take sites continuing in most states, although over time enforcement has improved (PAN, 2015). Despite the "poor" enforcement rating, no-take MPAs in Palau have, on average, nearly twice the biomass of resource fishes (i.e., those important commercially, culturally, or for subsistence) compared to nearby unprotected areas (Friedlander et al., 2017). In the Northern Reefs of Palau, the states of Ngarchelong and Kayangel passed their own statewide fisheries regulations in 2015. These regulations included temporary moratoria on the harvest of six fish species from the family Serranidae from 2015 to 2018 and on *Caranx ignobilis* from 2016 and 2017 for 3 years. Minimum size limits, which aimed to preserve at least 20% spawning potential ratio (SPR) were also implemented for 14 species from the families Serranidae, Lutjanidae, Lethrinidae, Acanthuridae, and Scaridae from 2016 and 2017 (Kayangel Public Law 15-16, Ngarchelong Public Law 15-57). Furthermore, the Northern Reef Fisheries Cooperative was set up in 2015 to recover fish stocks and promote sustainable fisheries (The Nature Conservancy, 2016a). Although these measures are important actions taken to preserve the nation's marine resources, there is little information on the status of these fisheries across Palau and this lack of information impedes the evaluation of the efficacy of these management actions.

In addition to the benefits they provide to humans, reef fishes also have important functional roles within coral reef ecosystems and overfishing can lead to a degradation of these key ecosystem functions (Bellwood et al., 2004; Pratchett et al., 2014). Herbivorous fishes increase reef resilience and reduce vulnerability to macroalgae phase-shifts by removing algae and sediment through grazing and exposing areas of the reef through bioerosion (Edwards et al., 2014; Bonaldo et al., 2014). This in turn encourages settlement, growth, and survival of coralline algae and coral (Bellwood et al., 2004). Increased fishing pressure can lead to a reduction in these ecosystem functions, with rates of bioerosion and coral predation particularly affected by human activity (Bellwood et al., 2012). Finally, predatory fishes are important for maintaining prey populations and exploitation of predators can lead to an increase in prey abundance, which can have negative ecological effects at the base of the food web (Dulvy et al., 2004).

To ensure sustainable fisheries and maintain healthy coral reefs for future generations, it is vital that effective fisheries management practices are implemented in Palau. This requires accurate assessment of coral reef fish stocks to evaluate the performance of past and present management efforts. To date, several fishery-dependent surveys have been conducted in discrete regions of Palau such as Koror (Palau's main population center) and the Northern Reefs (e.g., Kitalong and Dalzell, 1994; Moore et al., 2014; Prince et al., 2015; Lindfield, 2017; Linfield, 2016[1]; Prince, 2016a[2]; Prince, 2016b[3]). However, there has been limited research on fish populations in Palau using fishery-independent surveys at the archipelago scale (Dochez et al., 2019). It is therefore necessary for data to be collected on fish populations across the archipelago and evaluate the status of the fish stocks that comprise these fisheries.

Reef fishes are typically monitored by estimating the biomass of important species on a reef and tracking the changes in their biomass over time (MacNeil et al., 2015). However, formal fisheries stock assessments that specify the status of a given species in reference to an estimate of sustainable yield, have historically been beyond the capacity of Palau and similar small island nations to conduct (Johannes, 1998; Prince et al., 2015). Fortunately, novel data-limited methods are emerging that permit the assessment of data deficient fisheries and enable the status of a species to be quantitatively evaluated beyond monitoring changes in their biomass over time (Froese, 2004; Cope and Punt, 2009; Prince et al., 2011; Hordyk et al., 2015). One such method is the Spawning Potential Ratio (SPR) of a fish stock, which is defined as the proportion of the unfished reproductive potential left at any given level of fishing pressure in equilibrium and is a measure of the impact of fishing on the potential productivity of a stock (Goodyear, 1993). The length-based spawning potential ratio (LB-SPR) method uses length-composition data of a harvested fish population, instead of age data, together with life history parameters to estimate SPR (Hordyk et al., 2015). SPR can range from 100% in an unexploited stock, to 0% in a collapsed stock with no remaining spawning potential (Hordyk et al., 2015). An SPR of 40% is generally used as a proxy for maximum sustainable yield and an SPR of <20% indicates that recruitment rates are impaired and the stock is heavily exploited (Prince et al., 2015; Hordyk et al., 2015). In conjunction with biomass estimates from a diverse assemblage of species, estimates of SPR for keystone fisheries species can substantially improve our understanding of the status of data poor coral reef fisheries.

To this aim, the Palau International Coral Reef Center (PICRC) assessed commercially important reef fish populations across the main islands of Palau in 2017 (the Southwest Islands of Sonsorol and Hatohobei states were excluded from the survey due to their remoteness). Fishery-independent surveys using a diver operated stereo-video (stereo-DOV) system were conducted to 1) assess the current biomass and abundance of commercially important reef fish

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[1] Lindfield, S.J., 2016. Northern Reefs fishery-dependent data collection: Report on fish stocks – April 2016. Science and Monitoring for the Northern Reef Fisheries Management Project. Project Report, Palau International Coral Reef Center.

[2] Prince J., 2016a. Length based SPR assessment of eighteen Indo-Pacific coral reef fish populations in Palau. Unpublished report for The Nature Conservancy.

[3] Prince J., 2016b. Estimation of SPR based minimum lengths for Indo-Pacific coral reef fish in Palau. Unpublished report for The Nature Conservancy.

across Palau; 2) determine which assessed anthropogenic and biophysical factors are influencing the biomass of reef fishes in Palau; and 3) estimate the SPR of species with sufficient length data and available life history parameters. This study provides the first fishery-independent assessment of the status of commercially important reef fish stocks across the main islands of Palau and a baseline to assess changes in these resources over time.

2. Methods

2.1. Survey sites

In 2017, a total of 94 sites were surveyed across the Palau Archipelago within six reef habitats, including three back-reef sites, 19 channel sites, 20 fore-reef east sites, 22 fore-reef west sites, 16 fringing inner reef, and 14 patch reef sites (Fig. 1). Mapping of shallow-water benthic habitats for Palau was conducted in 2007 by the National Oceanic and Atmospheric Administration (NOAA) using high-resolution, multispectral satellite imagery and the total area of each habitat type was calculated based on these habitat maps (Battista et al., 2007). The number of sites was determined based on the total area of each habitat within the study area and previous sampling efforts for *B. muricatum* and *C. undulatus* in Palau (Friedlander and Koike, 2013; Polloi et al., 2014). Sites were then randomly selected using the open source Geographic Information System (GIS) software QGIS and any selected sites that were < 1 km apart or located inside an MPA were reallocated to another location. MPAs were excluded from this survey since the aim of this project was to assess the status of commercially important fish stocks in locations open to fishing.

2.2. Fish survey methodology

Fishery-independent surveys were conducted using a diver operated stereo-video system (stereo-DOV, Goetze et al., 2019), consisting of two GoPro Hero 4 cameras in waterproof housings mounted on a rigid base bar. The survey method involved two SCUBA divers swimming along the reef at two different depths where possible at each site: 15-20 m (deep) (n=90) and 5-10 m (shallow) (n=83). The lead diver operated the stereo-DOV system, pointing the cameras straight ahead along the reef for a 15-minute timed swim at each depth and maintaining a steady swimming speed of approximately 20 m/min if there was no current. For sites that did not have different depth strata, only one depth was used. The dive buddy followed closely behind the lead diver towing a floating Global Positioning System (GPS), which was used to calculate the transect length using Garmin BaseCamp software (https://www.garmin.com/en-US/software/basecamp/).

2.3 Data processing

Stereo videos were analyzed using the SeaGIS EventMeasure software (Version 4.42), with the length/3D rules set to: maximum range = 8,000 mm, maximum RMS = 20 mm, maximum precision to length ratio = 10%, minimum x coordinate = -2,500 mm and maximum x coordinate = 2,500 mm (Goetze et al., 2019). This ensured that only fish within a 5 m belt and up to 8 m distance away were included in the survey. The left and right videos were imported into EventMeasure and synchronized based on diver hand signals at the beginning of each transect. Fork length (FL) measurements were made for selected fish species, from 15 families, that are important for commercial, cultural or subsistence fishing in Palau (Supplementary Online Material - SOM 1), similar to the list of fish species used by Friedlander et al. (2017). When fish could not be identified to the species level, they were grouped into family or genus (e.g., Scaridae spp.). When the precision to length ratio exceeded 10% in EventMeasure, a 3D point was added for the fish and an estimated length was later calculated based on the mean length of all fish measured for that species. Estimated lengths were only used to calculate overall biomass at each survey site, they were not included in length analysis of individual taxa. Fish biomass was calculated using the length-based equation:

$$W = aFL^b$$

where W is the weight of the fish in grams, FL is the fork length of the fish in cm, and a and b are constant values derived from published biomass-length relationships (Kulbicki et al., 2005; Kamikawa et al., 2015; Gumanao et al., 2016; Cuetos-Bueno and Hernandez-Ortiz, 2017) and FishBase (Froese and Pauly, 2019). Weight was then divided by the area of the transect (transect length*5 m) in order to calculate biomass in g m^{-2}. Fishes were categorized into three trophic groups (piscivores, secondary consumers, and herbivores) based on Friedlander et al. (2017) and information from FishBase (Froese and Pauly, 2019).

2.4. Predictor variables

Site-specific predictor variables of fish biomass were compiled for input into mixed effects models (Table 1). These anthropogenic and biophysical variables were chosen based on previous studies assessing fishing pressure/impact on fish assemblages (e.g., Harborne et al., 2018; McLean et al., 2016) and data available in this study. Depth was recorded at each site during fish surveys and then classified as shallow (5-10 m) or deep (15-20 m). Habitat type was determined *a priori* based on NOAA’s benthic habitat map of Palau. The six reef habitats were then grouped into four main habitat types (channel, fore-reef east, fore-reef west, and inner reef [fringing inner, patch and back-reefs]) for analyses due to the small number of back-reef sites. Sites were also grouped into three main Regions (Northern Reefs, Babeldaob, and Southern Reefs, Fig. 1). Sites located in the extreme north (Kayangel and Ngarchelong states) were grouped into the Northern Reefs region. Sites located around Babeldaob, the largest island in Palau comprising 80% of the total land mass, were grouped into the Babeldaob region, and sites located in Koror, Peleliu, and Angaur states were grouped into the Southern Reefs region. This was done based on the presence of different management practices in the Northern Reefs and the different hydrogeological make up of Babeldaob (consisting of volcanic rock covered by soil with the presence of watersheds) and the Southern Reefs (consisting of carbonate rock islands).

A proxy for proximity to MPAs was calculated based on distance by water to the nearest MPA multiplied by MPA size, since both factors have been shown to affect fish biomass (e.g., Forcada et al., 2009; Friedlander et al., 2017). A proxy for fishing pressure from Koror was based on distance a boat has to travel to the main port. The total population of Palau is 17,661 and 65% of the population resides in Koror, making this the main source of fishing pressure. A proxy for local fishing pressure was calculated based on distance a boat has to travel from the nearest dock multiplied by the population of the nearest state. Population data were obtained from the 2015 Census of Population, Housing and Agriculture for the Republic of Palau (Office of Planning and Statistics, 2015). Distance to the nearest pass/channel was determined by measuring the linear distance to the mouth of the nearest channel or access point to the open ocean. A proxy for watershed pollution from Babeldaob, the only island with perennially flowing fresh water in Palau, was calculated by multiplying the percentage of altered land (urban, agricultural, and barren) within the adjacent watershed by the linear distance to the nearest river discharge (Houk et al., 2015). Vegetation data for Palau (2005-2006) was obtained from the United States Department of Agriculture (USDA) Forest Service (https://www.fs.usda.gov/detailfull/r5/forest-grasslandhealth/?cid=fsbdev3_046690&width=full)

and the coverage of each altered land type were calculated and then summed for each watershed in Babeldaob using QGIS. A proxy for accessibility (wave energy) was calculated for each site using 10-year wind speed records, fetch distance, and angle of exposure (QuikSCAT wind datasets from 1999 to 2009; https://winds.jpl.nasa.gov) (Houk et al., 2014).

Linear distances were measured using the distance matrix tool, whereas distance by water and boat were measured using the measure line tool in QGIS. For MPA proximity, fishing pressure from Koror, local fishing pressure, and watershed pollution, distances were inversely scaled so that increasing distances yielded higher MPA proximity, higher fishing pressure, and higher effect of watershed pollution, respectively. See SOM 2 for parameter values used for analysis for each survey site.

2.5. Statistical analysis

All statistical analyses were conducted using R version 4.0.3. Linear mixed effects models (LMM) were used to test the effect of predictor variables on fish biomass and to compare biomass between trophic groups using the 'lmer' function in the 'lme4' package. The four habitat types (channel, fore-reef east, fore-reef west, and inner reef [fringing inner, patch and back-reefs]) were also examined separately using LMM. Depth was added as a random effect to account for repeated measures at the same site. Stepwise model selection was carried out using the 'drop1()' function to find the most simplified model, where the least significant parameters were removed from the model until all variables were significant. Where significant effects were found, pairwise comparisons were conducted using the 'lsmeans' function. Prior to statistical analysis, continuous variables were normalized and tested for collinearity using the 'cor()' function with the "pearson" method; none of the variables were found to be correlated. In addition, biomass data were examined for normality using histograms and the Shapiro-Wilk test, and subsequently ln+1 transformed. Homogeneity of variances of discrete variables was tested using Levene's test; with no significant variance found between groups. Following analyses, residuals were plotted and checked for normality using the Shapiro-Wilk test. Biomass interpolation maps were created using the Inverse Distance Weighting method in QGIS. Data are presented as mean values ± 1 standard deviation.

2.6. Size structure and spawning potential ratio

The size structure of 12 species with sufficient actual length measurements ($n>100$ each) were examined. SPR was estimated for seven of these species that had locally available life history parameters using the LB-SPR method (Hordyk et al., 2015; Prince et al., 2015). LB-SPR uses maximum likelihood methods to estimate the ratio of fishing mortality to natural mortality (F/M) and selectivity-at-length parameters (SL_{50} and SL_{95}; i.e., the lengths at 50% and 95% selectivity by fishing), which in turn are used to calculate the SPR (Hordyk et al., 2015). Inputs to LB-SPR include L_{50} (length at which 50% of population reaches sexual maturity), L_{95} (length at which 95% of population reaches sexual maturity), L_{∞} (asymptotic length), M/K (natural mortality/rate at which L_{∞} is approached) and observed fish length data (Table 2). Life history ratios of M/K and L_m/ L_{∞} were derived at the family level from a meta-analysis of all available age, growth and maturity studies after going through a process of quality control to account for studies where the data has been constrained by heavy fishing pressure (J. Prince 2021, pers. comm., 7 April). The LB-SPR R Shiny application on The Barefoot Ecologist's Toolbox website (http://barefootecologist.com.au/) was used for SPR estimations.

3. Results

3.1. Fish biomass

3.1.1 Overall biomass

Biomass and abundance were recorded for 106 species (SOM 3). A total of 11,773 fishes were observed during the surveys, with actual length measurements for 5,518 individuals and estimated length measurements for the remaining 6,255. Total fish biomass varied by an order of magnitude across sites from 0.13 to 293 g m^{-2}, with a mean biomass of 17.83 ± 32.09 g m^{-2}. Hot spots of high biomass were observed at some Northern Reefs sites, including to the east of Ngarchelong and at Kayangel, and sites along the fore-reef west of Koror (Fig. 2A). Low biomass was observed at inner reef sites in the southern lagoon and around Babeldaob.

Mean biomass was significantly different between trophic groups (LMM: $p<0.001$), with significantly lower herbivore biomass (5.39 ± 10.11 g m^{-2}) than piscivore biomass (6.96 ± 27.63 g m^{-2}) ($p<0.001$). There was no significant difference in biomass between piscivores and secondary consumers (5.47 ± 11.48 g m^{-2}). The highest herbivore biomass was seen at a fore-reef site to the west of Koror (113.88 g m^{-2}). The lowest herbivore biomass was observed at sites to the east of Babeldaob, in the Northern Reefs and the Southern Reefs (Fig. 2B). The highest biomass of secondary consumers was observed at a fore-reef site to the west of Koror (79.42 g m^{-2}) and at several sites in the Northern Reefs. There was an overall low biomass of secondary consumers across the rest of Palau (Fig. 2C). The highest biomass of piscivores was seen in the Northern Reefs, including one site to the east of Ngarchelong (285.69 g m^{-2}) and to the northeast in Kayangel (156.35 g m^{-2}). High piscivore biomass was also seen at a fore-reef site in the southwest of the archipelago (122.95 g m^{-2}) and at other sites in the Northern Reefs. Low biomass of piscivores was seen within the lagoon around Babeldaob and in the western Northern Reefs (Fig. 2D).

Lutjanus gibbus, *Caranx sexfasciatus*, and *Sphyraena qenie* accounted for the highest percentages of total fish biomass observed during the surveys (16.12%, 11.75%, and 9.47%, respectively) (Fig. 3). *L. gibbus* was also the most abundant species observed (2,712), followed by *Naso lituratus* (1,314). *Chlorurus spilurus* had the highest frequency of occurrence, occurring in 68% of transects surveyed, followed by *L. gibbus* (59%) (SOM 3).

3.1.2 Drivers of fish biomass

Habitat and region were the only significant predictors of fish biomass (LMM: $p<0.001$ and $p=0.008$, respectively) (Table 3). The highest biomass was found in fore-reef west sites (30.38 ± 26.04 g m^{-2}) and the lowest was found in patch reef habitats (4.76 ± 2.59 g m^{-2}) and fringing inner reefs (6.03 ± 3.44 g m^{-2}). Significant differences were found between fore-reef west and channel ($p=0.001$), fore-reef west and fore-reef east ($p=0.044$), fore-reef west and inner reef ($p<0.001$), and fore-reef east and inner reef ($p=0.017$) (Fig. 4a; SOM 4). For region, a significant difference was found between the Northern Reefs (25.69 ± 33.19 g m^{-2}) and Babeldaob (7.37 ± 5.00 g m^{-2}) ($p=0.006$) (Fig. 4b; SOM 4).

In the channel habitat, region, MPA proximity, fishing pressure from Koror, local fishing pressure and wave energy significantly affected fish biomass (LMM: $p=0.041$, $p<0.001$, $p=0.013$, $p=0.007$ and $p=0.013$ respectively) (Table 3). However, when pairwise comparisons were conducted, there were no significant differences among the three regions (SOM 4). A positive relationship was observed for MPA proximity ($R^2=0.331$), whereas weak negative relationships were observed for fishing pressure from Koror ($R^2=0.048$), local fishing pressure ($R^2=0.041$) and wave energy ($R^2=0.037$) in the channel habitat (Fig. 5). In the fore-reef east habitat, fish biomass was significantly affected by region and MPA proximity (LMM: $p=0.016$

and p=0.002, respectively) (Table 3). However, when pairwise comparisons were conducted, there were no significant differences among the three regions and there was a weak negative relationship observed for MPA proximity (R^2=0.088) (Fig. 5; SOM 4). In the fore-reef west habitat, fish biomass was significantly affected by region (LMM: p=0.008) (Table 3). Significantly higher fish biomass was seen in the Northern Reefs compared to Babeldaob (p=0.016) and in the Southern Reefs compared to Babeldaob (p=0.010)(Fig. 5; SOM 4). In the inner reef habitat, fish biomass was significantly affected by MPA proximity (LMM: p=0.048) (Table 3), however the R^2 value (0.017) was very low (Fig. 5; SOM 4). Fishing pressure from Koror was also significant in the inner reef (LMM: p=0.010), with a negative relationship observed (R^2=0.056).

3.2. Size structure and spawning potential ratio

Size structure was examined for 12 species (SOM 5) and from the seven species where size at maturity values were available in Palau, the percentage of fish below L_{50} ranged from 27% for *Hipposcarus longiceps* to 70% for *Scarus rubroviolaceus* (Table 4). From these seven species with available life history parameters to calculate LB-SPR, the majority had SPR values between 20% and 40% (Table 5). *H. longiceps* had the highest SPR (53%), but as the length frequency distribution was bi-modal, this resulted in a poor fit of the model. This was due to a dominance of juvenile fish (< 200 mm) recorded on the fringing inner-reefs, patch reef and back reefs, and predominately sub-adult and adult fish recorded on the fore-reefs and channel habitats. If the model was run only including fish on the fore-reefs and channel habitats (*n* = 66), SPR was estimated at 34% and SL_{50} was 310 mm. The lowest SPR estimate was observed for *Siganus puellus* (16%).

4. Discussion

4.1. Fish biomass

4.1.1 Overall biomass

Biomass is an in situ measurement of the amount of living organisms on coral reefs and in this case, provides an indication of the availability of commercially important resource species across Palau. The results of this study indicate that fish biomass varied considerably across the survey sites, with the highest biomass observed in the Northern Reefs, driven primarily by large schools of piscivores (*S. qenie* and *C. sexfasciatus*) and secondary consumers (*L. gibbus*). The fore-reefs west of Koror also had a high fish biomass, driven by large schools of piscivores (*C. sexfasciatus*), secondary consumers (*L. gibbus*), and herbivores (*N. lituratus*). Harborne et al. (2018) calculated a potential standing stock of 107 g m^{-2} for the biomass of all reef fishes in Palau. Similarly, MacNeil et al. (2015) estimated resident reef fish biomass in the absence of fishing should equal ~100 g m^{-2}, with biomass <25 g m^{-2} potentially leading to negative ecosystem effects due to overexploitation. In this study only 16 out of 94 sites had biomass >25 g m^{-2} (averaged across depth), suggesting that 83% of sites may be overexploited. The fish biomass estimates calculated by Harborne et al. (2018) and MacNeil et al. (2015) include all non-cryptic reef fishes, whereas the current study was limited to a subset of commercially important reef fishes in Palau (SOM 1). In addition, all the study sites in MacNeil et al. (2015) and Harborne et al. (2018) were located in the fore-reef habitat, which typically supports higher biomass of reef fishes (Harborne et al., 2018). This study included data from different reef habitats, which may have led to lower overall biomass estimates. However, most fore-reef sites in our study had a total fish biomass much lower than 25 g m^{-2} (SOM 2).

MPAs provide a baseline to measure the difference in biomass of similar habitats that have been exploited by fisheries. In 2014, Friedlander et al. (2017) surveyed seven MPAs across Palau and found that total resource fish biomass ranged from ~80 g m^{-2} (patch reef habitat) to ~360 g m^{-2} (channel habitat). In contrast, three sites in this study had a total fish biomass >80 g m^{-2} and the majority of sites had much lower values. All sites surveyed in this study are open to fishing and it was therefore expected that biomass would be lower than MPA sites. However, the substantially lower biomass at the majority of sites suggests that reef fishes have been overexploited in Palau. It is noted that MacNeil et al. (2015), Harborne et al. (2018) and Friedlander et al. (2017) all used data collected using underwater visual census (UVC) surveys whereas the current study used stereo-DOV surveys to estimate fish biomass. It is possible that the stereo-DOV methodology used in this study could result in lower biomass estimates than UVC surveys due to differences in the swimming speed of the transect (Goetze et al., 2015). During slower moving and non-instantaneous UVC surveys, there is a greater likelihood of the larger mobile species moving into transect boundaries which can lead to overestimates of biomass (Ward-Paige et al., 2010). Furthermore, direct comparisons between UVC and stereo-DOV have been conducted by Holmes et al. (2013), which showed that although the total abundance of fish was similar between UVC and stereo-DOV, UVC recorded higher abundances of larger-bodied fisheries species compared to stereo-DOV due to visual observers having a greater ability than video cameras to recognize fish towards the edge visibility. UVC surveys have been shown to be less accurate at estimating fish lengths and sample area compared to stereo-DOV surveys (Harvey et al., 2001, 2004), however stereo-DOV has limitations on the number of actual measurements collected, with this study only able to measure ~50% of fish. Wilson et al. (2018) found that fish biomass estimates using UVC were ~50% greater than stereo-DOV, however once lengths were estimated for unmeasured fish (as we did in this study), biomass estimates between UVC and stereo-DOV were similar. Overall, fish biomass estimates from UVC and stereo-DOV should be broadly comparable when examined at higher taxonomic levels, and along with the added benefit of accurate length measurements, these results provides an important reference point from which large-scale changes in the amount of fish observed on Palau’s coral reefs can be evaluated.

4.1.2 Drivers of fish biomass

From the drivers investigated in this study, habitat was found to be the main driver of fish biomass across sites, with the highest biomass observed in western facing fore-reefs, and the lowest biomass observed in inner reefs (patch reefs and inner fringing reefs). Higher parrotfish abundance has been found in western and eastern fore-reefs compared to the inner reefs of Palau, which tend to have lower habitat complexity (Gouezo et al., 2019a). Furthermore, Roff et al. (2019) found substantial variability in herbivore biomass (5.6 ± 0.7 g m^{-2} to 66.4 ± 16.3 g m^{-2}) and predator biomass across sites in Palau, with 10-fold higher herbivore biomass and 17-fold higher predator biomass found in western facing reefs compared to eastern facing reefs. The west side of the archipelago likely has higher herbivore biomass due to its geomorphology and habitat heterogeneity, which may provide food subsidies and nursery habitats for herbivores (Roff et al., 2019); whereas higher predator biomass (Serranidae and Lutjanidae) may be due to the proximity of spawning aggregation sites (Colin, 2012). In addition, a recent study by Gouezo et al. (2021), showed that the western outer reefs of Palau have higher levels of particle retention and expected coral larval supply compared to the eastern outer reefs, which may also affect the supply and retention of fish larvae.

Region was also found to be a significant predictor of fish biomass, with significantly higher biomass observed in sites located in the Northern Reefs compared to sites around Babeldaob. The reefs around Babeldaob are easy to access and the inner reefs may be affected by watershed pollution, leading to lower overall biomass (Richmond et al., 2007). Conversely, the Northern Reefs are remote and located far away from Koror, with accessibility dependent on good weather conditions. However, fishing pressure from Koror and wave exposure, a proxy for accessibility, were not significant in our analyses. Other factors that could explain the high fish biomass in the Northern Reefs include naturally high productivity of the area and good management practices (The Nature Conservancy, 2016b). The Northern Reefs are often regarded as some of the best fishing grounds in Palau and in recent years this area has been managed differently to the rest of Palau, as detailed in the introduction (Lindfield, 2016[1]). These management strategies may have had a positive effect on fish biomass in this region; however, although fishers have shown a high degree of compliance with MPAs, there is evidence to suggest there is little compliance with other regulations such as species-specific laws (Carlisle and Gruby, 2018).

Fish biomass at channel sites was positively influenced by MPA proximity as fish biomass increased closer to large MPAs. MPAs can also act as a source of fish larvae to areas open to fishing, leading to increased recruitment and replenishment of fish populations (Harrison et al., 2012). Channel sites that had the highest fish biomass include those in Kayangel, located close to the large Ngeruangel Marine Reserve, protected since 1996, and in Ngarchelong near the large Ebiil Channel Marine Conservation Area, established in 1999. Similar to the high fish biomass found in Ebiil (Friedlander et al., 2017), previous monitoring has shown that the Ngeruangel MPA also has high biomass of resource fish (Gouezo et al., 2019b). Spillover of fishes and export of fish larvae could explain the higher fish biomass seen in channel habitats that are in close proximity to these MPAs. However, although MPAs also had a significant effect in the fore-reef east and inner reef habitats, only weak negative relationships were found. The reason that MPAs only had a significant positive effect in channels may be due to the close proximity of several survey sites to MPAs protecting channel habitats, which may have experienced a higher spillover of fish compared to other sites. For example, two sites are ~3 km from the center of Ebiil MPA, two sites are ~1 km from the center of Ngederrak MPA and one site is ~1 km from the center of Ngerumekaol MPA. Sand channels are corridors that provide transit pathways among hard bottom habitats and are important feeding and spawning locations for many vagile species (Friedlander et al., 2007). Channels near MPAs are important for energy transfer to and from these protected areas and can benefit fisheries through net emigration of adults and juveniles (“spillover”) (Rowley, 1994). The fact that these MPAs are protecting channel habitats increases the efficacy of the MPA, because these protected areas are high quality habitats that likely generate high spillover.

Fishing pressure from Koror and the nearest dock also had a weak effect on fish biomass in channels, with higher biomass seen at sites with lower fishing pressure. Fish biomass at inner reef sites were also weakly affected by proximity to Koror, with higher biomass seen at sites located further from Koror and biomass decreasing as distance to Koror decreased. This suggests that channel and inner reefs closer to Koror and channels closer to docks belonging to states with higher populations have greater fishing pressure. Channel sites with higher wave energy also had lower fish biomass, which is the opposite relationship expected, since sites with high wave energy should be more difficult to access. In the western facing fore-reefs, differences in fish biomass between the Southern Reefs and Babeldaob and the Northern Reefs and Babeldaob were primarily driven by large schools of fishes (e.g., *C. sexfasciatus*, *L. gibbus*, and *N. lituratus*) observed at the western facing fore-reefs in the south and north of Palau.

4.2 Size structure and spawning potential ratio

The high percentage of fish below L_{50} for some species such as *S. rubroviolaceus* (70%) and *Plectropomus leopardus* (65%), may indicate a lack of fish in larger size classes and therefore overfishing of adult fish. A low percentage of fishes below L_{50}, such as for *H. longiceps* (27%), may suggest there are low numbers of fish in smaller size classes and insufficient recruitment (Neumann and Allen, cited in Schultz et al., 2016).

SPR is a well-established biological reference point that can be used to inform management decisions in data-poor fisheries. However, due to limited the availability of life history parameters and sample sizes, the present study was only able to assess SPR for seven out of the 106 species observed. Reliable estimates of the biological parameters that describe the life history of a species are required to obtain accurate LB-SPR estimates, and these parameters can vary across region, they can be biased by sample size, and biased by sampling from stocks that have been subjected to intense fishing mortality. This prerequisite is a limitation in many coral reef fisheries that harvest diverse assemblages of fishes and although sampling programs in Palau have aimed to collect data to inform stock assessments (Prince et al., 2015; Prince, 2016a[2], 2016b[3]) life history estimates may continue to improve, this is especially true for *S. rubroviolaceus* and *S. puellus* where size at maturity estimates used in this study are considered preliminary. In addition to life history data, it is also important to have sufficient length measurements for each species since insufficient sample size can lead to an inaccurate assessment of size structure (Hordyk et al., 2015). This study made the assumption that fish originated from the same stock for all species assessed as in Prince et al. (2015), since dividing the data among regions or habitats would reduce sample sizes, and therefore, accuracy of the results.

For this study we used updated family-based life-history ratios (J. Prince 2021, pers. comm., 7 April) and updated size at maturity values for *H. longiceps* (Lindfield, Coral Reef Research Foundation, unpublished data) so these fishery-independent SPR assessments are not directly comparable to previous assessments in Palau (Prince et al., 2015; Prince, 2016a[2]). Overall, our results showed that SPR levels were typically greater than 20% indicating that there is enough spawning biomass for populations to replenish populations but remaining at levels typically less than SPR 40% which would equate to optimal sustainable yield in fisheries. Although it is clear that fishing pressure is impacting populations of reef fish in Palau, these levels of SPR are greater than the more dire estimates published by Prince et al. (2015) and Prince (2016a)[2] where SPR levels were less than 20% for the majority of species, indicative of heavy fishing pressure. Our results however should not be treated as a cause for optimism, as differences may be attributed to this study being the first to use fishery-independent data for LB-SPR assessments, not following the typical use of catch data for fishery assessments. The length-frequency data for *H. longiceps* provided insight into to the potential bias of data collection with surveys on the fringing inner reefs, patch reef and back reefs being dominated by small (< 200 mm) individuals, resulting in a bimodal size distribution from juvenile and adult populations (SOM 5). The corresponding selectivity-at-length (SL) values computed by the LB-SPR assessment were much smaller ($SL_{50\%}$ = 127 mm) compared to previous catch data ($SL_{50\%}$ = 276 mm) presented in Prince et al. (2015). As these LB-SPR models can only fit a single logistic selectivity curve and when there are high proportions of juvenile fish, this unrealistically assumes that the M/K which applies to adults also applies to equally juveniles, which would not be the case in nature. In an attempt to account for this, LB-SPR modelling on the subset of lengths from only fore-reef and channel habitats resulted in the fitting of a selectivity curve to the adult mode of the population and produced a lower and likely more realistic SPR level of 0.34. However, the reliability of this estimation is reduced due to a lower sample size of length measurements (*n* = 66) and further additional length measurements to refine the selectivity curve would be beneficial before making conclusions on this species.

Species with lower SPR values did not necessarily relate to low biomass values, and vice versa. For example, *L. gibbus* had a high mean biomass (4.92 g m^{-2} per site), due to their schooling behavior, and an SPR of 35%, whereas *H. longiceps* had a low mean biomass (0.69 g m^{-2} per site) and a greater SPR (or a similar SPR based on a presumably adult population). This could be reflective of ongoing density-dependent responses, where biomass is maintained despite reduced fish sizes, due to the removal of adult fish creating space for more juveniles (Houk et al., 2018). As *H. longiceps* is one of the most frequently landed species in Palau (Lindfield, 2017), the low density encountered during diving transects may also be reflective of the behavior of this species, being relatively shy of divers (Lindfield et al., 2014). Overall, the application of LB-SPR to our fishery-independent data provides another useful metric to track changes over time and assess the hopeful recovery of fish populations with improving management.

5. Conclusions

The results of this study indicate that reef fish biomass in the fished waters of Palau is generally low in comparison to previous research in both local MPAs and theoretical estimates of productivity for coral reef regions. Habitat was the most important predictor of fish biomass with the western facing fore-reefs naturally supporting the highest biomass of resource reef fish. High biomass was also associated with the Northern Reefs of Palau. As noted previously, the Northern Reefs are the most remote and have the most conservative fisheries management measures, including closed seasons, size limits, and limited entry, although compliance is variable. Fishing pressure from Koror explained patterns of fish biomass in the channels and inner reefs and local fishing pressure explained patterns of fish biomass in the channels only. SPR estimates showed that these stocks should be maintaining biomass, but likely have declined from their historical abundance. This suggests that Palau could benefit from a wider application of state specific fisheries management actions and/or nationwide policies that regulate the harvest of commercially important reef species.

These results highlight the need for improved fisheries management to ensure this resource continues to provide the ecosystem services that Palauan communities depend on. This study provides the first quantitative and fishery-independent baseline to detect future changes in fish biomass and SPR estimates over time; and as a reference to whether the fishery remains stable, improves, or continues to decline in response to future resource utilization patterns.

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Table 1. Assessed predictor variables of resource fish biomass.

Variable	**Category**	**Data type**	**Derivation**
Depth	Biophysical	Categorical	Recorded during fish surveys and categorized as shallow or deep
Habitat	Biophysical	Categorical	NOAA Palau habitat map
Region	Anthropogenic/ Biophysical	Categorical	Sites mapped and geographically divided into 3 main areas of Palau: Northern Reefs, Babeldaob and Southern Reefs
MPA proximity	Anthropogenic	Continuous	Distance by water to nearest MPA (inverse) multiplied by MPA size
Koror fishing pressure	Anthropogenic	Continuous	Distance by boat from Koror (inverse)
Local fishing pressure	Anthropogenic	Continuous	Distance by boat from the nearest dock (inverse) multiplied by the population of that state
Distance to pass	Anthropogenic/ Biophysical	Continuous	Linear distance to the nearest reef pass
Watershed pollution	Anthropogenic/ Biophysical	Continuous	Percentage of altered land in adjacent watershed multiplied by linear distance to nearest river discharge (inverse)
Wave energy	Anthropogenic/ Biophysical	Continuous	Wave energy calculated from wind speed, fetch distance and angle of exposure

Table 2. Life history parameters for seven commercially important resource species with sufficient actual length measurements for SPR estimates.

Species	**N**	**L_{50}**	**L_{95}**	**L_∞**	**M/K**	**L_{50}/L_∞**	**Source**
Lutjanus gibbus	385	245	320	340	0.977	0.72	1, 2
Acanthurus nigricauda	358	190	200	241	0.518	0.79	1, 2
Naso lituratus	334	205	238	238	0.518	0.79	1, 2
Scarus rubroviolaceus	207	292	390	448	0.94	0.652	1, 2
Siganus puellus	162	177	190	298	1.651	0.594	3, 2
Plectropomus leopardus	110	291	315	450	1.165	0.646	1, 2
Hipposcarus longiceps	107	251	273	385	0.94	0.652	4, 1

1 Prince (2016a)[2]
2 J. Prince (2021, pers. comm., 7 April)
3 Prince (2016b)[3]
4 Lindfield (Coral Reef Research Foundation, unpublished data)

Table 3. Results of mixed effects models (LMM) for predictors of fish biomass.

Predictor	**Df**	**AIC**	**LRT**	**Pr(>Chi)**
All habitats (LMM)				
		474.15		
Habitat	3	502.85	34.699	1.411e-07 ***
Region	2	479.89	9.742	0.008 **
Channel (LMM)				
		86.009		
Region	2	88.385	6.3757	0.041 *
MPA proximity	1	106.308	22.2989	2.333e-06 ***
Koror fishing pressure	1	90.192	6.1828	0.013 *
Local fishing pressure	1	91.396	7.3868	0.007 **
Wave energy	1	90.188	6.1794	0.013 *
Fore-reef east (LMM)				
		112.00		
Region	2	116.32	8.3222	0.016 *
MPA proximity	1	119.65	9.6489	0.002 **
Fore-reef west (LMM)				
		113.65		
Region	2	119.30	9.6516	0.008 **
Inner reef (LMM)				
		141.24		
MPA proximity	1	143.15	3.909	0.048 *
Koror fishing pressure	1	145.85	6.615	0.010 *

Significance codes: p<0.001(***), p<0.01(**) and p<0.05(*)

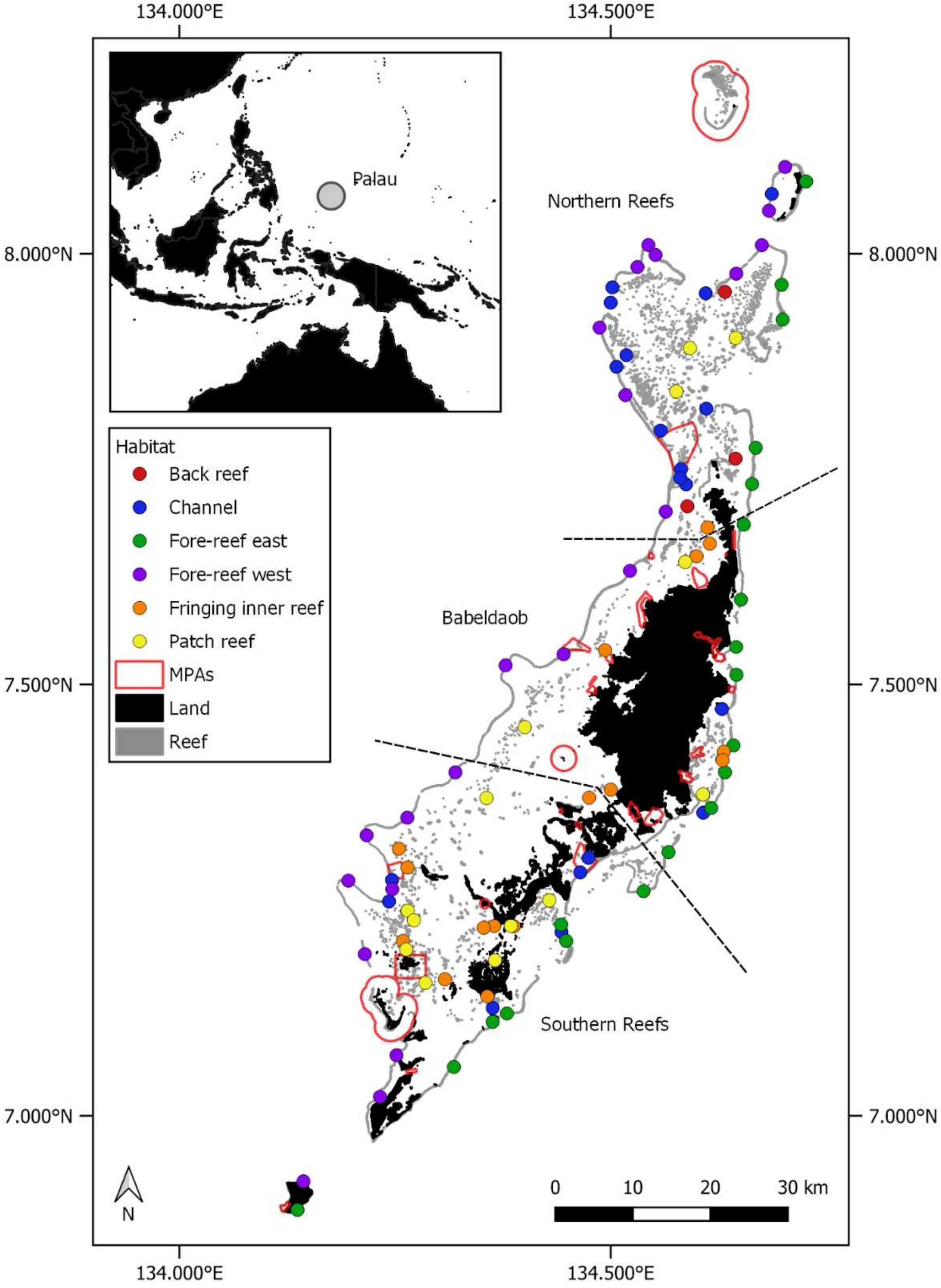
Table 4. Size structure of twelve resource fish species with sufficient actual length measurements.

Species	**N**	**Mean length (mm)**	**Median length (mm)**	**% below L_{50}**
Chlorurus spilurus	501	183	184	No L_{50} available
Lutjanus gibbus	384	248	249	45
Acanthurus nigricauda	358	199	200	40
Naso lituratus	334	202	200	55
Scarus schlegeli	226	183	181	No L_{50} available
Scarus rubroviolaceus	207	260	252	70
Siganus puellus	162	175	182	45
Lutjanus monostigma	129	302	303	No L_{50} available
Plectropomus leopardus	110	262	252	65
Hipposcarus longiceps	107	240	243	27
Kyphosus vaigiensis	105	265	264	No L_{50} available
Caranx sexfasciatus	101	341	359	No L_{50} available

Table 5. Output from LB-SPR assessment including spawning potential ratio (SPR) and selectivity-at-length (SL_{50} and SL_{95}), measurements are in fork length.

Species	**SPR (%)**	**SL_{50} (mm)**	**SL_{95} (mm)**
Lutjanus gibbus	35	212	282
Acanthurus nigricauda	38	160	193
Naso lituratus	20	169	208
Scarus rubroviolaceus	21	173	235
Siganus puellus	16	195	259
Plectropomus leopardus	31	168	202
Hipposcarus longiceps	53	127	166

909 **Figure 1.** Fish stock monitoring sites sampled in 2017 within each reef habitat across Palau.
910 MPAs are shown with red polygons and regions are delineated with black dashed lines.



911

Figure 2. Interpolation maps showing resource fish biomass across Palau for (A) total biomass, (B), herbivores, (C) secondary consumers and (D) piscivores. Color scale from blue to red, corresponds to increasing biomass in grams m^{-2}. Note that color ramps are on different scales.

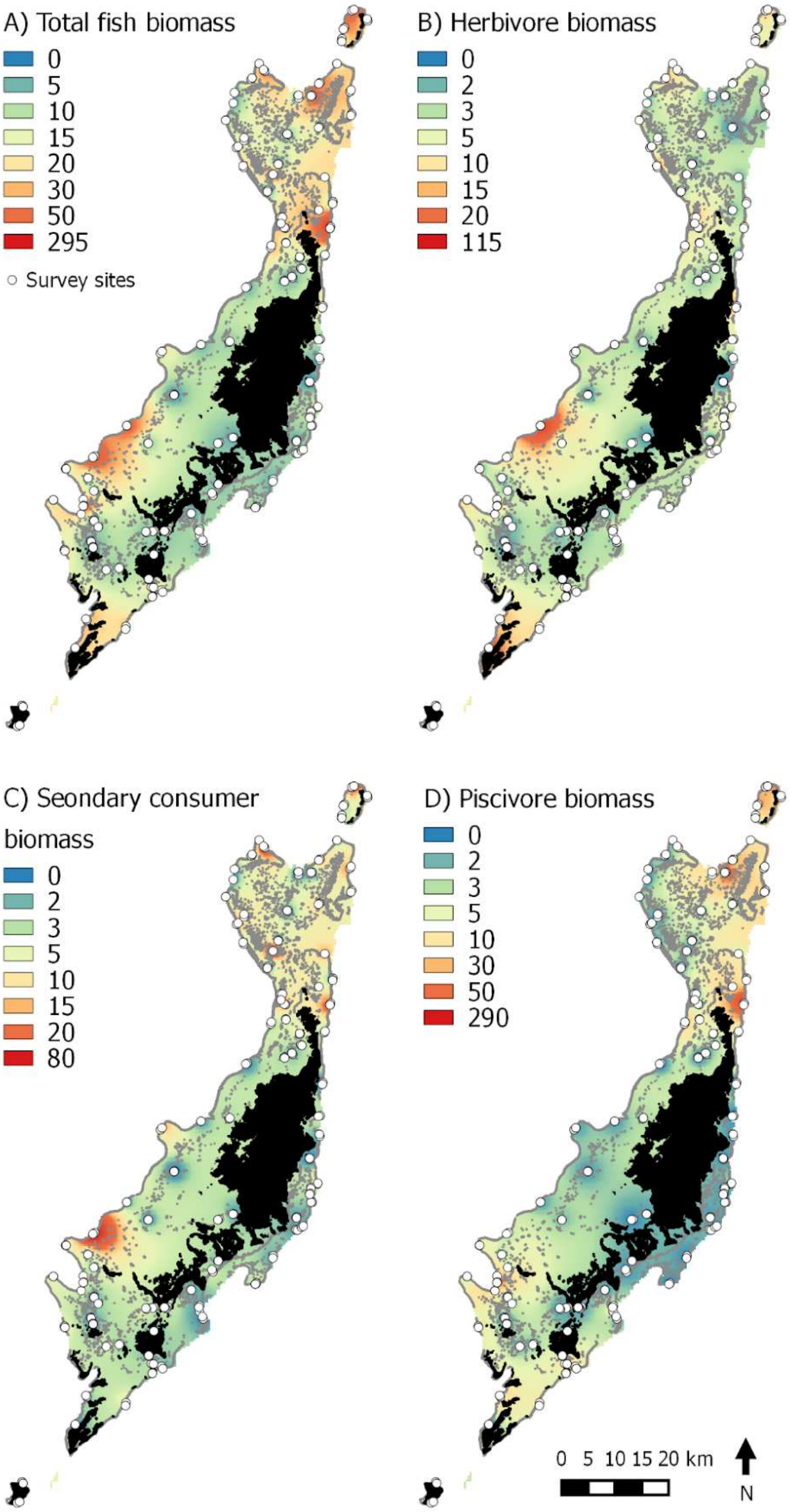


Figure 3. Resource fish species percentage contribution to total biomass. Only species that contributed >1% are included.

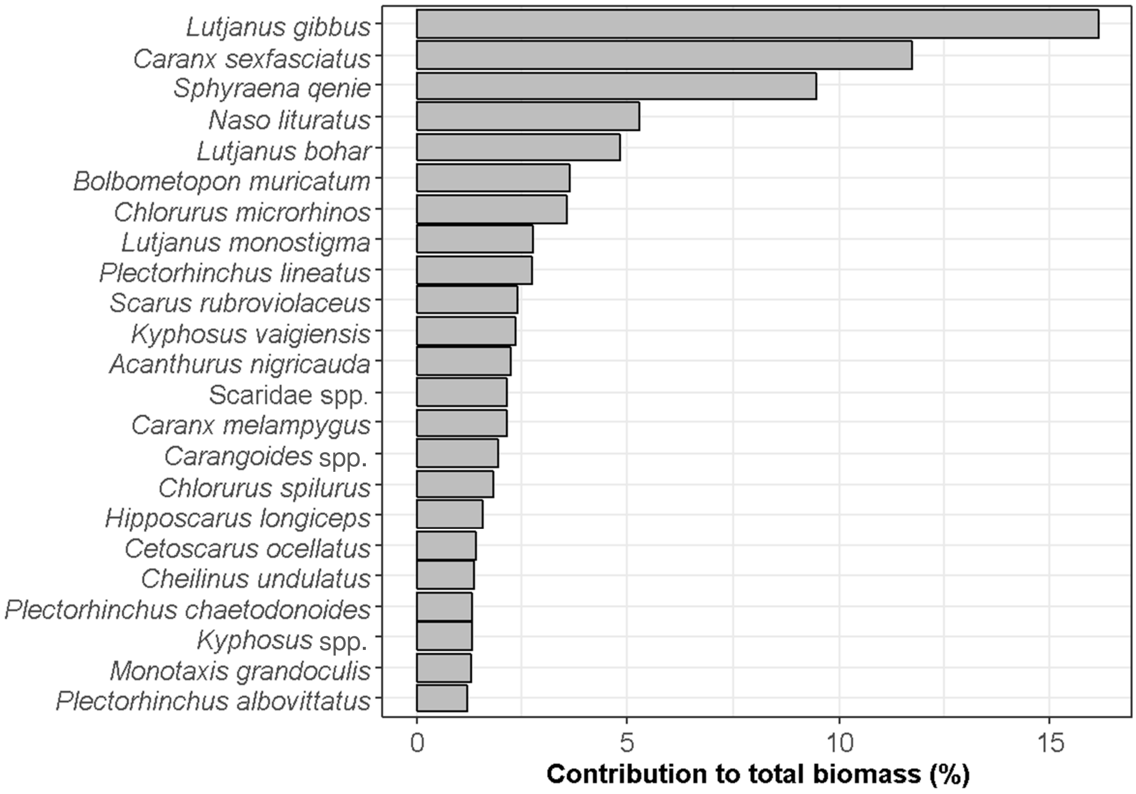


Figure 4. Box plots showing total resource fish biomass across habitats (a) and regions (b) with outliers removed. Median (black line), mean (♦), upper and lower quartiles, and 5th and 95th percentiles are shown. Habitat types and regions with the same letter are not significantly different (α = 0.05).

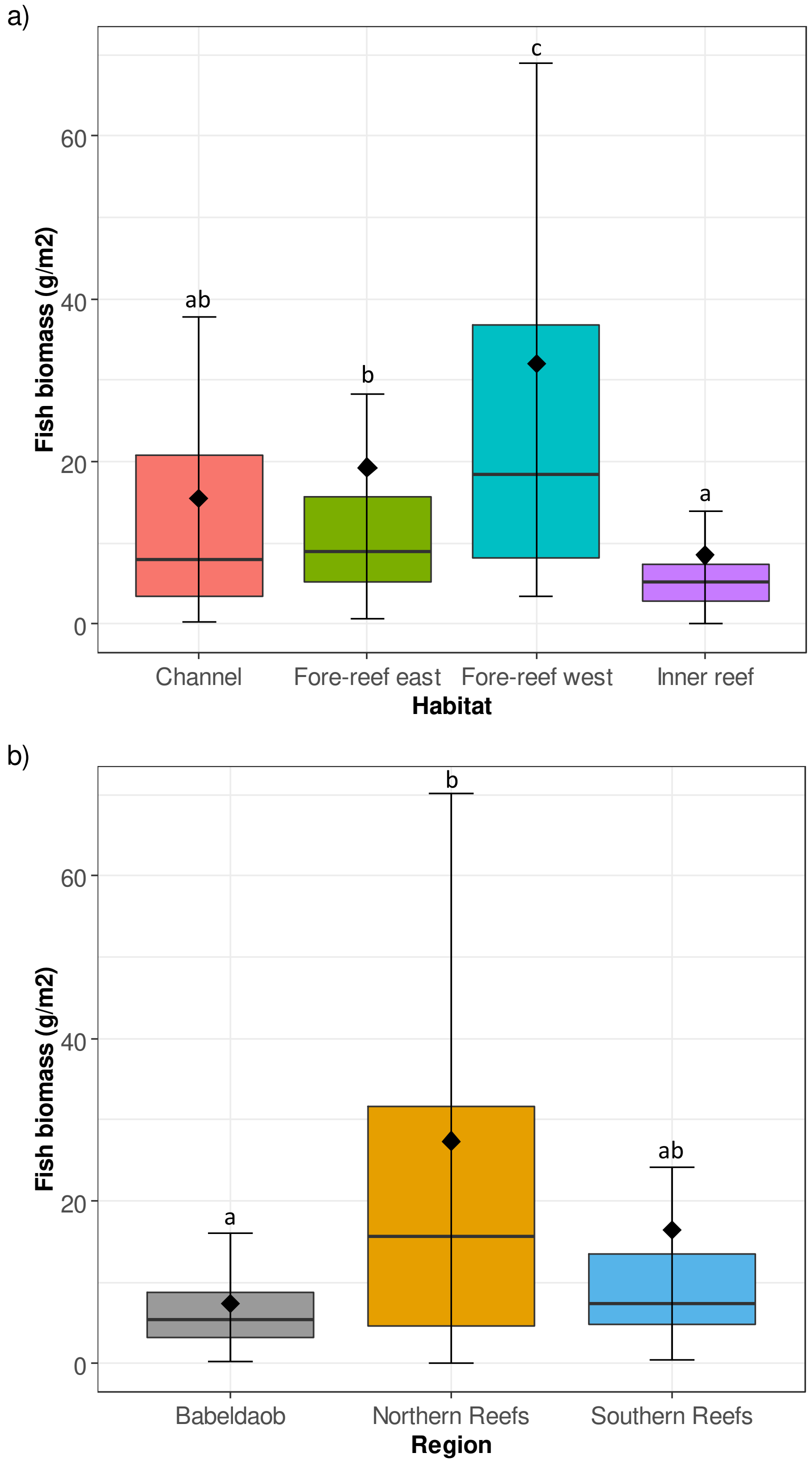
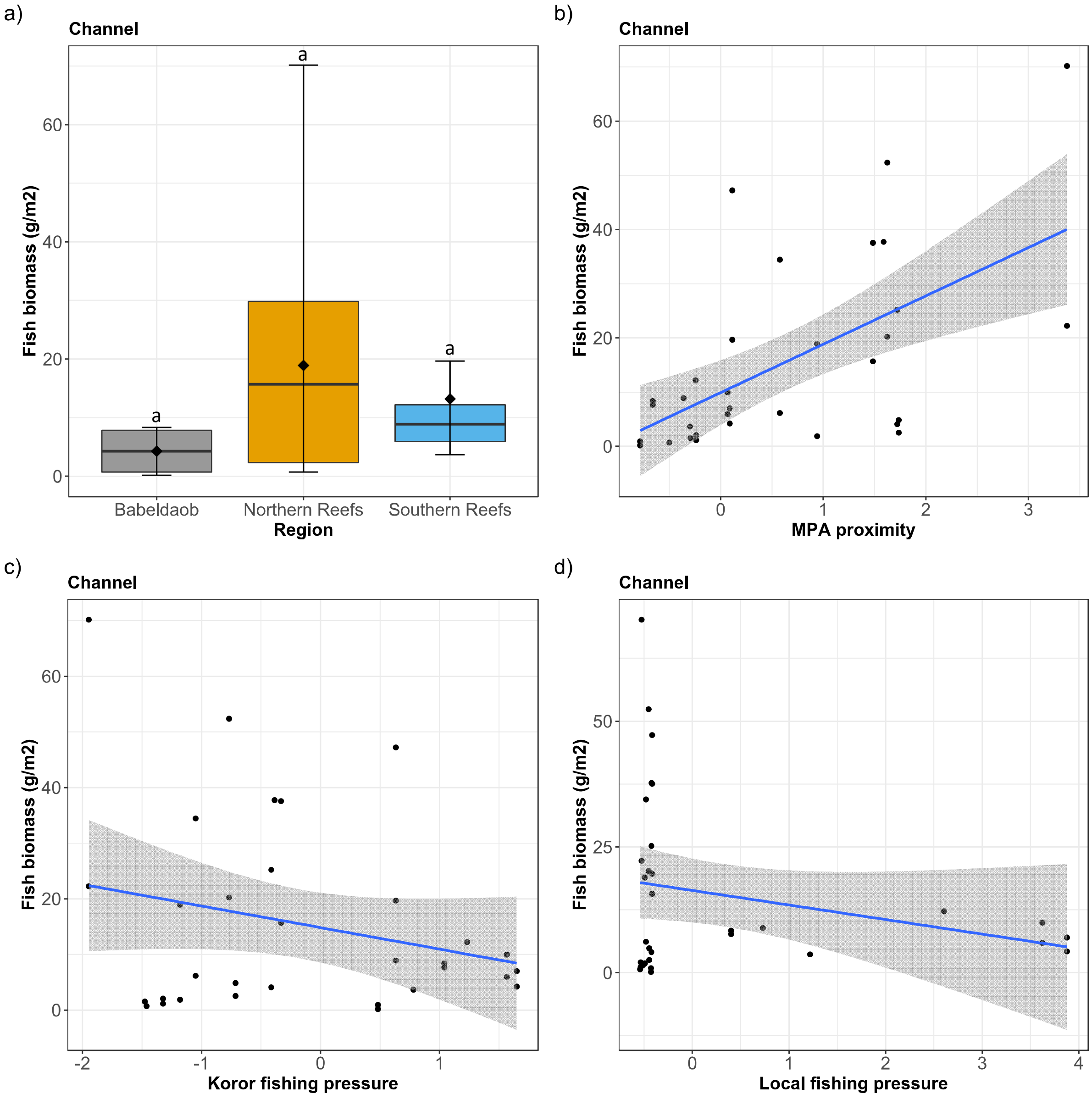
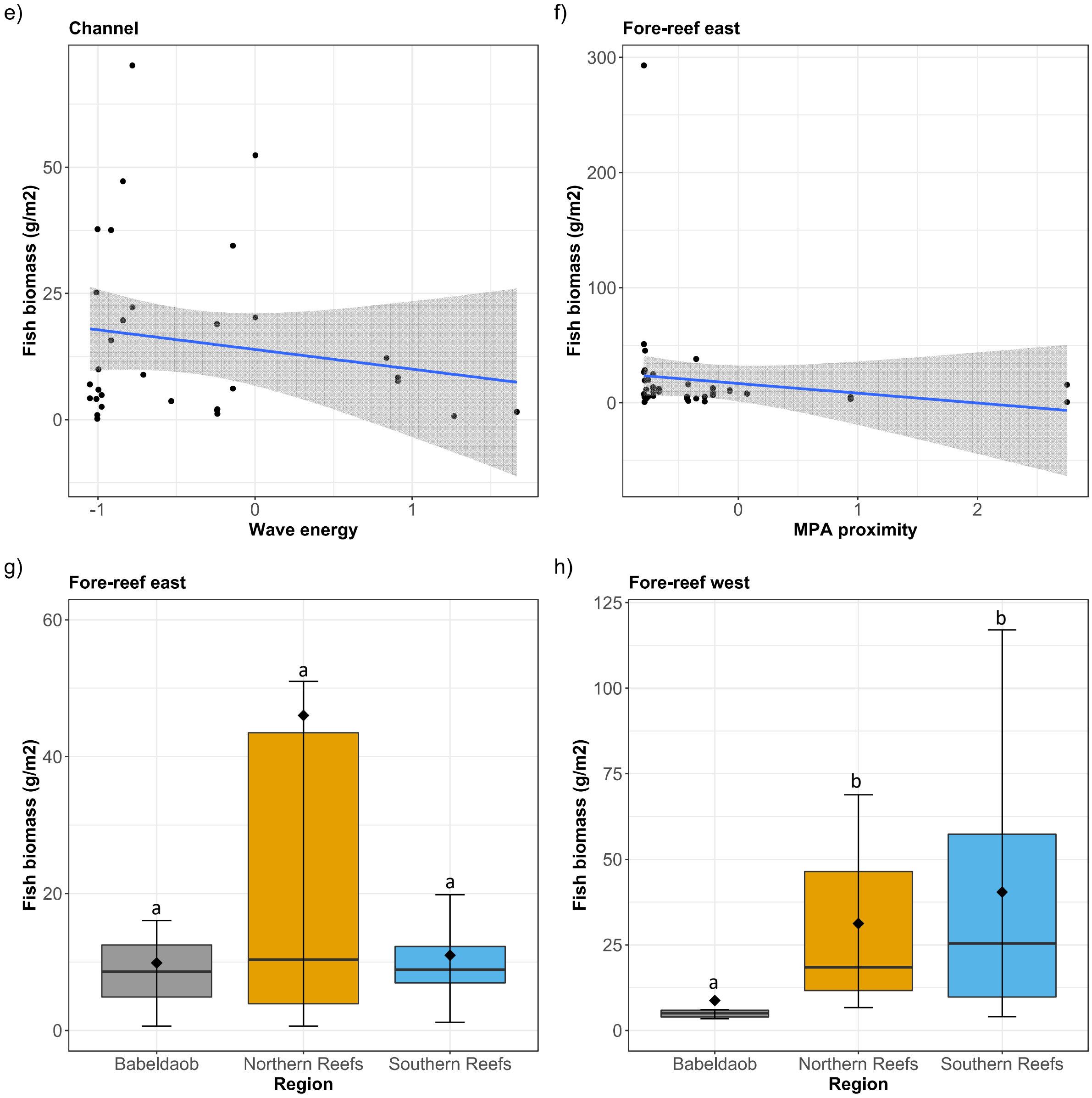
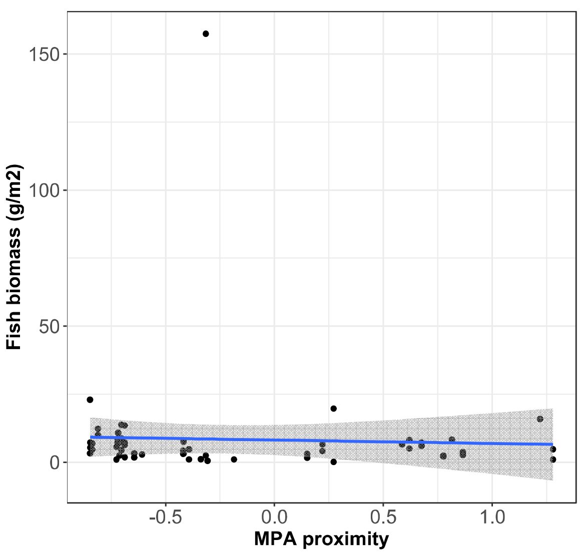


Figure 5. Regression plots and box plots showing assessed predictor variables that significantly affected resource fish biomass by habitat type. Continuous variables were normalized prior to analysis and distances used for MPA proximity, fishing pressure (local and Koror) and watershed pollution were inversely scaled. For the box plots, median (black line), mean (♦), upper and lower quartiles, and 5th and 95th percentiles are shown. Regions with the same letter are not significantly different (α = 0.05).

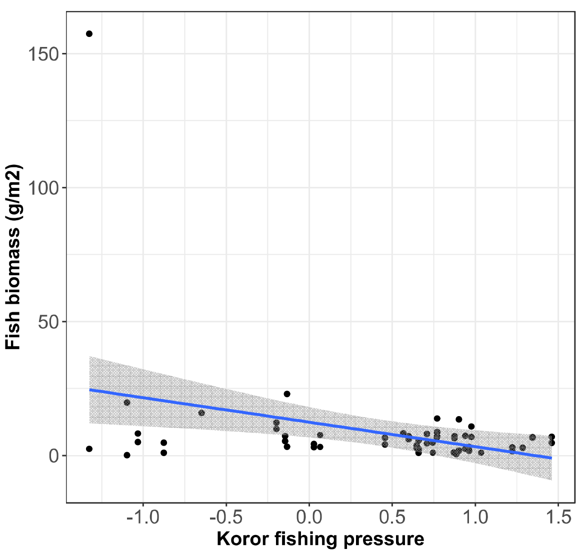



e)
Channel
Fish biomass (g/m2)
0
25
50
-1
0
1
Wave energy
f)
Fore-reef east
Fish biomass (g/m2)
0
100
200
300
0
1
2
MPA proximity
g)
Fore-reef east
Fish biomass (g/m2)
0
20
40
60
a
a
a
Babeldaob
Northern Reefs
Southern Reefs
Region
h)
Fore-reef west
Fish biomass (g/m2)
0
25
50
75
100
125
a
b
b
Babeldaob
Northern Reefs
Southern Reefs
Region

i)


Inner reef
Fish biomass (g/m2)
150
100
50
0
-0.5
0.0
0.5
1.0
MPA proximity

j)


Inner reef
Fish biomass (g/m2)
150
100
50
0
-1.0
-0.5
0.0
0.5
1.0
1.5
Koror fishing pressure