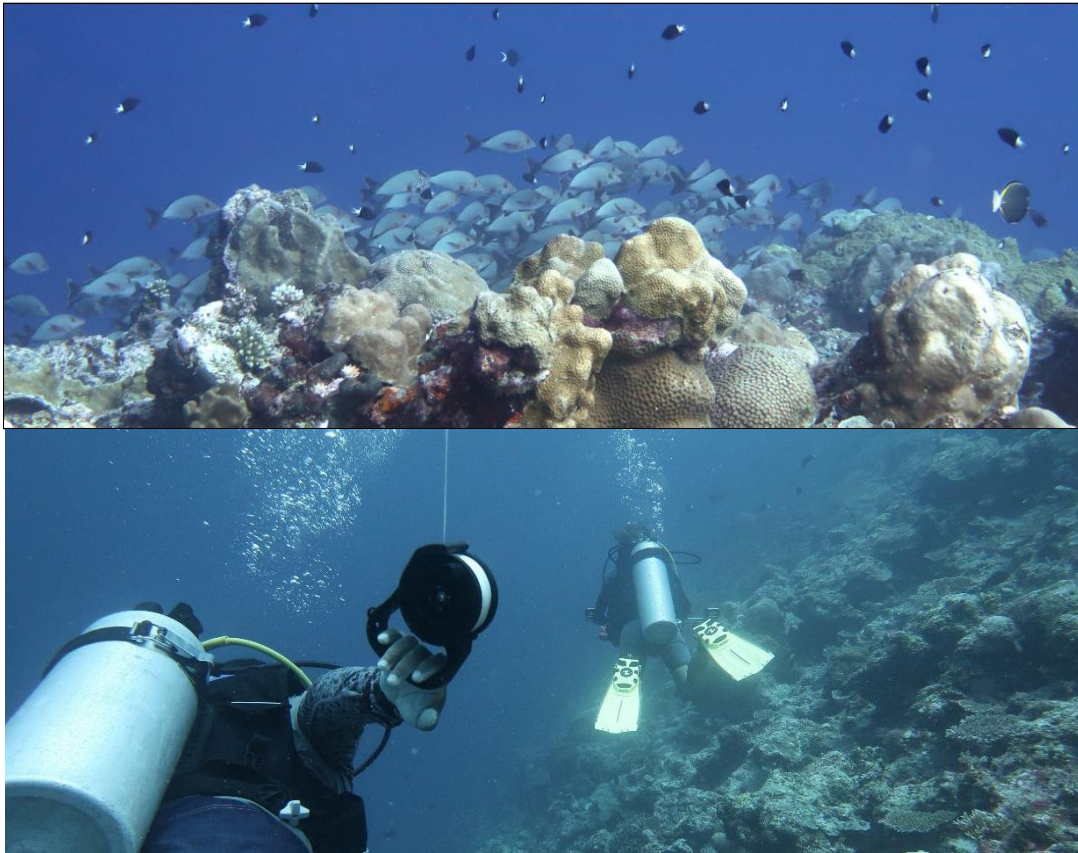


Fish populations in Palau in 2019 while still overexploited show signs of recovery



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Abstract

In recent years, there has been increasing concern that coral reef fish stocks are declining in Palau. Reef fisheries in Palau are data-poor and more information is needed on the abundance, biomass, and size structure of commercially important reef fish species in order to evaluate the current and future status of these resources. In 2017, the Palau International Coral Reef Center (PICRC) conducted the first nation-wide study to investigate the status of resource reef fish across Palau. This report presents the findings of the second survey conducted in 2019. In each year, fishery-independent surveys were conducted using a diver operated stereo-video (stereo-DOV) system at 94 sites, including six habitats and two depths, across the archipelago. Results showed that fish biomass varied from 0.103 to 392 g m⁻² across sites in 2019. There was no change in overall biomass over time, but at the trophic level there was a significant increase in herbivore biomass from 2017 to 2019. Habitat was the most significant predictor of fish biomass, with the highest biomass found in western fore-reef sites and the lowest in inner reef sites. Depth also affected fish biomass, with significantly higher biomass found in shallow transects (5-10 m) compared to deep (15-20 m). In channel habitats, marine protected area (MPA) proximity and wave energy significantly influenced fish biomass, with higher biomass seen closer to larger MPAs. In eastern facing fore-reefs, fish biomass was also significantly affected by MPA proximity, however the effect was opposite to the channel habitat. In western facing fore-reefs, fish biomass was only affected by depth. In the inner reefs, depth and fishing pressure from Koror had a significant effect on fish biomass, with increasing fishing pressure leading to lower biomass. Size structure was significantly different between 2017 and 2019 for six out of 10 assessed species. Spawning potential ratio (SPR) was <20% for two out of eight species in 2019, however most species had a SPR between 20% and 40%, with an increase from 2017 to 2019 seen for four out of six species. Overall, the low fish biomass at the majority of sites indicates overexploitation of fish stocks in the past, however the increase in herbivores and SPR for several species over time could indicate that fish stocks are starting to recover in Palau.

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. Before the export ban, around half of landed reef fish were sold commercially to residents, tourists, or exported (Prince et al., 2015; Dacks et al., 2020). In addition to the benefits they provide to humans, reef fishes also have important functional roles within coral reef ecosystems (Bellwood et al., 2004; Pratchett et al., 2014). Herbivorous fish are vital for regulating the abundance of macroalgae and turf algae on coral reefs (Edwards et al., 2014), whereas predatory fishes are important for maintaining prey populations (Dulvy et al., 2004). Overfishing of these groups can lead to a degradation of these key ecosystem functions. Since the 1970s, there have been increasing concerns among fishers that reef fish stocks have declined in Palau 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* (kemedukl) and *Cheilinus undulatus* (maml). 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 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). 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* (erobk) from 2016 and 2017 for 3 years. Minimum size limits were also implemented for 14 species from the families Serranidae, Lutjanidae, Lethrinidae, Acanthuridae, and Scaridae that restricted the take of immature fish 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.

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; Prince, 2016a; Prince, 2016b; Lindfield, 2016; Lindfield, 2017); however, there has been limited research on fish populations in Palau using fishery-independent surveys at the archipelago scale (Dochez et al., 2019; Muller-Karanassos et al., 2020; 2021). 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 changes over time (MacNeil et al., 2015). Another method of assessing the health of fish stocks is the spawning potential ratio (SPR), which is defined as the proportion of the unfished reproductive potential left at any given level of fishing pressure 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), which is ideal for assessing data-limited fisheries, such as the one in Palau. 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 (the maximum level at which a natural resource can be routinely exploited without long-term depletion) 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

estimates of biomass, estimates of SPR for keystone fisheries species can substantially improve our understanding of the status of data-poor coral reef fisheries.

In 2017, the Palau International Coral Reef Center (PICRC) conducted the first assessment of resource reef fish populations across the main islands of Palau (the Southwest Islands of Sonsorol and Hatohobei states were excluded from the survey due to their remoteness) (Muller-Karanassos et al., 2020; 2021). A second fishery-independent survey was carried out in 2019 using a diver operated stereo-video (stereo-DOV) system to 1) assess the current biomass and abundance of commercially important reef fish across Palau; 2) determine which assessed anthropogenic and biophysical factors are influencing the biomass of reef fishes in Palau; 3) estimate the SPR of species with sufficient length data and available life history parameters; and 4) compare data between 2017 and 2019.

2. Methods

2.1 Survey sites

In 2017 and 2019, 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 (Figure 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 were determined based on the total area of each habitat within the study area and previous sampling efforts for *B. muricatum* (kemedukl) and *C. undulatus* (maml) in Palau (Friedlander and Koike, 2013; Polloi et al., 2014). Sites were then randomly selected using Open Source Geographic Information Systems (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.

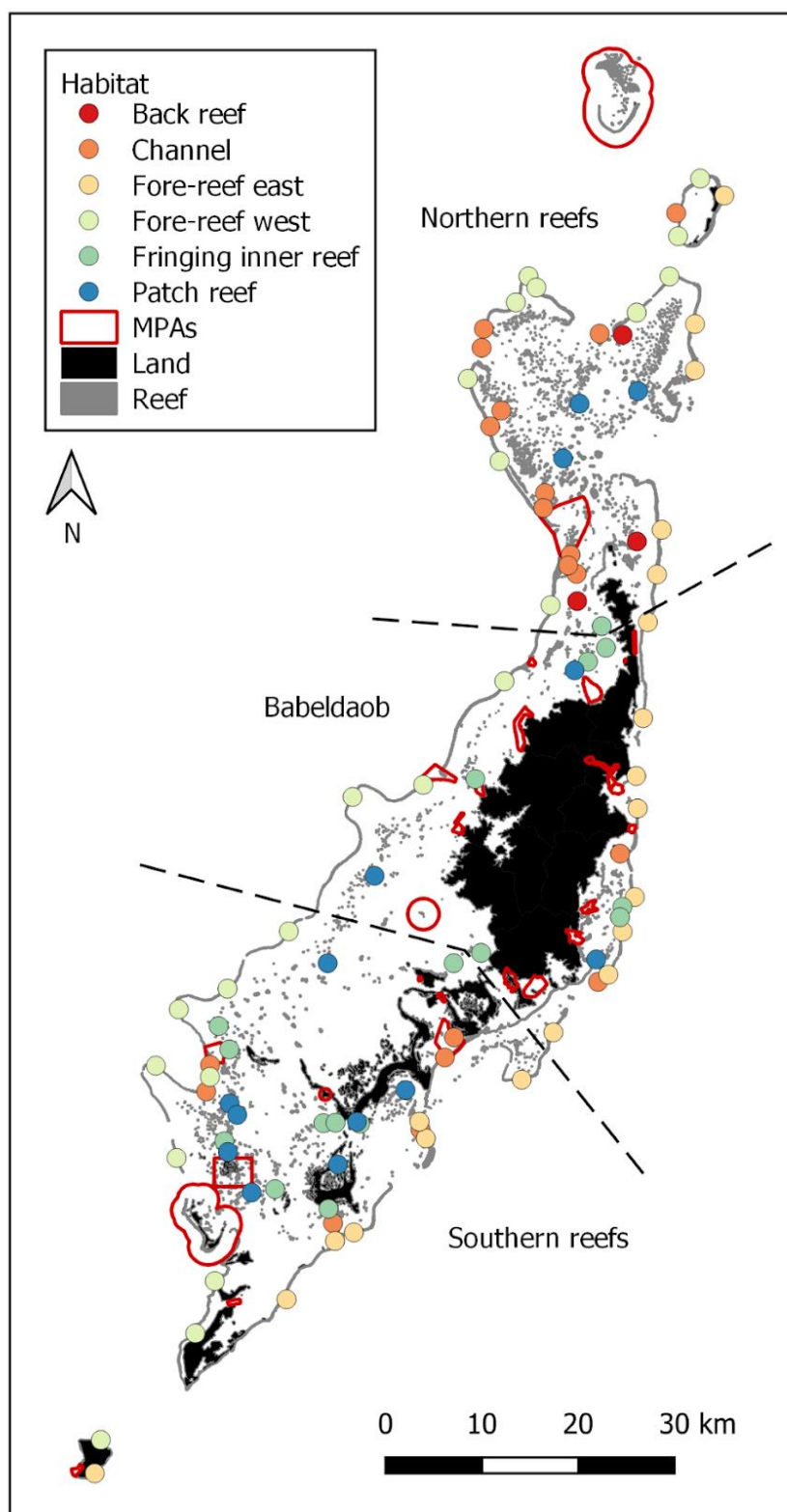


Figure 1. Fish stock monitoring sites sampled in 2017 and 2019 within each reef habitat across Palau. MPAs are shown with red polygons and regions are delineated with black dashed lines.

2.2 Fish survey methodology

Fishery-independent surveys were carried out using a stereo-DOV system, consisting of two GoPro Hero 4 cameras in waterproof housings mounted on an aluminum frame. In 2017, surveys took place from February to September, and in 2019, surveys took place from February to October, with 12 sites that were missed completed in May 2020. The survey method involved two SCUBA divers swimming along the reef at two different depths where possible at each site; this varied slightly between the two survey periods: 15-20 m (deep) ($n = 89$ in 2017 and $n = 88$ in 2019) and 5-10 m (shallow) ($n = 83$ in 2017 and $n = 88$ in 2019). At a few sites it wasn't possible to maintain the depth within the designated range due to the nature of the site, in which case the survey was grouped into the nearest depth class (e.g. if the depth ranged from 10 to 12 m, the survey was still classified as shallow). The lead diver operated the stereo-DOV system, which was used to take a video along the reef for a 15-minute timed swim at each depth. 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/>). The stereo-DOV system is calibrated once a year by PICRC, for data accuracy and precision.

2.3 Data processing

Stereo videos were analyzed using the SeaGIS EventMeasure software (Version 4.42), with the length/3D rules set up as in 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, for consistency. 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 (see Appendix 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 & 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 get 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). It is noted that biomass estimates for 2017 and 2019 were calculated using the most up-to-date a & b values and therefore the estimates for 2017 may vary slightly compared to the previous technical report (Muller-Karanassos et al., 2020).

2.4 Predictor variables

Site-specific predictor variables of fish biomass were compiled for input into mixed effects models (Table 1). These temporal, 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). Detailed information on the rest of the predictor variables can be found in Muller-Karanassos et al (2021).

Table 1. Assessed predictor variables of resource fish biomass.

Variable	Category	Data type	Derivation
Year	Temporal	Categorical	Year the survey was conducted
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

2.5 Data 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 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, to determine the effect of variables on specific habitat types. A generalized linear mixed effects model (GLMM, gamma distribution) was used to compare fish biomass between trophic groups and years using the 'glmer' function, since residuals did not conform to normality and homogeneity assumptions. For all GLMMs and LMMs, site was added as a random effect to account for repeated measures at the same sites over time. Models were selected based on Akaike Information Criterion (AIC) values. Where significant effects were found, pairwise comparisons were carried out using the 'lsmeans' function. Prior to statistical analysis, continuous data were normalized and tested for collinearity, and data were tested for normality and homogeneity of variances assumptions, as described in Muller-Karanassos et al (2021). Following LMM analyses, residuals were plotted and checked for normality. Biomass interpolation maps were created using the Inverse Distance Weighting method in QGIS. Data are presented as mean values \pm 1 standard error.

The size structure of 14 species with sufficient actual length measurements from 2019 ($n > 100$) were examined using length-frequency plots. Length-frequency plots were made for 10 of these species in 2017, and these were compared to the current size structures using Kolmogorov–Smirnov tests. One-way ANOVA tests were also performed to compare the mean length between 2017 and 2019 for each species. SPR was estimated for eight of these species that had locally available life history parameters using the LB-SPR method, as described in Muller-Karanassos et al (2021). The LB-SPR R Shiny application on The Barefoot Ecologist's Toolbox website (<http://barefootecologist.com.au/>) was used for SPR estimations. It is noted that SPR estimates for 2017 and 2019 were calculated using updated life-history parameters from J. Prince (2021, pers. comm., 7 April) and Lindfield (Coral Reef Research Foundation, unpublished data), therefore some estimates for 2017 are different compared to the previous technical report (Muller-Karanassos et al., 2020).

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

Species	Palauan name	N	L ₅₀	L ₉₅	L _∞	M/K	L ₅₀ /L _∞	Source
<i>Lutjanus gibbus</i>	Keremlal	556	245	320	340	0.977	0.72	1, 2
<i>Acanthurus nigricauda</i>	Chesengel	419	190	200	241	0.518	0.79	1, 2
<i>Naso lituratus</i>	Cherangel	242	205	238	238	0.518	0.79	1, 2
<i>Scarus rubroviolaceus</i>	Mesekelat mellemau	165	292	390	448	0.94	0.652	1, 2
<i>Hipposcarus longiceps</i>	Ngiaoch	148	251	273	385	0.94	0.652	3, 2
<i>Parupeneus barberinus</i>	Bang	144	230	250	391	1.871	0.588	1, 2
<i>Siganus puellus</i>	Reked	137	177	190	298	1.651	0.594	4, 2
<i>Chlorurus microrhinos</i>	Otord	133	309	345	474	0.94	0.652	1, 2

1. Prince (2016a)

2. J. Prince (2021, pers. comm., 7 April)

3. Lindfield (Coral Reef Research Foundation, unpublished data)

4. Prince (2016b)

3. Results

3.1 Fish biomass and abundance

3.1.1 Overall biomass and abundance

In 2019, biomass and abundance were recorded for 100 species (Appendix 2), whereas in 2017, 106 species were observed. In 2019, a total of 15,721 fishes were observed during the surveys, with actual length measurements for 8,115 individuals and estimated length measurements for the remaining 7,606. In 2017, 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. In 2019, total fish biomass varied across sites from 0.103 to 392 g m⁻², with a mean biomass of 21.37 ± 3.05 g m⁻². In 2017, total fish biomass varied across sites from 0.15 to 294 g m⁻², with a mean biomass of 17.86 ± 2.53 g m⁻² (Figure 2). Mean fish biomass was not significantly different between 2017 and 2019.

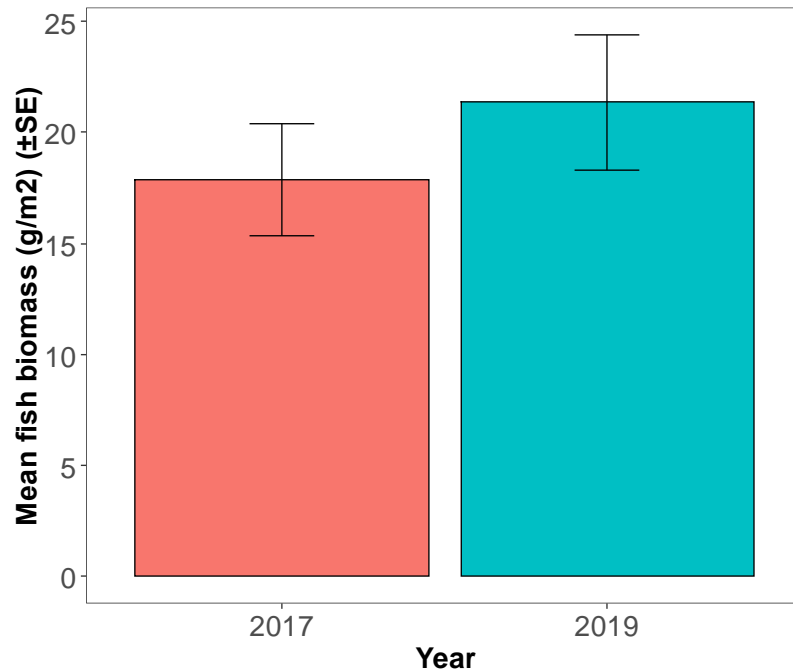


Figure 2. Bar plot showing mean overall fish biomass across years, including data for all sites and habitats. Error bars represent standard error.

In 2017, hot spots of high biomass were observed in the Northern Reefs and the south western reefs. In 2019, hot spots of high biomass were also observed in the Northern Reefs and in the south western fore-reefs. High biomass was also seen at eastern sites and in the south around Peleliu and Angaur. Low biomass was observed at inner reef sites in the southern lagoon and around Babeldaob in both years (Figure 3).

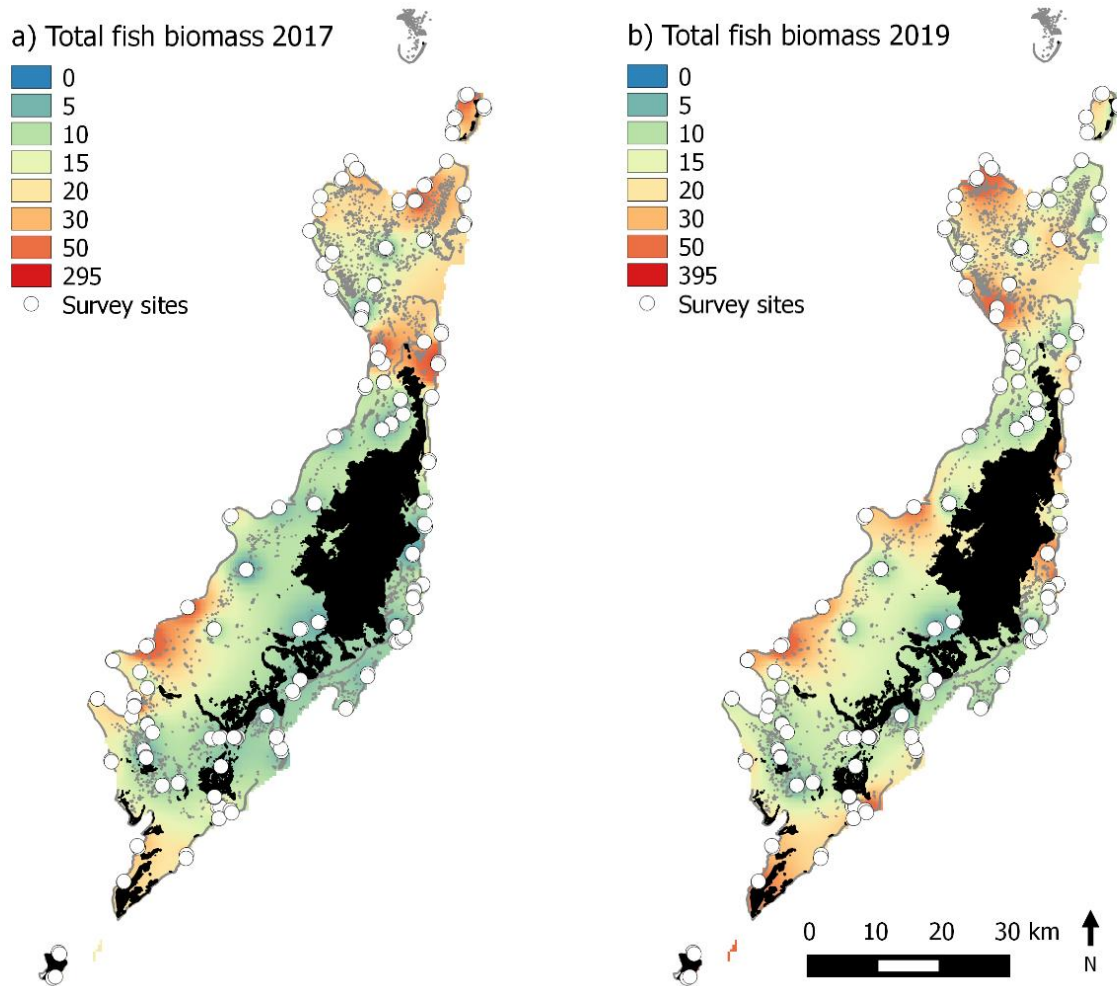


Figure 3. Interpolation maps showing total resource fish biomass across Palau in 2017 and 2019. Color scale from blue to red, corresponds to increasing biomass in grams m^{-2} . Note that color ramps are on different scales.

There was a significant interaction between trophic group and year (GLMM: $p < 0.001$). Mean herbivore biomass significantly increased from $4.98 \pm 0.75 \text{ g m}^{-2}$ in 2017 to $6.19 \pm 0.53 \text{ g m}^{-2}$ in 2019 ($p = 0.017$). There were no significant changes in secondary consumer or piscivore biomass over time. In 2017 and 2019, mean piscivore biomass ($7.02 \pm 2.12 \text{ g m}^{-2}$ and $6.65 \pm 2.50 \text{ g m}^{-2}$ respectively) was significantly higher than herbivore biomass ($p = 0.003$ and $p < 0.001$ respectively). In 2019, secondary consumer biomass ($8.53 \pm 1.42 \text{ g m}^{-2}$) was significantly higher than piscivore biomass ($p < 0.001$) and herbivore biomass ($p = 0.022$) (Figure 4). Although mean herbivore biomass was the lowest out of the three trophic groups in both years, herbivores had a higher number of fish per m^2 (density) compared to secondary consumers and piscivores in both years.

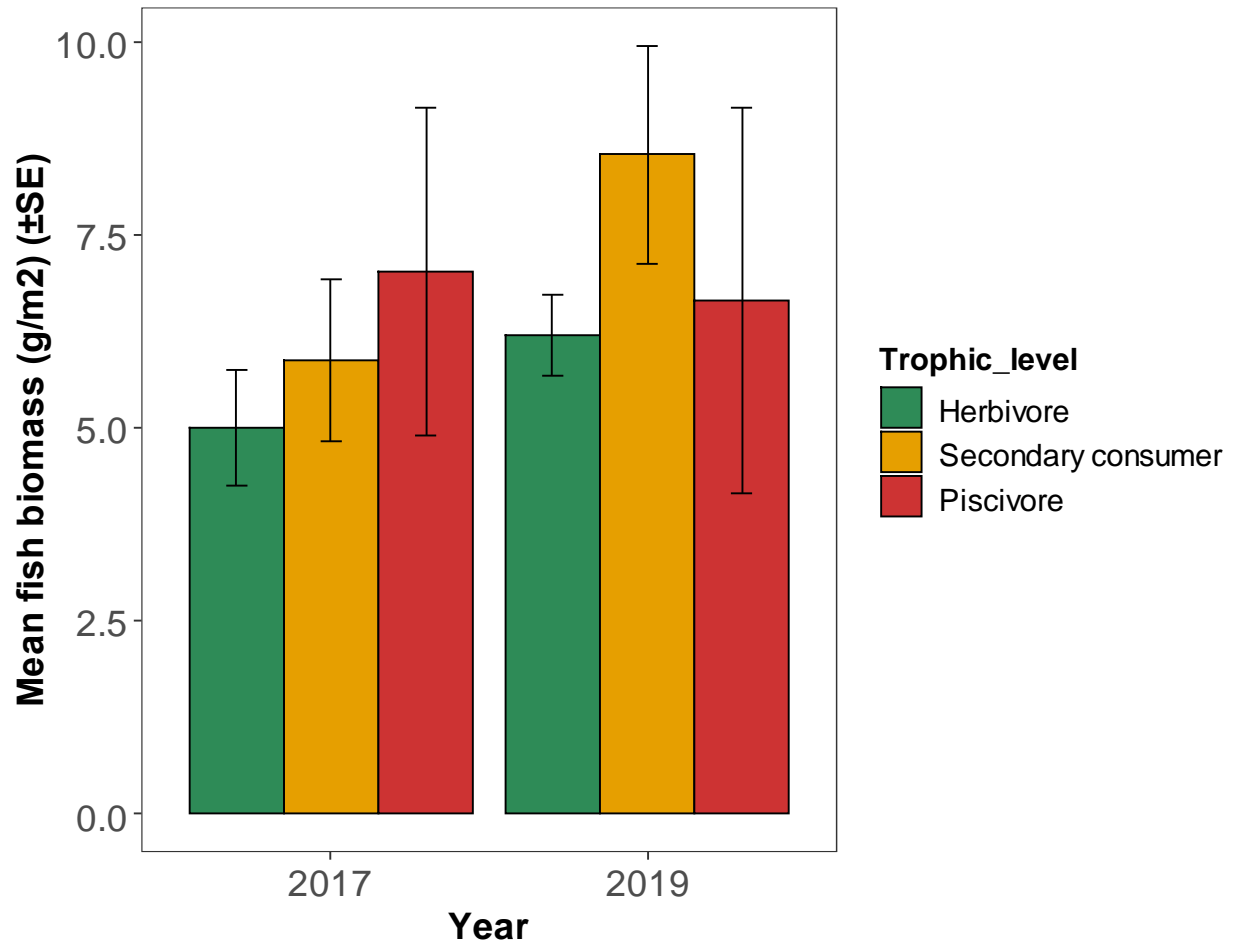


Figure 4. Bar plot showing mean fish biomass across trophic levels in 2017 and 2019. Error bars represent standard error.

Caranx sexfasciatus (chesuch) and *Lutjanus gibbus* (keremlal) accounted for the highest percentages of total fish biomass observed during the 2019 survey (22.12% and 22.04% respectively). In 2017, *L. gibbus* (keremlal), *C. sexfasciatus* (chesuch) and *Sphyraena qenie* (meyai) accounted for the highest percentages of total fish biomass (16.12%, 11.75%, and 9.47%, respectively) (Figure 5). In 2019, Scaridae spp. (mellemau) was the most abundant fish observed (4,218), followed by *L. gibbus* (keremlal) (4,117). *L. gibbus* (keremlal) was the most abundant species observed in 2017 (2,712). Scaridae spp. (mellemau) also had the highest frequency of occurrence in 2019, occurring in 93.33% of transects surveyed, followed by *Chlorurus spilurus* (mellemau) (63.33%). In 2017, *C. spilurus* (mellemau) had the highest frequency of occurrence (68.21%) (Appendix 2).

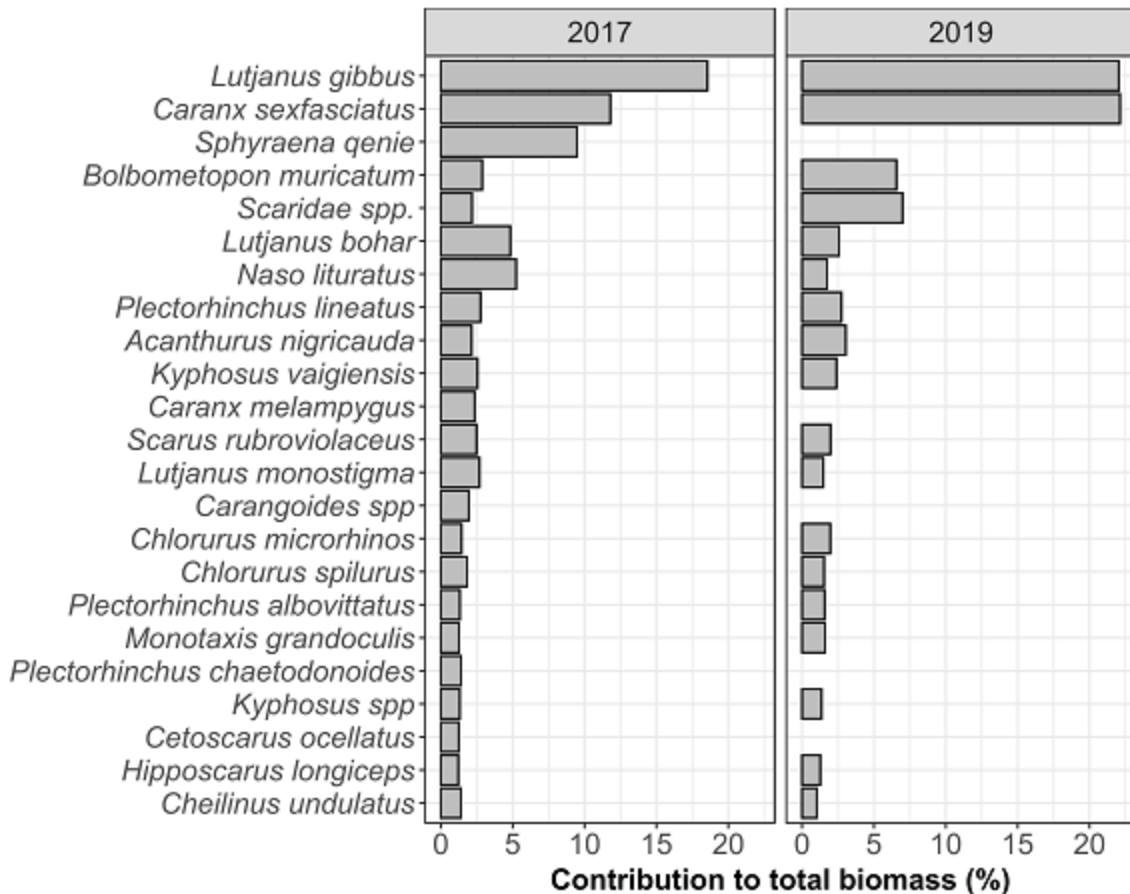


Figure 5. Resource fish species percentage contribution to total biomass in 2017 and 2019. Only species that contributed >1% are included.

3.1.2 Drivers of fish biomass

Habitat and depth were found to be significant predictors of fish biomass (LMM: $p < 0.001$ and $p = 0.005$ respectively). The highest biomass was found in the fore-reef west habitat ($35.64 \pm 5.75 \text{ g m}^{-2}$) and the lowest biomass was found in the inner reef habitat ($7.81 \pm 1.38 \text{ g m}^{-2}$) (Figure 6). Significant differences were found between channel and fore-reef west ($p = 0.012$), channel and inner reef ($p = 0.002$), fore-reef east and fore-reef west ($p = 0.017$), fore-reef east and inner reef ($p < 0.001$) and fore-reef west and inner reef ($p < 0.001$) habitats. Fish biomass was found to be significantly higher in shallow sites compared to deep sites, however mean fish biomass was similar between the two depths ($19.55 \pm 3.35 \text{ g m}^{-2}$ in deep and $19.76 \pm 2.06 \text{ g m}^{-2}$ in shallow). No significant differences were seen between deep and shallow within each habitat (Figure 6).

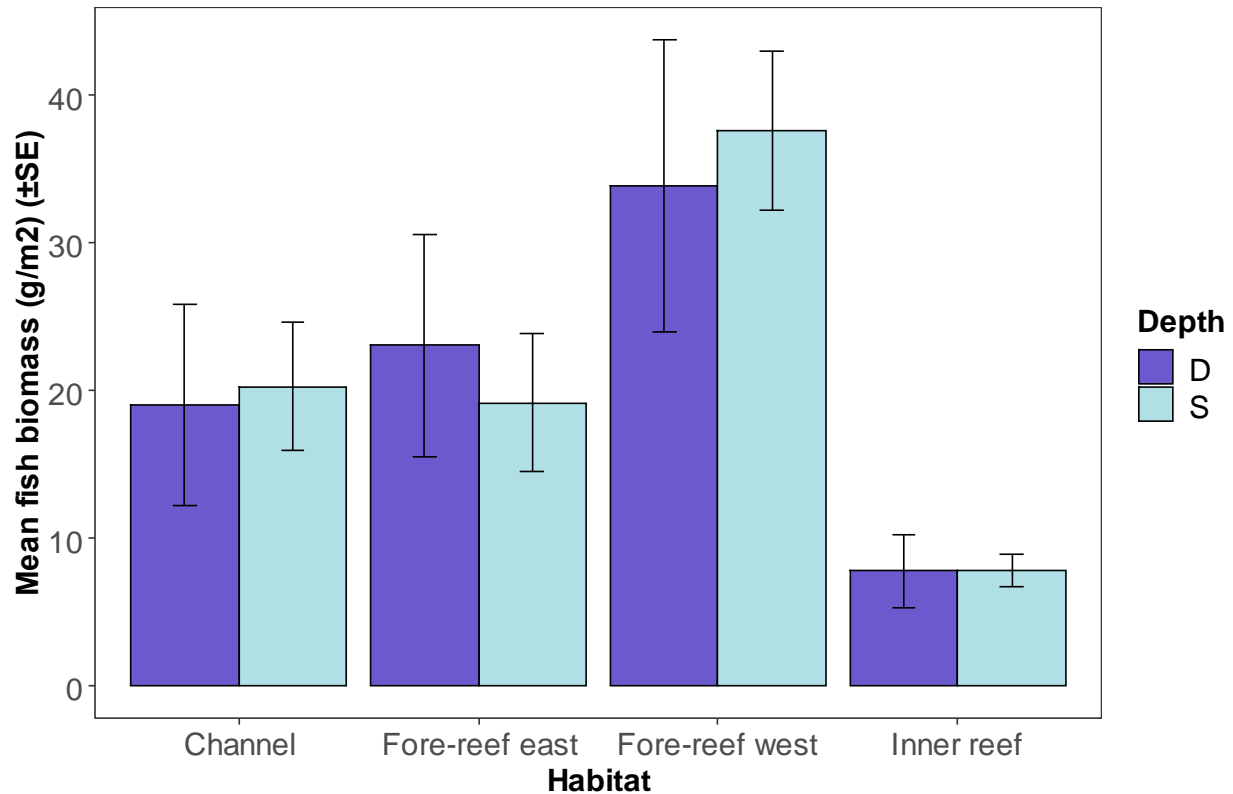


Figure 6. Bar plot showing mean resource fish biomass across habitats and depths (D=Deep, S=Shallow). Error bars represent standard error. Includes data from both 2017 and 2019.

3.1.2.1 Channel habitat

In the channel habitat, depth, MPA proximity and wave energy were found to significantly affect resource fish biomass (LMM: $p=0.047$, $p=0.030$ and $p=0.023$ respectively), however pairwise comparisons showed that fish biomass was not significantly different between shallow and deep sites ($S = 20.25 \pm 4.34 \text{ g m}^{-2}$ and $D = 19.04 \pm 6.80 \text{ g m}^{-2}$) (Figure 6). A weak positive relationship was observed for MPA proximity ($R^2 = 0.032$) (Figure 7a) and a very weak positive relationship was observed for wave energy ($R^2 = 0.015$) (Figure 7b).

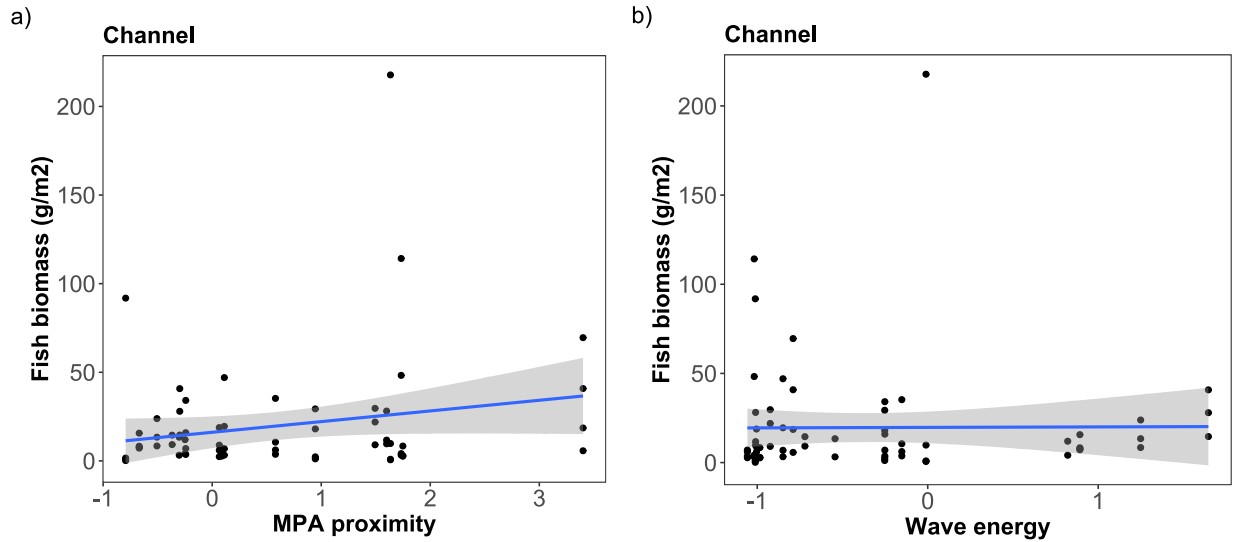


Figure 7. Regression plots showing effect of MPA proximity (a) and wave energy (b) on fish biomass within the channel habitat. Continuous variables were normalized prior to analysis and distances used for MPA proximity were inversely scaled. Includes data from both 2017 and 2019.

3.1.2.2 Fore-reef east habitat

In the fore-reef east habitat, MPA proximity was found to significantly affect fish biomass (LMM: $p=0.009$), with a weak negative relationship observed ($R^2 = 0.134$) (Figure 8).

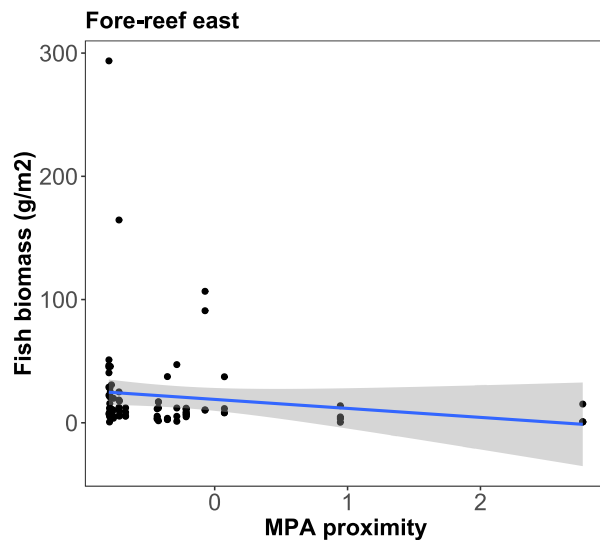


Figure 8. Regression plot showing effect of MPA proximity on fish biomass within the fore-reef east habitat. Continuous variables were normalized prior to analysis and distances used for MPA proximity were inversely scaled. Includes data from both 2017 and 2019.

3.1.2.3 Fore-reef west habitat

In the fore-reef west habitat, only depth significantly affected resource fish biomass (LMM: $p=0.024$). Mean fish biomass was significantly higher in the shallow depth ($37.58 \pm 5.37 \text{ g m}^{-2}$) compared to the deep ($33.88 \pm 9.89 \text{ g m}^{-2}$) (Figure 6).

3.1.2.4 Inner reef habitat

In the inner reef habitat, depth and fishing pressure from Koror significantly affected resource fish biomass (LMM: $p=0.032$ and $p=0.013$ respectively). Although mean fish biomass was similar between the deep ($7.80 \pm 2.48 \text{ g m}^{-2}$) and shallow ($7.82 \pm 1.08 \text{ g m}^{-2}$), pairwise comparisons revealed a significant difference ($p=0.035$). A weak negative relationship was observed for fishing pressure from Koror ($R^2 = 0.215$) (Figure 9).

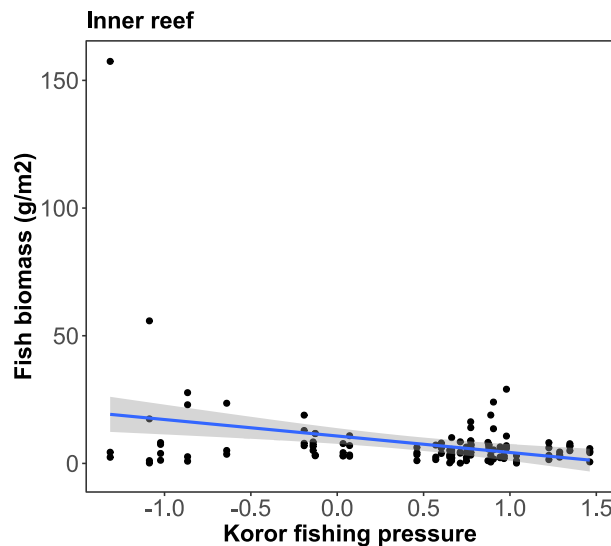


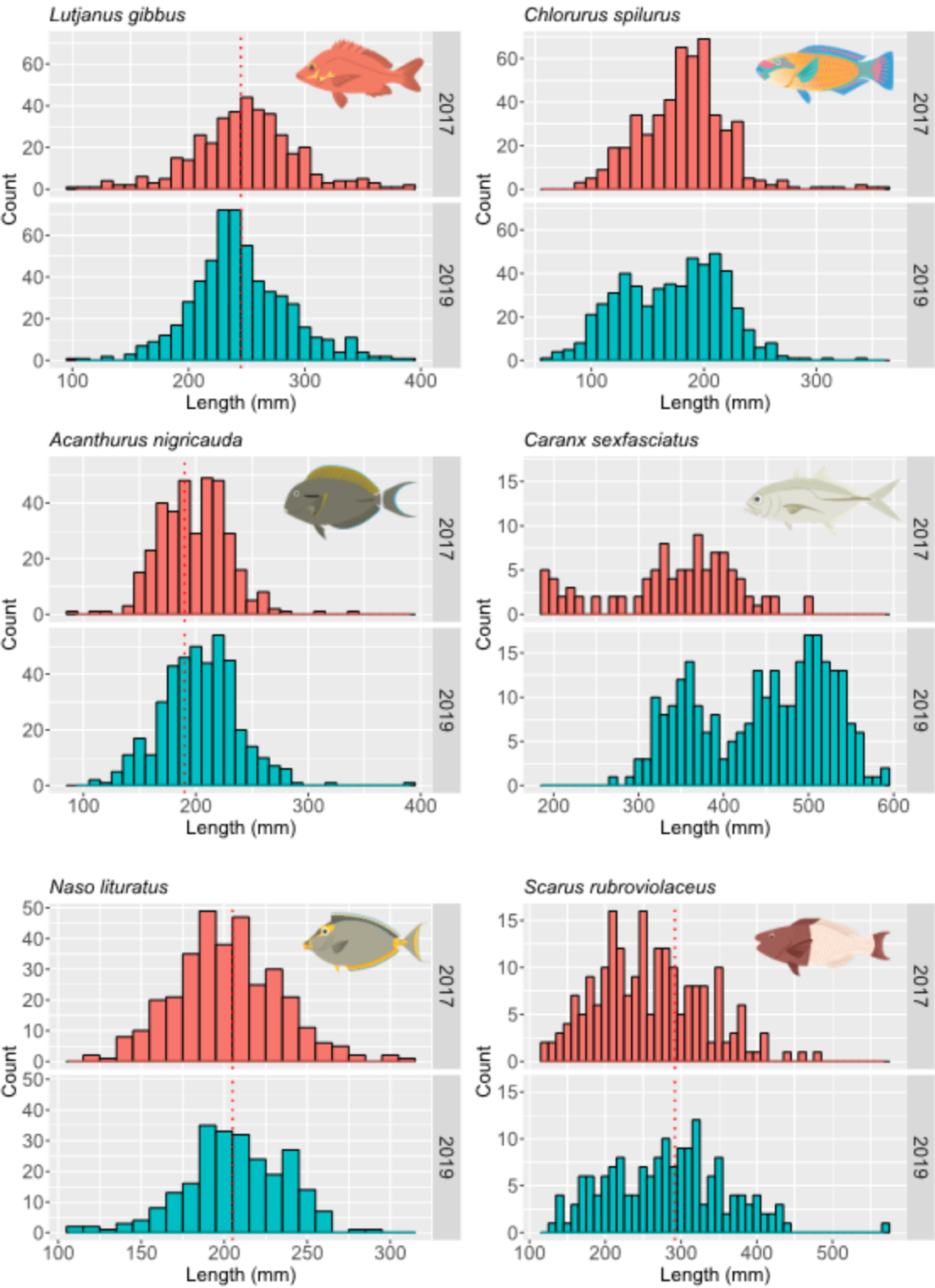
Figure 9. Regression plot showing effect of Koror fishing pressure on fish biomass within the inner reef habitat. Continuous variables were normalized prior to analysis and distances used for fishing pressure from Koror were inversely scaled. Includes data from both 2017 and 2019.

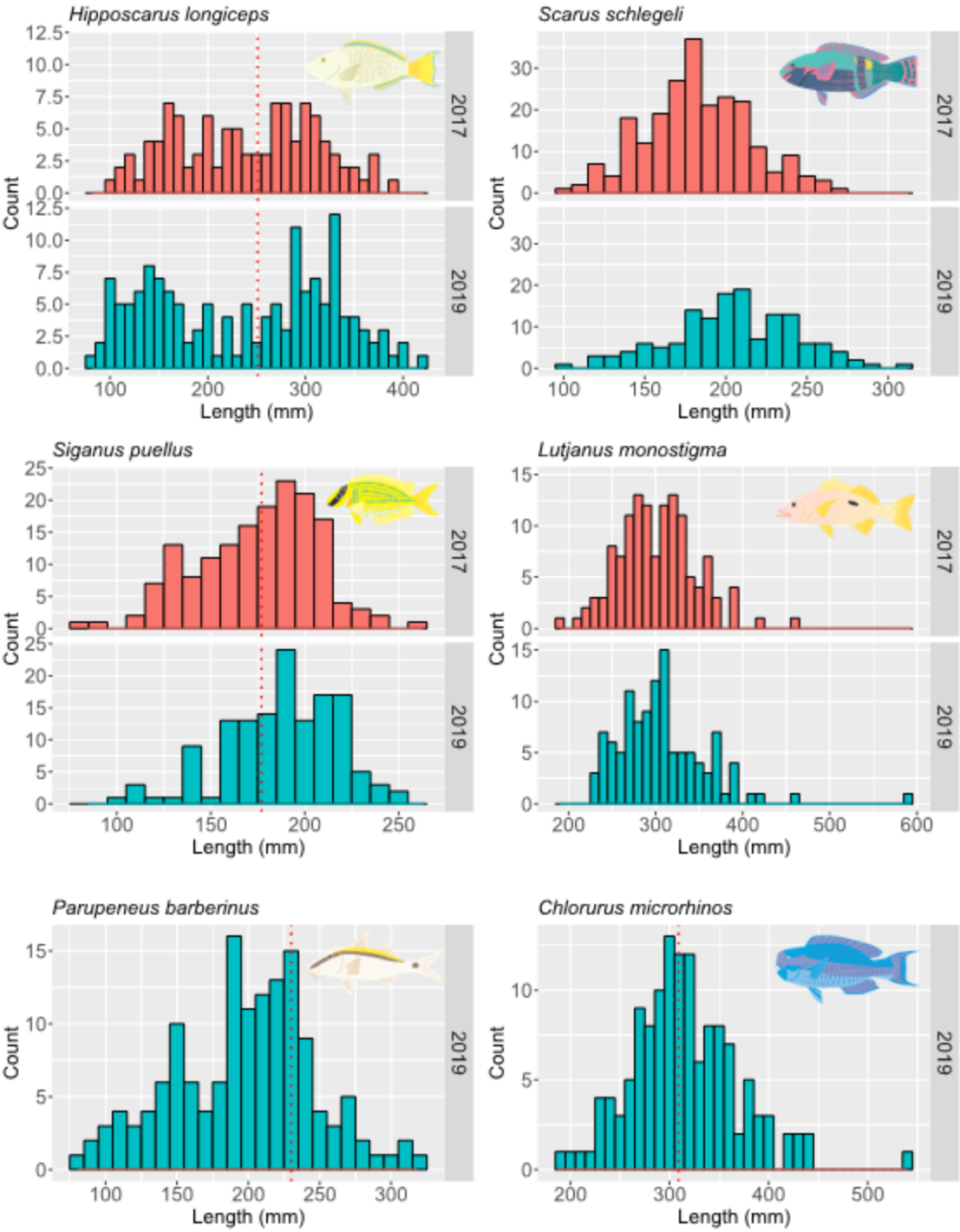
3.2 Size structure

3.2.1 Length-frequency distributions

Size structure was examined for 14 species using length-frequency plots, with lengths for 10 species compared to data collected in 2017 (Figure 10). Length distributions were significantly different between 2017 and 2019 for *L. gibbus* (keremlal) (KS test: $p=0.008$), *C. spilurus* (mellemau) (KS test: $p<0.001$), *C. sexfasciatus* (chesuch) (KS test: $p<0.001$), *Scarus rubroviolaceus* (mesekelat mellemau) (KS test: $p=0.013$), *Scarus schlegeli* (mellemau) (KS test: $p<0.001$) and *Siganus puellus* (reked) (KS test: $p=0.019$). Mean length was significantly different between 2017 and 2019 for *C. spilurus* (mellemau) ($p<0.001$), *C. sexfasciatus* (chesuch)

($p < 0.001$), *Scarus rubroviolaceus* (mesekelat mellemau) ($p = 0.006$), *Scarus schlegeli* (mellemau) ($p < 0.001$) and *Siganus puellus* (reked) ($p < 0.001$), with mean length increasing for all species, apart from *C. spilurus* which had a decrease. There was a big shift from smaller to larger fish seen for *C. sexfasciatus* (chesuch) with a mean length of 341 mm in 2017 to 446 mm in 2019. From the eight species where size at maturity values were available in Palau, the percentage of fish below L_{50} ranged from 32% for *Acanthurus nigricauda* (chesengel) to 75% for *Parupeneus barberinus* (bang). Six species out of these were also assessed in 2017, and all species apart from *L. gibbus* showed a decrease in the percentage of fish below L_{50} (Table 3).





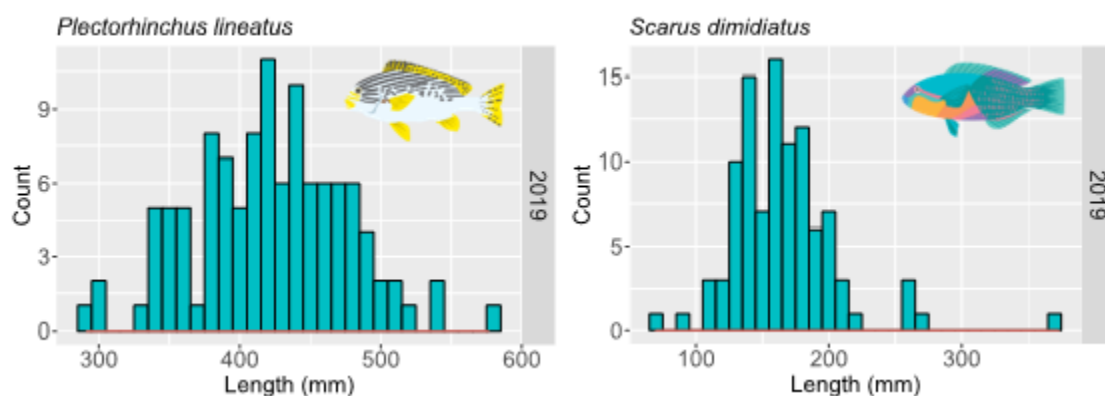


Figure 10. Length-frequency histograms for fourteen species with sufficient length measurements ($n > 100$), with L_{50} shown by red dashed line where available.

Table 3. Size structure of fourteen resource fish species with sufficient actual length measurements.

Species	Palauan name	N	Mean length (mm) 2017	Mean length (mm) 2019	Sig. change in mean length over time	% below L_{50} 2017	% below L_{50} 2019	Sig. change in size structure over time
<i>Lutjanus gibbus</i>	Keremlal	556	248	245	No	45	56	Yes
<i>Chlorurus spilurus</i>	Mellemau	536	183	173	Decrease	No L_{50}	No L_{50}	Yes
<i>Acanthurus nigricauda</i>	Chesengel	419	199	204	No	40	32	No
<i>Caranx sexfasciatus</i>	Chesuch	264	341	446	Increase	No L_{50}	No L_{50}	Yes
<i>Naso lituratus</i>	Cherangel	242	202	206	No	55	48	No
<i>Scarus rubroviolaceus</i>	Mesekelat mellemau	165	260	281	Increase	70	53	Yes
<i>Hipposcarus longiceps</i>	Ngiaoch	148	240	237	No	51	51	No
<i>Scarus schlegeli</i>	Mellemau	144	183	205	Increase	No L_{50}	No L_{50}	Yes
<i>Siganus puellus</i>	Reked	137	175	188	Increase	44	34	Yes
<i>Lutjanus monostigma</i>	Kesebii	114	302	308	No	No L_{50}	No L_{50}	No
<i>Parupeneus barberinus</i>	Bang	144	NA	197	NA	NA	75	NA
<i>Chlorurus microrhinos</i>	Otord	133	NA	315	NA	NA	52	NA
<i>Plectorhinchus lineatus</i>	Yaus	111	NA	422	NA	NA	No L_{50}	NA
<i>Scarus dimidiatus</i>	Mellemau	101	NA	165	NA	NA	No L_{50}	NA

NA = Not assessed

3.2.2 Length-based spawning potential ratio (LB-SPR)

From the eight species which had available life history parameters to calculate LB-SPR, the majority had SPR values above 20% (Table 4). *Hipposcarus longiceps* (ngiaoch) had the highest SPR (90%), but the length-frequency distribution was bi-modal (Figure 8), which 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 reefs and back reefs, and predominantly sub-adult and adult fish recorded on the fore-reefs and channel habitats. When the model was re-run including only fish on the fore-reefs and channel habitats ($n = 74$), SPR was estimated at 51% for 2019. The lowest SPR estimate was observed for *P. barberinus* (bang) (11%), with *Chlorurus microrhinos* (otord) also having a low SPR (18%). SPR estimates increased from 2017 to 2019 for *A. nigricauda* (chesengel), *S. rubroviolaceus* (mesekelat mellemau), *H. longiceps* (ngiaoch) and *S. puellus* (reked), remained the same for *Naso lituratus* (cherangel), and decreased for *L. gibbus* (keremlal) (Table 4).

Table 4. Output from LB-SPR assessment including spawning potential ratio (SPR) from 2017 and 2019 and selectivity-at-length (SL_{50} and SL_{95}) from 2019, measurements are in fork length.

Species	Palauan name	SPR (%) 2017	SPR (%) 2019	SL_{50} (mm) 2019	SL_{95} (mm) 2019
<i>Lutjanus gibbus</i>	Keremlal	35	29	209.26	259.94
<i>Acanthurus nigricauda</i>	Chesengel	38	51	162.41	207
<i>Naso lituratus</i>	Cherangel	20	20	188.93	243.01
<i>Scarus rubroviolaceus</i>	Mesekelat mellemau	21	32	185.31	261.23
<i>Hipposcarus longiceps</i>	Ngiaoch	53 (all data) 34 (excluding inner reefs)	90 (all data) 51 (excluding inner reefs)	84.79	89.32
<i>Parupeneus barberinus</i>	Bang	Not assessed	11	203.82	292.54
<i>Siganus puellus</i>	Reked	16	23	213.47	274.69
<i>Chlorurus microrhinos</i>	Otord	Not assessed	18	267.75	330.76

Note: **Green** SPR >40%, **orange** SPR ≥ 20% and **red** SPR <20%. An SPR of <20% indicates that recruitment rates are impaired.

4. Discussion

4.1 Overall fish biomass

Fish biomass varied considerably across sites in Palau, with differences in hotspots of high biomass seen between 2017 and 2019. In 2017 hotspots were seen mainly in the Northern Reefs and south western fore-reefs, whereas in 2019, hotspots were seen in more locations including

Angaur, the Northern Reefs, the eastern and south eastern fore-reefs and the western and south western fore-reefs. Fish biomass was mainly driven by large schools of fish such as *C. sexfasciatus* (chesuch) and *L. gibbus* (keremlal) in both years. It is important to note that each site was only surveyed once in each survey period and therefore values of fish biomass only provide a snapshot in time. Although the surveys both started at the same time of year (February), the sites were not surveyed in the same order and had different durations, due to logistical and weather restrictions. The 2017 survey ran from February to September whereas the 2019 survey ran from February to October, with a few missed sites sampled in May 2020.

Seasonal variations in fish abundance may occur due to the presence of spawning aggregations and other environmental factors. Many fish species are known to form spawning aggregations in specific months/moon phases and locations in Palau (e.g. groupers from April to July) (Sadovy, 2007). This could have affected measured fish biomass values at some sites located close to spawning aggregation sites, however the differences in fish biomass were mainly driven by species which commonly form large schools. It can be difficult to estimate the number of fish in a school and to only include the fish that lie within the transect boundaries, therefore differences between the two survey periods could also be caused by differences between observer estimates.

The slight increase in fish biomass seen from 2017 to 2019 appears to be caused by the significant increase in herbivores over time, which is a good sign for Palau's coral reef ecosystems. 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).

These results could indicate that reef fish biomass is recovering in reefs located around Palau, however since there are no comparable historic estimates for commercially important reef fish it is difficult to assess how well the stocks are doing, highlighting the importance of this study. Commercially important fish biomass values are comparable to data from other Pacific Island nations. For example, a study done in Hawaii found that total fish biomass of target fish species (reef species targeted or regularly exploited in the Main Hawaiian Islands) ranged from ~16 g m⁻² to ~88 g m⁻² across sites, with an average biomass of 46 g m⁻² in remote/inaccessible locations and 20.9 g m⁻² in accessible/populous locations (Williams et al., 2008). However, the target fish list used is different to the list used in this study, therefore these values only provide a rough

comparison. In terms of theoretical values, 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 reef fish biomass in the absence of fishing should equal $\sim 100 \text{ g m}^{-2}$, with biomass $<25 \text{ g m}^{-2}$ potentially leading to negative ecosystem effects due to overexploitation. In 2017, 78 out of the 94 sites had a biomass $<25 \text{ g m}^{-2}$ (averaged across depth), suggesting 83% of sites were overexploited. In 2019, slightly fewer sites (75 out of 94) had a biomass $<25 \text{ g m}^{-2}$, suggesting 80% of sites may be overexploited. Estimates of fish biomass 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 (Appendix 1), therefore biomass values may not be directly comparable. 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, even when only looking at fore-reef sites in this study, in order to get a more direct comparison, 62% of sites had a total fish biomass lower than 25 g m^{-2} .

The majority of sites in this study also had much lower values of fish biomass compared to values measured inside MPAs in Palau. In 2014, Friedlander et al. (2017) surveyed seven MPAs across Palau and found that total resource fish biomass ranged from $\sim 80 \text{ g m}^{-2}$ (patch reef habitat) to $\sim 360 \text{ g m}^{-2}$ (channel habitat). Only six sites in this study had a total fish biomass $>80 \text{ g m}^{-2}$ in 2019. 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. There are advantages and disadvantages to using both methods and these may result in different fish biomass estimates. UVC has been shown to overestimate biomass due to slower swimming speeds, allowing larger species to move into the transect boundaries (Ward-Paige et al., 2010). UVC has also been shown to record higher abundances of larger bodied fisheries species due to visual observers having a greater ability to recognize fish at the edge of visibility (Holmes et al., 2013). Stereo-DOV has limitations on the number of actual measurements collected, with this study only able to measure $\sim 50 \%$ of fish, however 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). Despite these differences, studies have found that the total abundance and biomass of fish were similar between UVC and

stereo-DOV (Holmes et al., 2013; Wilson et al., 2018) and estimates should be broadly comparable when examined at higher taxonomic levels. Along with the added benefit of accurate length measurements, these results provide an important reference point from which large-scale changes in the amount of fish observed on Palau's coral reefs can be evaluated.

4.2 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 the western facing fore-reefs, and the lowest biomass observed in the inner reefs (patch reefs, fringing inner reefs and back-reefs). The same results were found when the 2017 data was analyzed separately (Muller-Karanassos et al., 2020; 2021). Previous studies have also found lower fish biomass in the inner reefs of Palau, which tend to have lower habitat complexity compared to the outer reefs (Gouezo et al., 2019). Western facing reefs have also been found to have 10-fold higher herbivore biomass and 17-fold higher predator biomass compared to eastern facing reefs (Roff et al., 2019). 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 may be due to the proximity of spawning aggregation sites (Colin, 2012). In addition, a 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.

Higher fish biomass was found in shallow transects compared to deep transects, however differences were not seen between depths within habitats. Other studies have also found that fish density and diversity decrease with increasing depth in coral reef ecosystems (e.g. Jankowski et al., 2015; MacDonald et al., 2016). Comparatively, Pereira et al. (2018) found the opposite effect, with higher fish abundance, species richness and larger fish found in deep reefs (>25 m) compared to shallow reefs (<6 m). In this study, mean biomass in the deep and shallow were similar (~20 g m⁻² for both), therefore the effect of depth doesn't seem to be an important predictor of fish biomass.

Region was not found to significantly predict fish biomass, when the 2017 and 2019 data were combined. In 2017, the Northern Reefs were found to have significantly higher biomass compared to reefs around Babeldaob. The interpolation map from 2019 showed hotspots of high biomass at reefs in all three regions, which explains why region was not a significant predictor when the 2019 data was included in the analysis.

When habitats were analyzed separately, fish biomass at channel sites was positively influenced by MPA proximity, with fish biomass increasing closer to larger MPAs. This is the same result that was found for the 2017 data alone. Spillover of fish could explain the higher fish biomass seen in channel habitats that are in close proximity to MPAs (McClanahan and Mangi, 2000). 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). However, MPAs only had a significant effect in the channel habitat. This 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 the Ebiil Channel Marine Conservation Area, two sites are ~1 km from the center of the Ngederrak Reef Conservation Area and one site is ~1 km from the center of the Ngerumekaol Spawning Area. 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 in or 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. Fish biomass at eastern fore-reef sites were also significantly affected by MPA proximity, however the relationship was negative instead of positive.

Western fore-reef and inner reef habitats were significantly affected by depth. Mean biomass was similar between depths for the inner reef sites, however in the fore-reef west sites, biomass was higher in the shallow compared to deep transects. This could be due to changes in habitat availability and complexity with increasing depth, leading to differences in reef fish composition (MacDonald et al., 2016). Biomass in the inner reefs was also significantly affected by fishing pressure from Koror, which was also the case for the 2017 data alone. Fish biomass decreased as fishing pressure increased, suggesting inner reefs located closer to Koror have higher fishing pressure and therefore lower total fish biomass. A previous study conducted across several Pacific islands, found that total reef fish biomass was lowest at densely-populated islands and highest (4x more fish biomass) on reefs distant from human populations, with fishing pressure identified as one of the main driving factors (Williams et al., 2010). This suggests that fishing pressure from Koror is mainly affecting fish biomass in the inner reef sites compared to the other habitats. The inner reefs are more accessible to fishermen since they require travelling a shorter distance and are less exposed than the outer reefs. However, wave energy, which is a proxy for accessibility, was only slightly significant in the channel habitat.

4.3 Size structure

The size structure of several species changed from 2017 to 2019, with most showing a shift to larger fish (e.g. *C. sexfasciatus* - chesuch), indicating recovery of these species. Large fish are important for population replenishment because they produce more eggs which are larger compared to smaller fish (Barneche et al., 2018). However, *L. gibbus* (keremlal) showed a shift to smaller size classes over time, also reflected by a decrease in SPR, which could indicate overfishing of larger fish for this species (Robinson et al., 2016). In addition, *P. barberinus* (bang), which was not assessed in 2017, had a high percentage of immature fish. The changes in size structure seen between survey periods could also be caused by differences in the number of length measurements, since having a larger sample size increases the precision of results. For example, in 2017, *C. sexfasciatus* (chesuch) had a lower sample size of 101 compared to 2019, which had 264 measurements.

Due to low sample sizes of fish measured and limited availability of locally derived size at maturity values, only eight out of the 100 species observed were assessed for SPR. The majority of assessed species had an SPR $\geq 20\%$, indicating there is enough spawning biomass for populations to replenish themselves, but most were still below SPR 40%, which would equate to maximum sustainable yield in fisheries (Mace, 1994). SPR estimates also increased over time for most species which had data for 2017 and 2019 indicating recovery over time. However, *P. barberinus* (bang) and *C. microrhinos* (otord) had low SPR estimates $< 20\%$ indicating heavy fishing pressure on these species, although the sample sizes for these two species were low (< 150). Updated family-based life-history ratios (J. Prince 2021, pers. comm., 7 April) and updated size at maturity values for *H. longiceps* (ngiaoch) (Lindfield, Coral Reef Research Foundation, unpublished data) were used, so these fishery-independent SPR assessments are not directly comparable to previous assessments in Palau (Prince et al., 2015; Prince, 2016a). In addition, this study used fishery-independent data for LB-SPR assessments, not following the typical use of catch data for fishery assessments, which can lead to differences in SPR estimates. For example, *H. longiceps* (ngiaoch) had a bi-modal size distribution due to fringing inner reefs, patch reefs and back reefs being dominated by small (< 200 mm) individuals. Since 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 equally to juveniles, which would not be the case in nature, leading to a higher SPR estimate.

Although sampling programs in Palau have aimed to collect life history data to inform stock assessments (Prince et al., 2015; Prince, 2016a, 2016b), ongoing data collection will continue to improve the accuracy of assessments. This is especially true for *S. rubroviolaceus* (mesekelat

mellemau) and *S. puellus* (reked) where size at maturity estimates used in this study are considered preliminary. In addition to life history data, increasing the sample size of length measurements would improve the precision of assessments as all species had less than the optimal sample size of 1000 fish (Hordyk et al., 2015). This study made the assumption that fish originated from the same stock for all species assessed as in Prince (2016a), since dividing the data would reduce sample sizes, and therefore, accuracy of the data. Overall, the application of LB-SPR to the fishery-independent data provides another useful metric to track changes over time and assess the recovery of fish populations with improving management.

5. Conclusions

The results from this study indicate that reef fish biomass in the fished waters of Palau is still generally low in comparison to local MPAs and theoretical estimates of productivity; however, the increase in herbivores over time could be an indication that fish stocks are starting to recover. Habitat was the most important predictor of fish biomass with the western facing fore-reefs supporting the highest biomass of resource reef fish. Proximity to MPA was significant only in the channel habitat, whereas fishing pressure from Koror was only significant in the inner reef habitat, reaffirming the results from 2017. SPR estimates showed that most stocks should be maintaining biomass, but some species may be overexploited. These results highlight the need for improved fisheries management to regulate the harvest of commercially important reef species. Some management suggestions include increasing the size of MPAs to make sure fish species with larger home ranges are being protected, improving enforcement, and potentially developing size limits for species with low SPRs. A third survey was completed in May 2021, and monitoring will continue every two years, which will provide more information on whether fish stocks are improving, remaining stable or declining.

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Appendices

Appendix 1. List of reef fish species used in surveys.

Family	Taxa	Trophic level	a	b	Source
Acanthuridae	<i>Acanthurus</i> spp.	Herbivore	0.028	2.983	1
	<i>Acanthurus nigricauda</i>	Herbivore	0.0525	2.77	2
	<i>Acanthurus xanthopterus</i>	Herbivore	0.033	2.92	2
	<i>Naso</i> spp.	Herbivore	0.0085	3.25	1
	<i>Naso lituratus</i>	Herbivore	0.0205	3.05	2
	<i>Naso unicornis</i>	Herbivore	0.0267	2.92	2
Carangidae	<i>Carangoides</i> spp.	Piscivore	0.0361	2.812	1
	<i>Carangoides ferdau</i>	Piscivore	0.0316	2.91	2
	<i>Carangoides fulvoguttatus</i>	Piscivore	0.0329	2.808	1
	<i>Carangoides orthogrammus</i>	Piscivore	0.0223	2.98	2
	<i>Carangoides plagiotaenia</i>	Piscivore	0.0782	2.598	5
	<i>Caranx</i> spp.	Piscivore	0.0198	2.986	1
	<i>Caranx ignobilis</i>	Piscivore	0.0164	3.059	1
	<i>Caranx lugubris</i>	Piscivore	0.025	2.94	2
	<i>Caranx melampygus</i>	Piscivore	0.0228	2.95	2
	<i>Caranx sexfasciatus</i>	Piscivore	0.0501	2.71	2
	<i>Elagatis bipinnulata</i>	Piscivore	0.01	2.85	3
	<i>Trachinotus blochii</i>	Secondary Consumer	0.02951	2.8	3
Chanidae	<i>Chanos chanos</i>	Herbivore	0.0047	3.389	1
Haemulidae	<i>Diagramma pictum</i>	Secondary Consumer	0.0144	2.988	1
	<i>Plectorhinchus</i> spp.	Secondary Consumer	0.0197	2.969	1
	<i>Plectorhinchus albovittatus</i>	Secondary Consumer	0.0197	2.969	1 - <i>Plectorhinchus</i> spp.
	<i>Plectorhinchus chaetodonoides</i>	Secondary Consumer	0.0173	3.04	1
	<i>Plectorhinchus chrysotaenia</i>	Secondary Consumer	0.0197	2.969	1 - <i>Plectorhinchus</i> spp.
	<i>Plectorhinchus gibbosus</i>	Secondary Consumer	0.0226	2.962	1
	<i>Plectorhinchus lessonii</i>	Secondary Consumer	0.0197	2.969	1 - <i>Plectorhinchus</i> spp.
	<i>Plectorhinchus lineatus</i>	Secondary Consumer	0.0126	3.079	1
	<i>Plectorhinchus picus</i>	Secondary Consumer	0.00683	3.23	2

	<i>Plectorhinchus vittatus</i>	Secondary Consumer	0.0197	2.969	1 - <i>Plectorhinchus</i> spp.
Kyphosidae	<i>Kyphosus</i> spp.	Herbivore	0.0129	3.151	1
	<i>Kyphosus cinerascens</i>	Herbivore	0.0306	2.94	2
	<i>Kyphosus vaigiensis</i>	Herbivore	0.031	2.93	2
Labridae	<i>Cheilinus undulatus</i>	Secondary Consumer	0.0184	3.02	2
	<i>Choerodon anchorago</i>	Secondary consumer	0.01862	3.08	3
Lethrinidae	<i>Gymnocranius</i> spp.	Secondary Consumer	0.0302	2.909	1
	<i>Lethrinus</i> spp.	Secondary Consumer	0.0165	3.043	1
	<i>Lethrinus atkinsoni</i>	Secondary Consumer	0.0227	3	2
	<i>Lethrinus erythracanthus</i>	Secondary Consumer	0.0183	3.02	2
	<i>Lethrinus erythropterus</i>	Secondary Consumer	0.0103	3.417	5
	<i>Lethrinus harak</i>	Secondary Consumer	0.0281	2.89	2
	<i>Lethrinus obsoletus</i>	Secondary Consumer	0.0165	3.06	2
	<i>Lethrinus olivaceus</i>	Secondary Consumer	0.02	2.93	2
	<i>Lethrinus ornatus</i>	Secondary Consumer	0.0293	3.067	5
	<i>Lethrinus rubrioperculatus</i>	Secondary Consumer	0.0228	2.94	2
	<i>Lethrinus xanthochilus</i>	Secondary Consumer	0.0179	3	2
	<i>Monotaxis grandoculis</i>	Secondary Consumer	0.023	3.022	1
Lutjanidae	<i>Aprion virescens</i>	Piscivore	0.0241	2.89	2
	<i>Lutjanus</i> spp.	Secondary Consumer	0.0151	3.057	1
	<i>Lutjanus argentimaculatus</i>	Secondary Consumer	0.0188	2.96	2
	<i>Lutjanus bohar</i>	Piscivore	0.0156	3.059	1
	<i>Lutjanus ehrenbergii</i>	Secondary Consumer	0.0367	2.96	5
	<i>Lutjanus fulvus</i>	Secondary Consumer	0.0134	3.12	2
	<i>Lutjanus gibbus</i>	Secondary Consumer	0.0176	3.06	2
	<i>Lutjanus monostigma</i>	Piscivore	0.0222	2.913	1
	<i>Lutjanus rivulatus</i>	Piscivore	0.0084	3.02	1
	<i>Symphoricichthys spilurus</i>	Secondary Consumer	0.0123	3.03	3
Mugilidae	<i>Ellochelon vaigiensis</i>	Secondary Consumer	0.0141	3.023	1 - <i>Liza</i> spp.

	<i>Crenimugil seheli</i>	Secondary Consumer	0.0061	3.275	1
Mullidae	<i>Parupeneus</i> spp.	Secondary Consumer	0.0145	3.13	1
	<i>Parupeneus barberinus</i>	Secondary Consumer	0.0233	2.93	2
	<i>Parupeneus cyclostomus</i>	Piscivore	0.0136	3.11	2
	<i>Bolbometopon muricatum</i>	Secondary Consumer	0.01413	3.04	3
Scaridae	<i>Cetoscarus ocellatus</i>	Herbivore	0.0276	2.92	2 - <i>Cetoscarus bicolor</i>
	<i>Chlorurus</i> spp.	Herbivore	0.0234	2.956	1 - <i>Scarus</i> spp.
	<i>Chlorurus bleekeri</i>	Herbivore	0.0415	2.946	5
	<i>Chlorurus frontalis</i>	Herbivore	0.0172	3.08	2
	<i>Chlorurus japanensis</i>	Herbivore	0.01413	3.04	3
	<i>Chlorurus microrhinos</i>	Herbivore	0.0174	3.07	2
	<i>Chlorurus spilurus</i>	Herbivore	0.02	3.04	2
	<i>Hipposcarus longiceps</i>	Herbivore	0.0161	3.05	2
	<i>Scarus</i> spp.	Herbivore	0.0234	2.956	1 - <i>Scarus</i> spp.
	<i>Scarus altipinnis</i>	Herbivore	0.0206	3	2
	<i>Scarus chameleon</i>	Herbivore	0.0234	2.956	1 - <i>Scarus</i> spp.
	<i>Scarus dimidiatus</i>	Herbivore	0.0278	3.049	5
	<i>Scarus flavipectoralis</i>	Herbivore	0.0228	3.134	5
	<i>Scarus forsteni</i>	Herbivore	0.0142	3.13	2
	<i>Scarus frenatus</i>	Herbivore	0.02089	3.09	3
	<i>Scarus ghobban</i>	Herbivore	0.02	2.99	2
	<i>Scarus globiceps</i>	Herbivore	0.0162	3.09	2
	<i>Scarus niger</i>	Herbivore	0.0134	3.16	1
	<i>Scarus oviceps</i>	Herbivore	0.0144	3.14	4
	<i>Scarus prasiognathos</i>	Herbivore	0.0234	2.956	1 - <i>Scarus</i> spp.
	<i>Scarus psittacus</i>	Herbivore	0.0141	3.14	2
	<i>Scarus quoyi</i>	Herbivore	0.0565	2.818	5
	<i>Scarus rivulatus</i>	Herbivore	0.0175	3.074	1
	<i>Scarus rubroviolaceus</i>	Herbivore	0.0114	3.18	2
	<i>Scarus schlegeli</i>	Herbivore	0.0187	3.03	2
	<i>Scarus spinus</i>	Herbivore	0.0234	2.956	1 - <i>Scarus</i> spp.
	<i>Scarus tricolor</i>	Herbivore	0.0229	3.106	5
	<i>Scarus xanthopleura</i>	Herbivore	0.0234	2.956	1 - <i>Scarus</i> spp.
Scombridae	<i>Grammatorcynus bilineatus</i>	Piscivore	0.00647	3	3
	<i>Gymnosarda unicolor</i>	Piscivore	0.01047	3.05	3
	<i>Scomberomorus commerson</i>	Piscivore	0.0162	2.856	1

Serranidae	<i>Aethaloperca rogaa</i>	Piscivore	0.0066	3.277	1 - <i>Cephalopholis sonnerati</i>
	<i>Anyperodon leucogrammicus</i>	Piscivore	0.0014	3.548	1
	<i>Cephalopholis</i> spp.	Piscivore	0.0115	3.109	1
	<i>Cephalopholis argus</i>	Piscivore	0.0119	3.13	2
	<i>Cephalopholis cyanostigma</i>	Piscivore	0.0345	2.944	5
	<i>Cephalopholis miniata</i>	Piscivore	0.0107	3.114	1
	<i>Cephalopholis sonnerati</i>	Piscivore	0.0066	3.277	1
	<i>Cromileptes altivelis</i>	Piscivore	0.0962	2.489	1
	<i>Epinephelus</i> spp.	Piscivore	0.0122	3.053	1
	<i>Epinephelus coeruleopunctatus</i>	Secondary Consumer	0.018	2.938	1
	<i>Epinephelus corallicola</i>	Piscivore	0.01363	3	3
	<i>Epinephelus fuscoguttatus</i>	Piscivore	0.0134	3.057	1
	<i>Epinephelus melanostigma</i>	Piscivore	0.01633	3	3
	<i>Epinephelus polyphekadion</i>	Secondary Consumer	0.0106	3.14	2
	<i>Gracila albomarginata</i>	Piscivore	0.0122	3.053	1 - <i>Epinephelus</i> spp.
	<i>Plectropomus</i> spp.	Piscivore	0.0107	3.086	1
	<i>Plectropomus areolatus</i>	Piscivore	0.0107	3.086	1 - <i>Plectropomus</i> spp.
	<i>Plectropomus laevis</i>	Piscivore	0.0059	3.238	1
	<i>Plectropomus leopardus</i>	Piscivore	0.00846	3.16	2
	<i>Plectropomus oligacanthus</i>	Piscivore	0.0155	2.9721	4
	<i>Variola albimarginata</i>	Piscivore	0.0187	3	2
	<i>Variola louti</i>	Piscivore	0.013	3.09	2
Siganidae	<i>Siganus</i> spp.	Herbivore	0.0145	3.122	1
	<i>Siganus argenteus</i>	Herbivore	0.0153	3.06	2
	<i>Siganus corallinus</i>	Herbivore	0.0023	3.821	1
	<i>Siganus doliatus</i>	Herbivore	0.0104	3.272	1
	<i>Siganus fuscescens</i>	Herbivore	0.0137	3.068	1
	<i>Siganus lineatus</i>	Herbivore	0.0219	2.998	1
	<i>Siganus puellus</i>	Herbivore	0.0176	3.028	1
	<i>Siganus punctatissimus</i>	Herbivore	0.0145	3.122	1 - <i>Siganus</i> spp.
	<i>Siganus punctatus</i>	Herbivore	0.0199	3.07	2
Sphyraenidae	<i>Sphyraena barracuda</i>	Piscivore	0.0062	3.011	1
	<i>Sphyraena forsteri</i>	Piscivore	0.0053	3.034	1

	<i>Sphyraena qenie</i>	Piscivore	0.0058	3.013	1 - <i>Sphyraena</i> spp.
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1 Kulbicki et al. (2005)

2 Kamikawa et al. (2015)

3 Froese and Pauly (2019) (FishBase)

4 Cuetos-Bueno & Hernandez-Ortiz (2017)

5 Gumanao et al. (2016)

Appendix 2. List of commercially important reef fish observed during this study including total biomass, abundance and frequency of occurrence.

Species	Abundance	Total biomass (g/m ²)	Frequency of occurrence (%)
<i>Acanthurus nigricauda</i>	841	117.08	51.67
<i>Acanthurus</i> spp.	59	8.34	6.11
<i>Acanthurus xanthopterus</i>	5	2.33	1.11
<i>Aethaloperca rogaa</i>	17	1.56	8.89
<i>Anyperodon leucogrammicus</i>	1	0.41	0.56
<i>Aprion virescens</i>	4	11.53	2.22
<i>Bolbometopon muricatum</i>	80	252.58	15.56
<i>Carangidae</i> spp.	2	1.83	0.56
<i>Carangoides ferdau</i>	14	31.88	3.33
<i>Carangoides orthogrammus</i>	1	1.36	0.56
<i>Carangoides</i> spp.	8	11.20	3.33
<i>Caranx lugubris</i>	1	0.29	0.56
<i>Caranx melampygus</i>	27	24.82	8.33
<i>Caranx sexfasciatus</i>	938	850.99	5.56
<i>Caranx</i> spp.	3	4.91	1.67
<i>Cephalopholis argus</i>	79	12.91	26.11
<i>Cephalopholis</i> spp.	12	1.48	5.56
<i>Cetoscarus ocellatus</i>	62	33.00	17.78
<i>Cheilinus undulatus</i>	40	39.53	17.78
<i>Chlorurus bleekeri</i>	32	6.83	11.67
<i>Chlorurus microrhinos</i>	149	75.72	23.89
<i>Chlorurus spilurus</i>	705	58.97	63.33
<i>Choerodon anchorago</i>	12	1.06	5.56
<i>Cromileptes altivelis</i>	1	1.68	0.56
<i>Elagatis bipinnulata</i>	1	0.40	0.56
<i>Epinephelus corallicola</i>	1	0.34	0.56
<i>Epinephelus fuscoguttatus</i>	2	2.93	1.11
<i>Epinephelus polyphekadion</i>	3	2.52	1.67
<i>Epinephelus</i> spp.	4	1.52	2.22
<i>Gracila albomarginata</i>	7	1.77	3.89
<i>Gymnosarda unicolor</i>	2	8.12	1.11
<i>Haemulidae</i> spp.	1	0.58	0.56
<i>Hipposcarus longiceps</i>	245	48.84	38.89
<i>Kyphosus cinerascens</i>	3	0.43	1.11
<i>Kyphosus</i> spp.	114	52.26	4.44
<i>Kyphosus vaigiensis</i>	176	92.14	7.78
<i>Labridae</i> spp.	1	0.31	0.56
<i>Lethrinus erythropterus</i>	26	8.61	10.56

<i>Lethrinus harak</i>	3	0.58	1.11
<i>Lethrinus obsoletus</i>	15	3.13	6.67
<i>Lethrinus olivaceus</i>	19	17.22	5.56
<i>Lethrinus</i> spp.	30	5.95	10.00
<i>Lethrinus xanthurus</i>	2	0.26	0.56
<i>Lutjanus bohar</i>	95	98.98	23.33
<i>Lutjanus ehrenbergii</i>	16	3.14	1.67
<i>Lutjanus fulvus</i>	47	6.46	11.67
<i>Lutjanus gibbus</i>	4117	847.62	54.44
<i>Lutjanus monostigma</i>	178	56.87	19.44
<i>Lutjanus rivulatus</i>	1	0.12	0.56
<i>Lutjanus</i> spp.	4	1.73	0.56
<i>Monotaxis grandoculis</i>	325	61.53	41.67
<i>Naso lituratus</i>	489	66.77	54.44
<i>Naso</i> spp.	3	1.57	1.67
<i>Naso unicornis</i>	14	13.86	4.44
<i>Parupeneus barberinus</i>	226	22.45	50.00
<i>Parupeneus cyclostomus</i>	22	3.51	8.33
<i>Plectorhinchus albobittatus</i>	32	60.52	7.78
<i>Plectorhinchus chaetodonoides</i>	56	38.00	17.78
<i>Plectorhinchus chrysotaenia</i>	21	18.08	1.67
<i>Plectorhinchus gibbosus</i>	3	3.16	0.56
<i>Plectorhinchus lessonii</i>	72	18.89	18.33
<i>Plectorhinchus lineatus</i>	132	105.53	13.33
<i>Plectorhinchus</i> spp.	10	5.70	3.89
<i>Plectorhinchus vittatus</i>	36	10.02	10.56
<i>Plectropomus areolatus</i>	57	14.83	13.89
<i>Plectropomus laevis</i>	3	3.63	1.67
<i>Plectropomus leopardus</i>	100	22.78	23.33
<i>Plectropomus</i> spp.	25	5.13	8.89
Scaridae spp.	4218	268.83	93.33
<i>Scarus altipinnis</i>	1	0.02	0.56
<i>Scarus chameleon</i>	12	1.40	3.33
<i>Scarus dimidiatus</i>	134	14.63	20.56
<i>Scarus flavipectoralis</i>	16	1.87	4.44
<i>Scarus forsteni</i>	102	18.08	23.89
<i>Scarus frenatus</i>	25	10.10	7.78
<i>Scarus ghobban</i>	27	5.85	10.56
<i>Scarus globiceps</i>	20	2.37	1.67
<i>Scarus niger</i>	80	9.97	11.67
<i>Scarus oviceps</i>	92	14.68	24.44

<i>Scarus prasiognathos</i>	40	14.89	13.89
<i>Scarus psittacus</i>	4	0.45	1.67
<i>Scarus rubroviolaceus</i>	222	76.17	33.33
<i>Scarus schlegeli</i>	163	20.62	36.11
<i>Scarus spinus</i>	40	4.84	13.33
<i>Scarus tricolor</i>	2	1.90	1.11
Serranidae spp.	2	0.63	1.11
<i>Siganus argenteus</i>	116	14.10	9.44
<i>Siganus corallinus</i>	11	1.25	3.33
<i>Siganus doliatus</i>	77	5.81	15.56
<i>Siganus fuscescens</i>	2	0.50	0.56
<i>Siganus lineatus</i>	35	10.21	2.78
<i>Siganus puellus</i>	220	18.92	42.22
<i>Siganus punctatissimus</i>	61	4.15	15.00
<i>Siganus punctatus</i>	92	12.28	26.67
<i>Siganus</i> spp.	37	1.92	9.44
<i>Sphyræna barracuda</i>	1	2.92	0.56
<i>Variola albimarginata</i>	1	0.16	0.56
<i>Variola louti</i>	35	15.36	14.44
<i>Variola</i> spp.	1	0.33	0.56