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Modelling and mapping regional-scale patterns of fishing impact and fish stocks to support coral-reef management in Micronesia

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BIOSKETCH

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Modelling and mapping regional-scale patterns of fishing impact and fish stocks to support coral-reef management in Micronesia

Running title: Mapping Micronesian fishing and fishes

ABSTRACT

Aim: Use a fishery-independent metric to model and map regional-scale fishing impact, and demonstrate how this metric assists with modelling current and potential fish biomass to support coral-reef management. We also examine the relative importance of anthropogenic and natural factors on fishes at biogeographical scales.

Location: Reefs of five jurisdictions in Micronesia.

Methods: A subset of 1127 fish surveys (470 sites) was used to calculate site-specific mean parrotfish lengths (a proxy for cumulative fishing impact), which were modelled against 20 biophysical and anthropogenic variables. The resulting model was extrapolated to each 1 ha reef cell in the region to generate a fishing impact map. The remaining data (657 sites) were then used to model fish biomass using 15 response variables, including fishing impact. This model was used to map estimated current regional fish standing stocks and, by setting fishing impact to 0, potential standing stocks.

Results: Human population pressure and distance to port were key anthropogenic variables predicting fishing impact. Total fish biomass was negatively correlated with fishing, but the influence of natural gradients of primary productivity, sea surface temperature, habitat quality, and larval supply were regionally more important.

Main conclusions: Mean parrotfish length appears to be a useful fishery-independent metric for modelling Pacific fishing impact, but considering environmental covariates is critical. Explicitly modelling fishing impact has multiple benefits, including generation of the first large-scale map of tropical fishing impacts that can inform conservation planning. Using fishing impact data to map current and potential fish stocks provides further benefits, including highlighting the relative importance of fishing on fish biomass and identifying key biophysical variables that cause maximum potential biomass to vary significantly across the region. Regional-scale maps of fishing, fish standing stocks, and the potential benefits of protection are likely to lead to improved conservation outcomes during reserve network planning.

Keywords

Biophysical gradients, Boosted regression trees, Coral reef fishes, Fish standing stocks, Fishing impact, Marine reserves, Marine spatial planning, Micronesia

1 INTRODUCTION

The myriad anthropogenic stressors that affect the world's oceans have led to immense efforts to conserve the ecosystem services they provide (Mora et al., 2006; Halpern et al., 2008). Fisheries are often a key target of these management initiatives, particularly in the tropics and subtropics where coral reefs provide food, livelihoods, and incomes for millions of people (Sadovy, 2005). Typically, efforts to sustainably manage reef fishes strive for networks of no-take marine reserves that have a variety of benefits, including rebuilding populations and exporting individuals to fished areas (Graham et al., 2011). Designing these networks effectively often requires matching multiple biological and social criteria (Sala et al., 2002; Fernandes et al., 2005), and there are sophisticated computational tools to assist spatial planning (Ball, Possingham, & Watts, 2009; Krueck et al., 2017). However, these design tools rely on the availability of spatially comprehensive, good-quality data, and a lack of data layers often limits the planning process (Pittman, & Brown, 2011). This scarcity of comprehensive data is particularly problematic for regional-scale initiatives that have been established in areas such as the Caribbean (Knowles et al., 2015), Micronesia (Houk et al., 2015), and Coral Triangle (White et al., 2014).

The increasing availability of extensive online data offers a potential solution for at least some of the data requirements for marine spatial planning (Pittman, & Brown, 2011; Sbrocco, & Barber, 2013). Furthermore, these data can be used as key explanatory variables to derive other useful variables. For example, combining multiple biophysical and socioeconomic drivers has facilitated modelling variables including fish biomass and richness (Mellin, Bradshaw, Meekan, & Caley, 2010; McClanahan, Maina, Graham, & Jones, 2016), climate-change impacts (Wolff et al., 2015), and ecosystem services (Hutchison, Manica, Swetnam, Balmford, & Spalding, 2014; Spalding et al., 2017). These derived data layers, particularly fish biomass, can have considerable value for configuring potential regional-scale marine reserve networks (McClanahan et al., 2016). However, maps of fish biomass at a scale and resolution appropriate for regional or national spatial planning remain scarce, and even when available the underlying models may be limited by the difficulties of obtaining data for many key covariates (McClanahan et al., 2016).

While maps of fish biomass are uncommon within marine spatial planning exercises, high-resolution maps of fishing derived from biological or social data are even rarer (e.g. generic distance-to-shore decay functions are used in the few cases where fishing is incorporated, Magris, Treml, Pressey, & Weeks, 2016). The scarcity of these maps is surprising given that reserves are often explicitly designed to manage fisheries. For example, a map of fishing has value for displaying national or regional patterns and "scorecard" assessments of fishery status to a range of stakeholders, facilitating quantitative comparisons within or between countries, providing some information on fishing-derived employment, food security or economic importance, and for monitoring change. Furthermore, a fishing map could be included in spatial planning algorithms to achieve goals such as siting marine reserves in areas with low fishing to minimise conflicts with fishers (Sala et al., 2002). Finally, fishing can be included in a model of fish biomass as a single explicit variable, rather than by using multiple proxies such as human population density and distance to market (e.g. Cinner et al., 2016; McClanahan et al., 2016). Using a single variable of fishing in biomass models, and thus obtaining a single partial dependency plot, facilitates easier visualisation and quantification of important biogeographic questions such as its relative importance in determining fish biomass compared to biophysical gradients. Finally, a single functional relationship between fishing and fish biomass is useful when investigating the impacts of management scenarios, such as reducing fishing to predict the benefits of reserves.

Despite the potential benefits, quantifying coral-reef fishing is challenging because the fisheries are typically characterised by many boats that exploit multiple species using a variety of gear types across large, remote areas (Dunn et al., 2010). Furthermore, many tropical countries have limited resources to monitor fisheries, and there are concerns about some fisheries-dependent data (Pauly, & Zeller, 2014). A few comprehensive fisheries-dependent data sets are available to map reef fishing effort directly, but they are typically at relatively small spatial scales (Chollett, Canty, Box, & Mumby, 2014; Hamilton et al., 2016; Thiault, Collin, Chlous, Gelcich, & Claudet, 2017). Consequently, most large-scale investigations of reef fisheries have used fishery-independent data, particularly examining how human population density correlates with fish biomass recorded in underwater censuses (Williams et al., 2015b; Cinner et al., 2016; McClanahan et al., 2016). These studies have clearly demonstrated the effects of fishing on fish assemblages, but using total biomass has limits such as mixing fished and non-fished species, combining size and abundance metrics that may respond differently to exploitation, and a need for surveys of all non-cryptic species.

Some of the problems associated with using total fish biomass may be addressed by considering individual functional groups or species (e.g. Williams et al., 2015b). However, there is a growing recognition of the value of other indicators of fishing, such as length-based metrics, size-spectra, and mean trophic level (reviewed by Nash, & Graham, 2016). Among these metrics, the derivation of fishing from the sizes of herbivorous species, especially parrotfishes, seems particularly promising. Although parrotfishes are typically secondary targets compared to more valuable species such as grouper (Mumby et al., 2012), large-bodied parrotfishes are often rare on heavily fished reefs, with assemblages shifting towards smaller-bodied species (Clua, & Legendre, 2008; Taylor, Houk, Russ, & Choat, 2014). Consequently, mean parrotfish size, but not density or total biomass, appears to be a better metric of Caribbean fishing than the biomass of some more commercially important species (Vallès, & Oxenford, 2014; Vallès, Gill, & Oxenford, 2015). In addition, parrotfishes are rarely absent even under very high fishing pressure, allowing mean size to be calculated at all sites. Parrotfish data are also routinely recorded during fish surveys because of their functional importance in controlling macroalgal abundance and as bioeroders (e.g. Bellwood, Hughes, Folke, & Nyström, 2004).

This study utilises mean parrotfish size to model the drivers and patterns of fishing impact across Micronesia, and uses the model to generate the first large-scale fishing map and support marine spatial planning in the region. We then show how a map of fishing impact can be used to help map fish biomass across the region to further assist resource management, and provide a single functional relationship between fishing and fish standing stocks. Within the models for both fishing and fish biomass we include an extensive range of biophysical and social covariates that may affect parrotfish size and fish biomass. Approximately 50% of studies considering indicators of fishing have not adequately accounted for these potentially confounding covariates, limiting a full assessment of their use (Nash, & Graham, 2016). Furthermore, this comprehensive investigation of the relative importance of the anthropogenic and biophysical drivers of fish biomass provides new insights into the biogeography of Micronesian fish assemblages. Finally, we utilise the relationship between fishing impact and fish biomass to demonstrate how it can be used to estimate the maximum biomass of fishes on reefs in the absence of fishing, and map the potential benefits of marine reserves that can help identify priority areas for protection.

2 METHODS

2.1 Study area

The study encompassed the spatial extent of the Micronesia Challenge, which aims to conserve >30% of the marine resources by 2020 (Houk et al., 2015). The area consists of five jurisdictions: the Republic of Palau, the Federated States of Micronesia, the Territory of Guam, the Commonwealth of the Northern Marianas, and the Republic of the Marshall Islands (subsequently Palau, FSM, Guam, CNMI, and RMI respectively) (Figure 1). Micronesian reefs are typically found around either atolls or high (volcanic origin) islands with or without extensive lagoons (Dalzell, Adams, & Polunin, 1996; Taylor, Lindfield, & Choat, 2015). Reefs are threatened by overexploitation through subsistence and commercial fisheries, although the status of fisheries varies significantly from populous to uninhabited islands and atolls (Williams et al., 2015b). Throughout the Pacific, surgeonfishes, parrotfishes, groupers, and snappers are the primary fishery targets (Rhodes, & Tupper, 2007; Houk et al., 2012; Bejarano, Golbuu, Sapolu, & Mumby, 2013). To increase the sustainability of these fisheries, some marine protected areas and no-take reserves have been established (Mumby et al., 2013), and are complemented in some locations by seasonal closures of spawning aggregations (Rhodes, & Tupper, 2007) and bans on catching vulnerable species such as the bumphead parrotfish (*Bolbometopon muricatum*) (Houk et al., 2012).

This study focused on fringing, barrier, and atoll reef slopes, which typically support the highest biomass of fishes, are heavily targeted by fishers, and are more commonly surveyed by researchers. These habitats were delineated using the level 4 marine classes of the Millennium Coral Reef Mapping Project that mapped reefs worldwide using Landsat 7 ETM+ satellite images (MCRMP, Andréfouët et al., 2006). Level 4 of the classification scheme includes 39 habitat classes, of which 13 were used for this study (see Appendix S1). Reef slope polygons were rasterised into 320,715 1 ha cells in ArcGIS for association with predictor variables.

2.2 Fish survey data

Reef fish data were derived from 1127 survey sites throughout the region, including each jurisdiction and state within the FSM (see Appendix S1 in Supporting Information). The data were collected for different projects and purposes, and therefore did not utilise a standard methodology (see Appendix S1 for details of data sets). Briefly, all surveys were quantitative counts within defined areas (depths of 1-23 m), facilitating the calculation of fish abundance per unit area, but included visual surveys along belt transects (30 – 50 m in length), visual surveys using stationary point counts (10-15 m in diameter), and video surveys (5 m wide x 3 min long). Although results are typically comparable between belt transects and stationary point counts (Samoilys, & Carlos, 2000), survey method was included in subsequent models to account for any systematic biases. In all surveys, fishes were counted and sized, facilitating calculation of biomass using allometric relationships (Froese, & Pauly, 2010). Coral cover at each site was quantified using photo-quadrats, *in situ* visual assessment of quadrats, video transects, or *in situ* visual estimates. Visual estimates of benthic cover have been demonstrated to be similar to quadrats and transects (Wilson, Graham, & Polunin, 2007).

Surveys were haphazardly separated into two groups for use in the fishing and fish biomass models, ensuring broad geographical coverage throughout the region for each model (470 and 657 sites in the fishing and biomass models respectively). For fishing impact, mean parrotfish length (independent of species identity) was calculated for each site. Family-level mean parrotfish length was calculated from fishes larger than 15 cm to make the analyses robust to recruitment variability. Furthermore, records of *Bolbometopon muricatum* were excluded because they are absent from the Marshall Islands (Froese, & Pauly, 2010) and may skew values elsewhere because of their large size and shoaling behaviour. For the biomass data set, we first identified 19 species that occur throughout the region (Froese, & Pauly, 2010) and were surveyed at every site (two acanthurids, a carangid, a kyphosid, a labrid, three lethrinids, two lutjanids, five scarids, three serranids, and two siganids, see Appendix S1 for species list). Although reducing the data sets to these key species involved using only a subset of the data, it did ensure consistent estimates of current standing stock across the region and among data sets. Furthermore, biomass of these 19 key taxa represents a good proxy of the total assemblage biomass because they represent a range of families and fishery values (see Appendix S1). Abundances of the 19 species at each site were summarised as biomass per m^2 (subsequently ‘total biomass’). Each species was also assigned to a trophic group (primary consumer, secondary consumer, or piscivore, Sandin, & Williams, 2010), and biomass data were summarised for each group. Site-level estimates of mean parrotfish size, total biomass, and biomass of each trophic group were combined with *in situ* data on coral cover, depth, latitude, longitude, and year of collection for inclusion within the models.

2.3 Predictor variables

Additional site-specific predictor variables that may be biophysical or anthropogenic drivers of fishing and fish abundances were compiled to inform the fishing impact and total biomass models (Table 1). The derivation of each predictor at each fish survey site is described in detail in Appendix S2, but briefly the MCRMP map was used to derive the distance to the nearest reef pass (that may provide access for fishers or increase water flow), island geomorphology, and habitat type. The MCRMP map was also used to derive the fetch (distance to land or reef crest) at each location, which was combined with QuikSCAT data (wind direction and mean speed in 25 km^2 cells during 2005 to 2009) using linear wave equations to estimate wave exposure (Chollett, & Mumby, 2012). Finally, the MCRMP map was used to estimate the potential area of fishable reef within both 20 and 200 km of each survey site (see Appendix S1), which were combined with human population size within the same distances to estimate population density per km^2 of reef (i.e. separate populations densities within 20 km and within 200 km). Human population size data was from the Global Rural-Urban Mapping Project within the Socioeconomic Data and Applications Center (SEDAC), and 20 km represents the typical range of local artisanal fishers while 200 km represents the influence of longer-range commercial vessels (Nadon et al., 2012; Williams et al., 2015b). Tourist numbers within 20 and 200 km per km^2 of fishable reef were calculated by using estimates of total arrivals in 2011 and distributing them in proportion to indigenous populations. Other anthropogenic predictors of fishing were distance to the nearest major port (potential market), an expert-based rank (low, medium, high) of reef fish exports by air, an expert-based assessment of the protected status of each reef area (open or effectively open to fishing, partly effective reserve, or effective reserve), and a principle coordinates analysis (PCA) of jurisdiction-scale indicators of socio-economic development (e.g. GDP) that may influence fishing pressure (Cinner et al., 2009). Socio-economic development was then quantified using two predictor variables from the first two axes of the PCA. Oceanic net primary productivity was derived using the mean values from 2010-2013 that were estimated using a chlorophyll-based model (Behrenfeld, & Falkowski, 1997), after removing values confounded by bottom reflectance (Gove et al., 2013). Sea surface temperature data were obtained from the Coral Reef Temperature Anomaly Database, and the metric used was the mean temperature from the coldest month of each year between 2008 and 2012 (following Nadon et al., 2012 and Williams et al., 2015b, where this metric was also highly correlated with other metrics of temperature). Finally, relative larval supply to each reef from upstream sources (excluding self-recruitment) was estimated using a biophysical model (see Mora et al., 2012 for full model description).

2.4 Data analysis

Models of fishing impact, total biomass, and biomass of primary consumers and piscivores (only three of the 19 species were secondary consumers and so this group was not analysed) were generated using boosted regression trees (BRTs) (Elith, Leathwick, & Hastie, 2008). All covariates were first tested for co-linearity (pairwise *r* threshold of 0.75), which led to the removal of latitude, tourist pressure, and the second axis of socio-economic development from the PCA in the fishing model. Latitude was removed from the total biomass model. Variance inflation factors were below recommended limits (Dormann et al., 2013). Covariates were untransformed within the BRTs, but mean parrotfish size, total biomass, and the biomass of each trophic group were log transformed to better fit the assumptions of Gaussian error distributions. BRT parameters (learning rate, tree complexity, and bag fraction) were calculated for each model by testing across a series of values, and then using the values that gave the lowest model deviance (Elith et al., 2008). In addition to covariates, each BRT included a variable comprising of random numbers: variables with less explanatory power than this random number variable were removed to generate final, minimal models (Soykan, Eguchi, Kohin, & Dewar, 2014). Evidence of spatial autocorrelation was examined by testing the residuals of each model with Moran's *I* statistic. Model performance was assessed using the amount of deviance explained and the Pearson's correlation coefficient between observed and model-predicted values.

Fishing impact and fish biomass maps were generated by using final models to predict values for all 1 ha cells on reef slopes. The full fishing impact model predicts the mean size of parrotfishes, which is influenced by biophysical, anthropogenic, and methodological factors. However, mapping fishing impact required isolating the human influence on parrotfish size, and therefore cell-specific values were used for each anthropogenic factor (Table 1), while mean values were used for biophysical variables and year of data collection. Belt transect was used in predictions as the data collection method for all 1 ha cells as it the most common protocol used among the data sets. Predicted values of parrotfish size were back-transformed and then rescaled from 0 (largest mean parrotfish size) to 1 (smallest mean size) before map production. Total biomass and the biomass of each trophic group in each 1 ha cell were predicted using the full final model (i.e. spatially variable values for each 1 ha cell) except for methodological variables (standardised to mean year of collection and collection by belt transect) and coral cover and depth (mean values used in the absence of spatially continuous maps of coral cover or bathymetry). Finally, predictions for the potential biomass in each cell in the absence of fishing were generated using the total biomass model and setting fishing impact to 0 in every cell. This allowed the calculation of the potential absolute and percentage gain in biomass in each cell following reserve establishment.

3 RESULTS

3.1 Fishing impact model

The final model for fishing impact included eight anthropogenic and biophysical variables influencing mean parrotfish size (Figure 2), plus the year of data collection (all partial dependency plots including year, and the largest interaction, are in Figures S3.4 and S3.5 in Appendix S3). The anthropogenic variables of distance to port and population density within 200 km were responsible for ~35% of the explained variance, with mean parrotfish size increasing (fishing decreasing) with increasing distance from port and decreasing population density. The distance to pass variable was considered to represent both an anthropogenic component (reefs far from passes are less accessible to fishers, Thiault et al., 2017) and biophysical component (reefs close to passes may be more productive, Schrimm, Heussner, & Buscail, 2002). Consequently, the relationship with parrotfish size was adjusted to only include the anthropogenic component prior to mapping predicted fishing impact (Figure 2).

The fishing impact model explained 36% of the variability in mean parrotfish length, and the correlation between observed and predicted values was 0.602. There was significant (Moran's I; p =

0.041) spatial autocorrelation among the residuals of the BRT model. However, this correlation was negative with residuals at sites close together more dissimilar than residuals among more distant sites, suggesting spatial autocorrelation was not influencing model performance (Stuart-Smith et al., 2013).

3.2 Biomass models

The final model for total biomass of the 19 focal fish species included 11 anthropogenic, biophysical, and methodological variables (eight most important variables shown in Figure 3; partial dependency plots for data collection year, method, and distance to pass shown, along with the largest interaction, in Figures S3.6 and S3.7 in Appendix S3). The most important correlations were with biophysical variables, and total biomass was particularly high in deeper, cooler, more productive water and on reefs with high larval supply from upstream reefs (Figure 3). Total biomass (log transformed) decreased approximately linearly with increasing fishing, and represented ~7% of the variation explained by the model (Figure 3). The model explained 52% of the variability in total biomass, and the correlation between observed and predicted values was 0.721. There was no significant spatial autocorrelation among model residuals (Moran's I; $p = 0.129$).

The models for primary consumers and piscivores were qualitatively similar to the model for total standing stock (eight most important variables shown in Figures 4 and 5; partial dependency plots for all variables are in Figures S3.8 and S3.9 in Appendix S3). Biomass of primary consumers appeared particularly sensitive to larval supply, and the negative correlation with fishing was stronger (Figure 4). Biomass of piscivores was most clearly correlated with temperature, and piscivores were more abundant on windward reefs and reef with nearby lagoons (potentially containing nursery habitats) (Figure 5). The models explained 50% and 45% of the variability in primary consumer and piscivore biomass respectively, and the correlations between observed and predicted values were 0.708 and 0.669.

3.3 Maps of fishing impact, total biomass, and predicted gain in biomass

Extrapolating values of fishing impact and total biomass throughout the region generated 1 ha resolution maps of each variable (Figures 6a, b). Total biomass was predicted to be generally higher where fishing was predicted as lower, but also reflects the various biophysical gradients within the model (e.g. decreasing temperatures from south to north). Setting fishing impact to 0 allowed the generation of a map of predicted potential biomass in each cell, and the percentage potential gain in biomass following the cessation of fishing (Figures 6c, d). Potential percentage gains in standing stock were predicted to be highest where fishing was predicted to be highest (e.g. Guam), but absolute increases were constrained by biophysical gradients. The maps also facilitated jurisdictional summaries of fishing and fish stocks, which are likely to be valuable tools for outreach to a range of stakeholders (Figure 7). Additional maps for primary consumers and piscivores were also generated (see Appendix S3).

Using a correlative relationship between the total biomass of all species and the 19 focal species used in this study, calculated from the large NOAA CRED data set, mean current standing biomass and mean potential biomass for all non-cryptic fishes across all cells were 497 kg ha^{-1} and 567 kg ha^{-1}. However, these values were sensitive to the values assumed for coral cover and depth (mean values were 21.7% and 6.0 m respectively). For example, estimating potential standing stock at a depth of 10 m, which is a typical survey depth for many other studies, generated a regional mean of 841 kg ha^{-1}. In the most biomass-rich waters the means using a depth of 10 m were 1066 (RMI) and 1070 kg ha^{-1} (Palau), which are close to global averages (1000 kg ha^{-1}, MacNeil et al., 2015). Future generation of maps of bathymetry and coral cover would significantly aid mapping fish stocks across the region.

4 DISCUSSION

A strength of marine reserve selection algorithms, namely the simultaneous analysis of multiple spatially explicit data layers to identify priority areas, is also a weakness because of the reliance on comprehensive data sets that are often onerous or impossible to collect. Fishing is a good example of spatial information that is rarely available to planners (Thiault et al., 2017), even though fish production represents one of the major ecosystem services driving tropical conservation (Russ, 2002). Here we build on previous work that has used fishery-independent data to identify the major drivers of human impacts on fish assemblages, but show how modelling fishing as a separate, first step towards modelling fish biomass can produce an additional data layer that has a range of ecological, biogeographical, and conservation uses.

We deliberately use the term fishing ‘impact’ to avoid conflating it with the more common fishing ‘pressure’ that often refers to current fishing effort or mortality in the fisheries literature (Piet, Quirijns, Robinson, & Greenstreet, 2007). In contrast, our metric of fishing is a relative, unitless pattern of cumulative exploitation. For example, it identifies areas that have been heavily impacted by fishing (small mean size of parrotfishes), where fishers may have subsequently moved to more profitable locations, rather than necessarily identifying areas that are currently heavily fished. This relationship between fishery-independent and dependent variables is an important topic for future research.

However, our map of fishing impact does mirror known contemporary regional patterns of effort, such as northwards declines through CNMI with increasing distance from populous islands (Williams et al., 2015b) and generally low fishing impact in RMI away from Majuro (Martin et al., 2017). More importantly, measures of fishing impact represent the only realistic method of generating insights into patterns of exploitation in the absence of high resolution fishery-dependent data.

Micronesia represents an ideal place to further examine parrotfish mean size as a metric of fishing impact because of the unusually high value of herbivores in the region's fisheries (Houk et al., 2012). Although this study did not aim to test parrotfish mean length as a proxy of fishing, the results are consistent with it representing a useful indicator. Firstly, the correlates of parrotfish size, particularly human density and distance from market, were similar to those identified previously (Cinner, Graham, Huchery, & MacNeil, 2013). Secondly, when incorporated into the model of fish standing stock, using an independent data set, increasing fishing impact was correlated with a decrease of standing stocks. Consequently, we suggest that this first large-scale use of mean parrotfish size as an indicator of fishing, and novel use in the Pacific, is consistent with smaller-scale work that identified its practical and theoretical advantages in the Caribbean (Vallès, & Oxenford, 2014; Vallès et al., 2015). However, the importance of a range of biophysical variables in the fishing impact model, some of which were more important than human population density, underscores the importance of controlling for these factors when using fishery-independent metrics (Nash, & Graham, 2016).

Mapping fishing impact in this study provided a rarely available data layer for both spatial planning and more informal comparisons among reefs and jurisdictions that may prove useful for encouraging stakeholders towards conservation goals. The approach can also be extended to other habitats (e.g. soft-bottom lagoons) and fisheries (e.g. invertebrates), and can be used with other proxies of fishing impact. Furthermore, our approach generated a single metric of fishing that could be included in a model of fish biomass, which more clearly identified their relationship than representing fishing by multiple interacting proxies. The relationship between fishing and fish stocks, and the importance of fishing compared to biophysical gradients, is critical for understanding human impacts on reefs (Williams, Gove, Eynaud, Zgliczynski, & Sandin, 2015a; Williams et al., 2015b; Heenan, Hoey, Williams, & Williams, 2016). This study demonstrates that increased fishing correlated with approximately linear decreases in log fish biomass, meaning that previously unexploited stocks can be rapidly depleted by relatively small increases in fishing. This non-linear relationship between fishing and fish biomass is consistent with previous studies (Cinner et al., 2013; D'agata et al., 2016; McClanahan et al., 2016).

The impact of fishing on total biomass across the region was less significant than five biophysical variables. Clearly fishing is a critical local driver of fishing biomass, as demonstrated by increased abundances inside marine reserves (Tupper, 2007) and significant reductions in species not considered here (e.g. *Bolbometopon muricatum*, Bellwood, Hoey, & Choat, 2003). However, regional-scale biophysical variables predominate in our model, to a degree not typically seen in smaller-scale studies with less pronounced biophysical gradients and where the effect of fishing is more significant (e.g. D'agata et al., 2016). In comparison with many other reef areas, Micronesia includes large areas of lightly fished remote reefs, and has a history of traditional forms of sustainable reef management (Houk et al., 2015).

The fish biomass model demonstrated the primary influence of correlations with biogeographical-scale gradients in net primary productivity and sea-surface temperature. Although acknowledged theoretically, empirical evidence of these influences has only relatively recently emerged for reef fishes (Nadon et al., 2012; Williams et al., 2015b; Cinner et al., 2016; Heenan et al., 2016). Increasing temperature was negatively correlated with the total biomass of Micronesian fishes, which is consistent with concerns about how global climate change may affect fisheries (Cheung et al., 2013). Furthermore, the presence of large-scale oceanographic features that affect net primary productivity, and potentially bottom-up forcing of reef ecosystems (Gove et al., 2013), appears to limit standing stocks around islands in less productive waters (e.g. Guam). Fish standing stocks increased with increasing depth and coral cover, with apparent thresholds at ~10m and ~10% coral cover that reflect high fish abundance on mid-depth reefs (Mumby et al., 2008) and the importance of coral for fish habitat (Coker, Wilson, & Pratchett, 2014). Intriguingly, fish standing stocks were also positively correlated with increasing larval supply from upstream sources, despite using a regional-scale connectivity model. Despite a widespread acknowledgment of the importance of inter-reef connectivity to fish demographics (Harrison et al., 2012), evidence of high larval supply significantly increasing the biomass of entire assemblages is scarce (see Stier, Hein, Parravicini, & Kulbicki, 2014 for another example). However, our model suggests larval supply has a significant effect on the abundance of multiple Micronesian fish species, despite the connectivity model not resolving self-recruitment that also affects population persistence (Green et al., 2015).

An advantage of including a single variable representing fishing within fish biomass models is the ease of simulating various management options. We used this functionality to reduce fishing impact to 0 to investigate the effects of marine reserves, particularly the potential increases in fish biomass towards maximum local limits. Such targets may be used both within reserve planning exercises and as baselines for monitoring the efficacy of established reserves. Although eliminating fishing is perhaps the most obvious scenario to explore, the single fishing impact variable allows investigations into other management options, such as reducing fishing by some proportion to represent potential gear restrictions or size limits. Furthermore, the model allows exploration of the benefits to fisheries of other scenarios, such as increasing coral cover by improving water quality (Klein et al., 2012). Having estimates of current and potential standing stock also facilitates the calculation of the proportion of fishable biomass remaining, providing insights into the time to recovery following protection (MacNeil et al., 2015). Finally, reducing fishing to 0 demonstrates the significant natural variations in potential maximum biomass on reefs, which complements a growing literature suggesting that such variations are critical when assessing fishing impacts or the scope for recovery (Nadon et al., 2012; Williams et al., 2015b; Heenan et al., 2016; Valdivia, Cox, & Bruno, 2017).

Many marine spatial planning exercises lack comprehensive data to maximise the benefits of marine reserves for fisheries, including the status of the resource (e.g. current stocks), the level of threat (e.g. fishing), and which areas are likely to provide the most benefits if protected (e.g. current stocks low compared to potential maximum). Here we provide a promising new approach for using fishery-independent metrics to map fishing impact, and then using this variable to estimate current and maximum standing stocks. These products can then be used in marine spatial planning to identify areas that are heavily fished, contain high standing stocks, and have the greatest scope for recovery. Indeed, the value of these products has already been demonstrated in the region. For example, the maps have been used to validate the selection of a new, large no-take zone in northern Palau, develop localized policy briefs to highlight key messages for a range of stakeholders, and will be used in new marine spatial planning exercises (Spalding, Brumbaugh, & Landis, 2016). More generally, the maps are now online for local practitioners to explore the patterns and obtain summary statistics (http://maps.oceanwealth.org/), and the approach has been extended to support marine spatial planning in The Bahamas (the Bahamian data products are also available at the Mapping Ocean Wealth data portal). The wider availability of similar maps for other regions would embed a key ecosystem service in marine spatial planning, and help ensure the best possible outcomes for people and nature.

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DATA ACCESSIBILTY

If accepted for publication, all data underlying the models will be archived in Dryad. Map products can be viewed at http://maps.oceanwealth.org/.

SUPPORTNG INFORMATION

Additional Supporting Information may be found in the online version of this article:

APPENDIX S1 Details of fish survey data

APPENDIX S2 Details of predictor variables not collected *in situ*

APPENDIX S3 Additional analytical results and maps

TABLE 1 Predictor variables used in the models of fishing impact and fish biomass. Further details of the derivation of each variable are in Appendix S2.

Variable	**Category**	**Derivation**	**Fishing model?**	**Biomass model?**
Coral cover	Biophysical	From *in situ* fish surveys (continuous)	✓	✓
Depth	Biophysical	From *in situ* fish surveys (continuous)	✓	✓
Distance to pass	Biophysical / Anthropogenic	Distance to the nearest reef pass mapped by MCRMP (continuous)	✓	✓
Distance to port	Anthropogenic	Distance to nearest major port (continuous)	✓	×
Export	Anthropogenic	Extent of reef fish exports from each jurisdiction (categorical)	✓	×
Fishing impact	Anthropogenic	Fishing impact estimated by this study		✓
Geomorphology	Biophysical	Reef type within MCRMP (categorical)	✓	✓
Habitat type	Biophysical	Habitat type within MCRMP (categorical)	✓	✓
Human density (20 km)	Anthropogenic	Human population within 20 km per km^2 of fishable reef (continuous)	✓	×
Human density (200 km)	Anthropogenic	Human population within 200 km per km^2 of fishable reef (continuous)	✓	×
Larval supply	Biophysical	Estimate of larval supply to each reef from upstream sources only (continuous)	×	✓
Latitude	Biophysical	From *in situ* fish surveys (continuous)	✓	✓
Longitude	Biophysical	From *in situ* fish surveys (continuous)	✓	✓
Net primary productivity	Biophysical	Oceanic net primary productivity estimated from satellite data (continuous)	✓	✓
Protected status	Anthropogenic	Level of protection from fishing (categorical)	✓	✓
Sea surface temperature	Biophysical	Sea surface temperature estimated from satellite data (continuous)	✓	✓
Socio-economic development	Anthropogenic	Socio-economic status of jurisdiction (continuous)	✓	×
Survey method	Methodological	From *in situ* fish surveys (categorical)	✓	✓
Tourist pressure (20 km)	Anthropogenic	Estimated tourist numbers within 20 km (continuous)	✓	×
Tourist pressure (200 km)	Anthropogenic	Estimated tourist numbers within 200 km (continuous)	✓	×
Wave exposure	Biophysical	Wave theory using satellite data on wind speeds and fetch from MCRMP (continuous)	✓	✓
Year	Methodological	From *in situ* fish surveys (continuous)	✓	✓

FIGURE LEGENDS

FIGURE 1 Geographic area encompassed by the study, representing the islands and marine resources considered by the Micronesia Challenge. FSM = Federated States of Micronesia, CNMI = the Commonwealth of the Northern Marianas. States within FSM are delineated.

FIGURE 2 Partial dependence plots for the eight most influential variables (anthropogenic variables in bold) retained in the minimal boosted regression tree model of mean parrotfish length in Micronesia. Figures in parentheses represent percentage of explained deviance attributable to each variable. SST = sea surface temperature. Y axes centred to have zero mean over the data distribution (15 – 47.5 cm prior to transformation). Rug plots inside the top of plots show distribution of values, in deciles. For distance to pass, dotted line shows modification of fitted function used for fishing impact predictions.

FIGURE 3 Partial dependence plots for the eight most influential variables retained in the minimal boosted regression tree model of total biomass of the 19 focal fish species in Micronesia. Figures in parentheses represent percentage of explained deviance attributable to each variable. SST = sea surface temperature; NPP = net primary productivity. Y axes centred to have zero mean over the data distribution (0 - 517.9 g m^{-2} prior to transformation). Rug plots inside the top of plots show distribution of values, in deciles.

FIGURE 4 Partial dependence plots for the eight most influential variables retained in the minimal boosted regression tree model of total biomass of fish primary consumers in Micronesia. Figures in parentheses represent percentage of explained deviance attributable to each variable. SST = sea surface temperature; NPP = net primary productivity. Y axes centred to have zero mean over the data distribution (0 - 201.4 g m^{-2} prior to transformation). Rug plots inside the top of plots show distribution of values, in deciles.

FIGURE 5 Partial dependence plots for the eight most influential variables retained in the minimal boosted regression tree model of total biomass of piscivorous fishes in Micronesia. Figures in parentheses represent percentage of explained deviance attributable to each variable. SST = sea surface temperature; NPP = net primary productivity. Y axes centred to have zero mean over the data distribution (0 - 110.2 g m^{-2} prior to transformation). Rug plots inside the top of plots show distribution of values, in deciles.

FIGURE 6 Regional maps of (a) predicted fishing impact (0-1 scale), (b) predicted current total biomass of the 19 focal fish species, (c) predicted potential fish standing stock of the 19 focal fish species in the absence of fishing, and (d) predicted potential percentage gain in total biomass of the 19 focal fish species in the absence of fishing. Each panel includes larger-scale insets of Palau and Guam to show actual map resolution.

FIGURE 7 Summary plots of the proportion of 1 ha reefs cells separated by (a) predicted fishing impact, (b) predicted current fish standing stock of the 19 focal fish species, (c) predicted potential absolute gain in fish standing stock of the 19 focal fish species under a 0 fishing impact scenario, and (d) predicted potential percentage gain in fish standing stock of the 19 focal fish species under a 0 fishing impact scenario. Values are separated by jurisdiction (and states in FSM) and by remote (within 20 km of the most populated islands) and populous (>20 km from the most populated islands) areas in Micronesia. Categories in (c) and (d) are defined by 25%, 50%, and 75% quantiles.

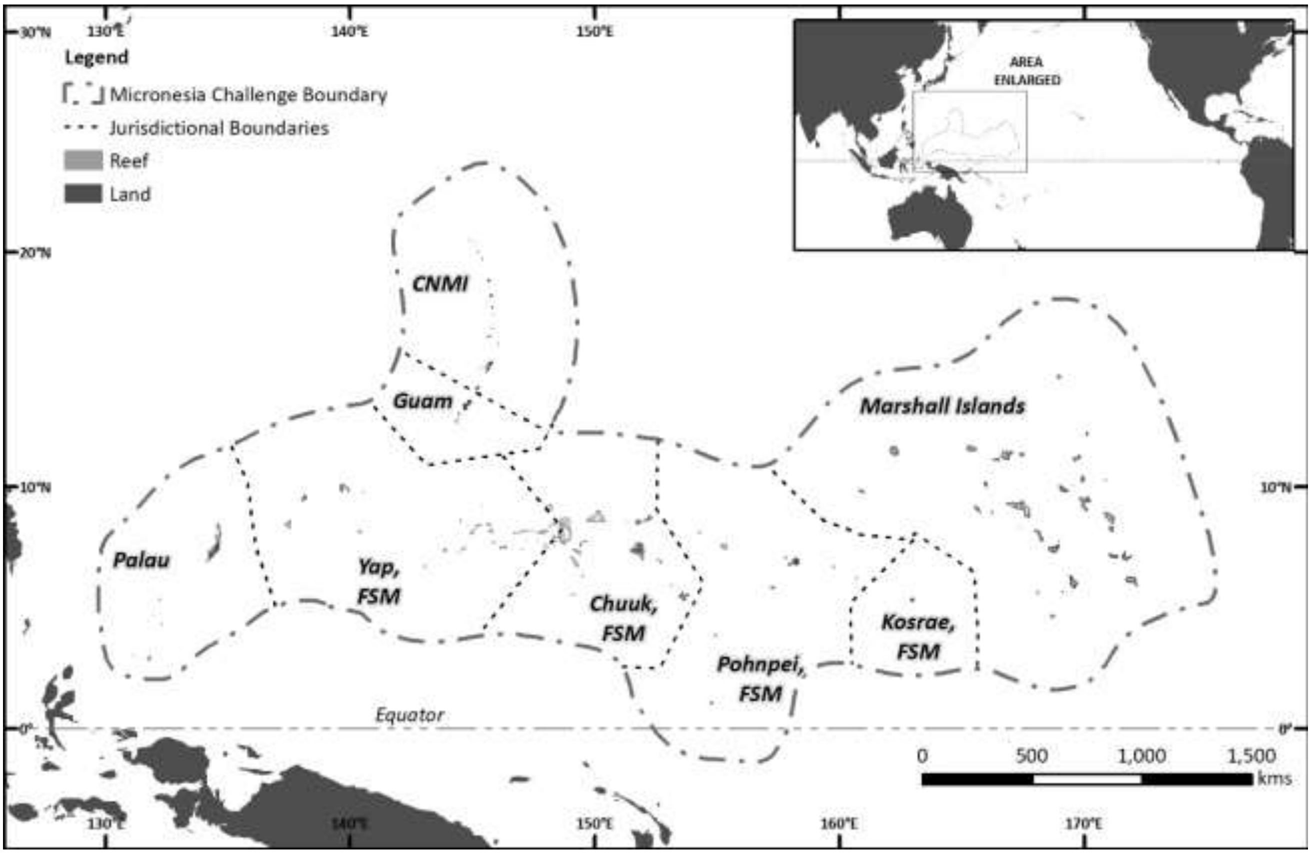
30°N
130°E
140°E
150°E
160°E
170°E
20°N
10°N
0°
Legend
Micronesia Challenge Boundary
Jurisdictional Boundaries
Reef
Land
AREA ENLARGED
CNMI
Guam
Marshall Islands
Palau
Yap, FSM
Chuuk, FSM
Pohnpei, FSM
Kosrae, FSM
Equator
0
500
1,000
1,500
kms

FIGURE 1

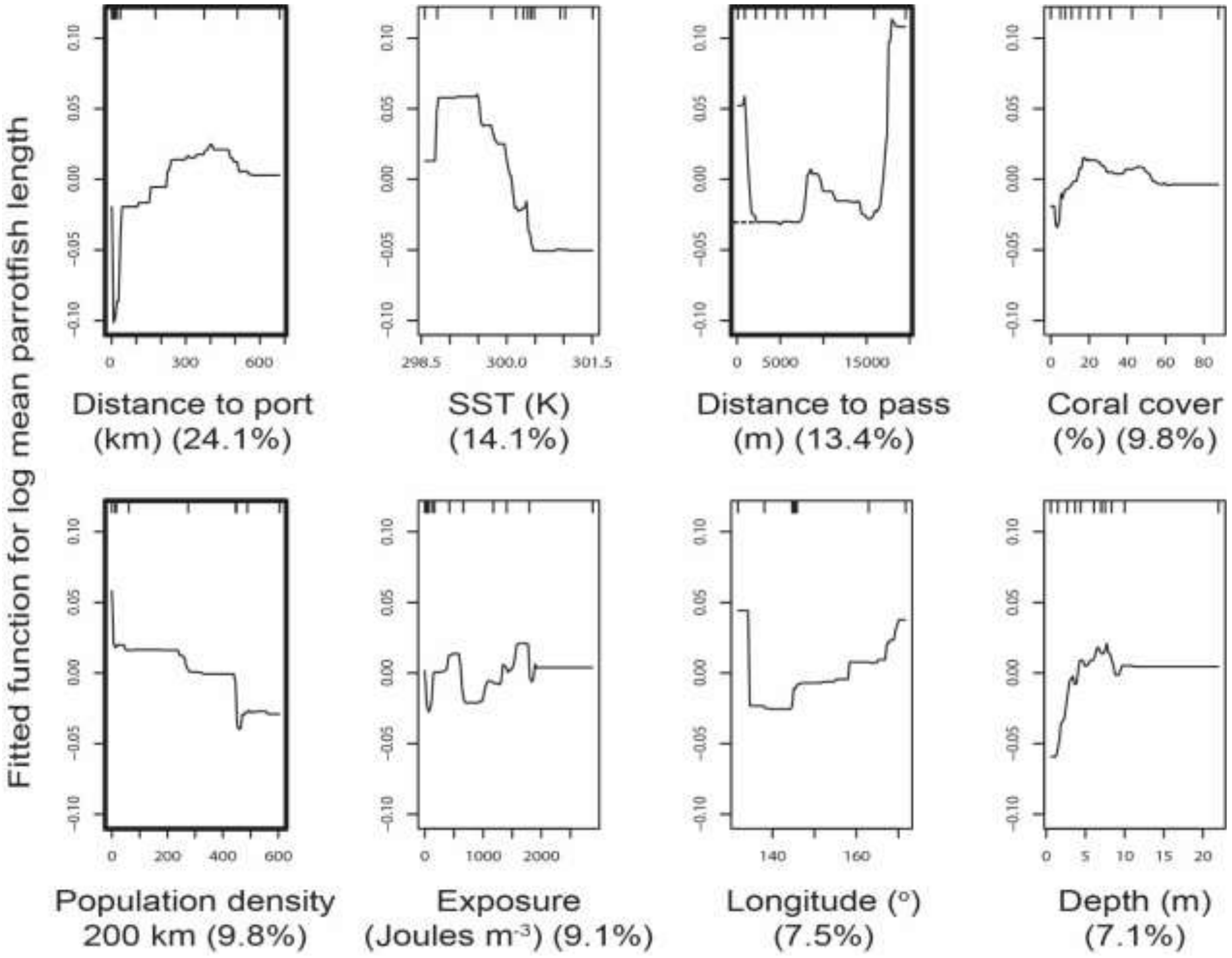
Fitted function for log mean parrotfish length
0.10
0.05
0.00
-0.05
-0.10
0
300
600
Distance to port (km) (24.1%)
298.5
300.0
301.5
SST (K) (14.1%)
0
5000
15000
Distance to pass (m) (13.4%)
0
20
40
60
80
Coral cover (%) (9.8%)
0
200
400
600
Population density 200 km (9.8%)
0
1000
2000
Exposure (Joules m^{-3}) (9.1%)
140
160
Longitude (°) (7.5%)
0
5
10
15
20
Depth (m) (7.1%)

FIGURE 2

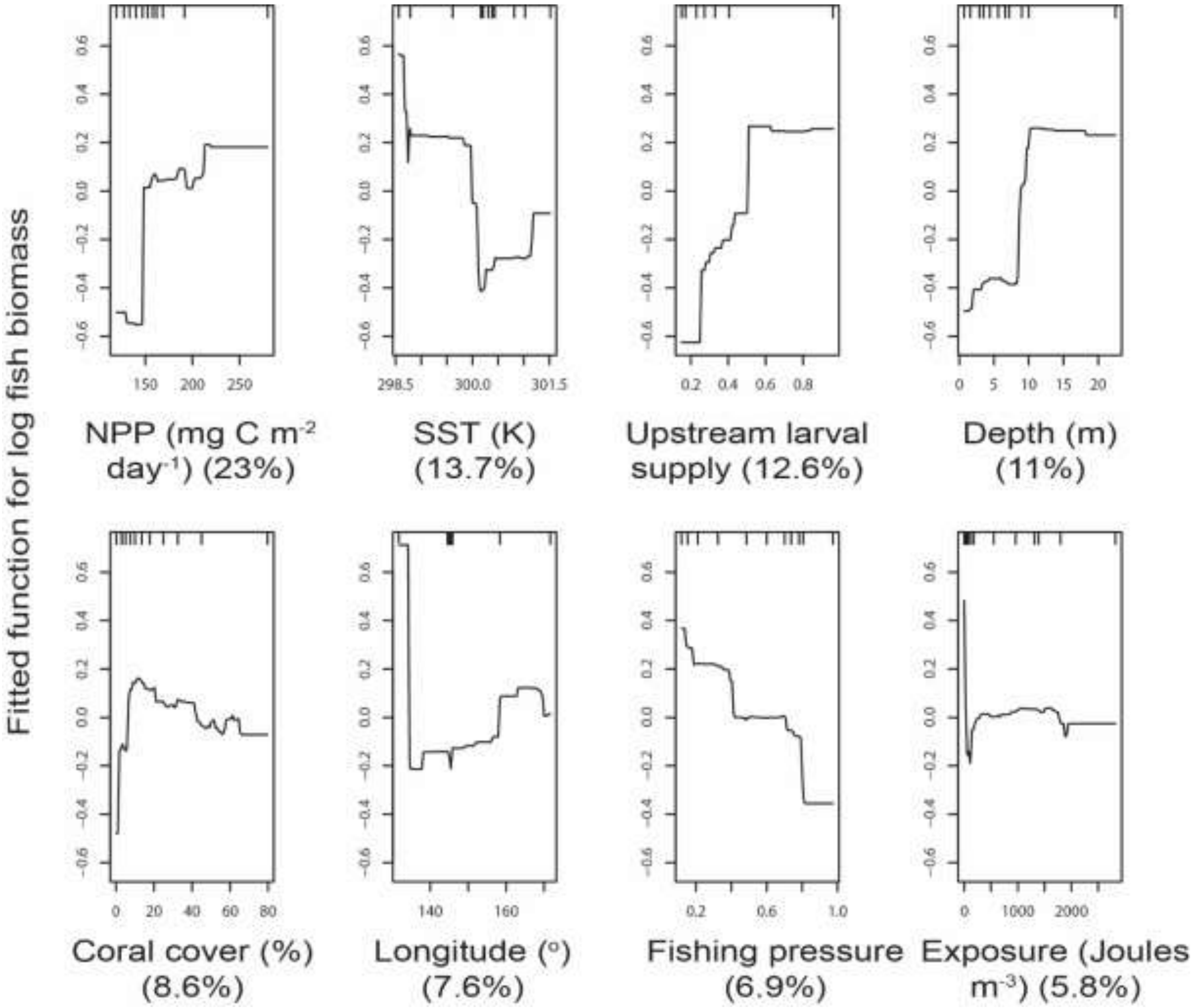
Fitted function for log fish biomass
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
150
200
250
NPP (mg C m-2 day-1) (23%)
298.5
300.0
301.5
SST (K) (13.7%)
0.2
0.4
0.6
0.8
Upstream larval supply (12.6%)
0
5
10
15
20
Depth (m) (11%)
0
20
40
60
80
Coral cover (%) (8.6%)
140
160
Longitude (°) (7.6%)
0.2
0.6
1.0
Fishing pressure (6.9%)
0
1000
2000
Exposure (Joules m-3) (5.8%)

FIGURE 3

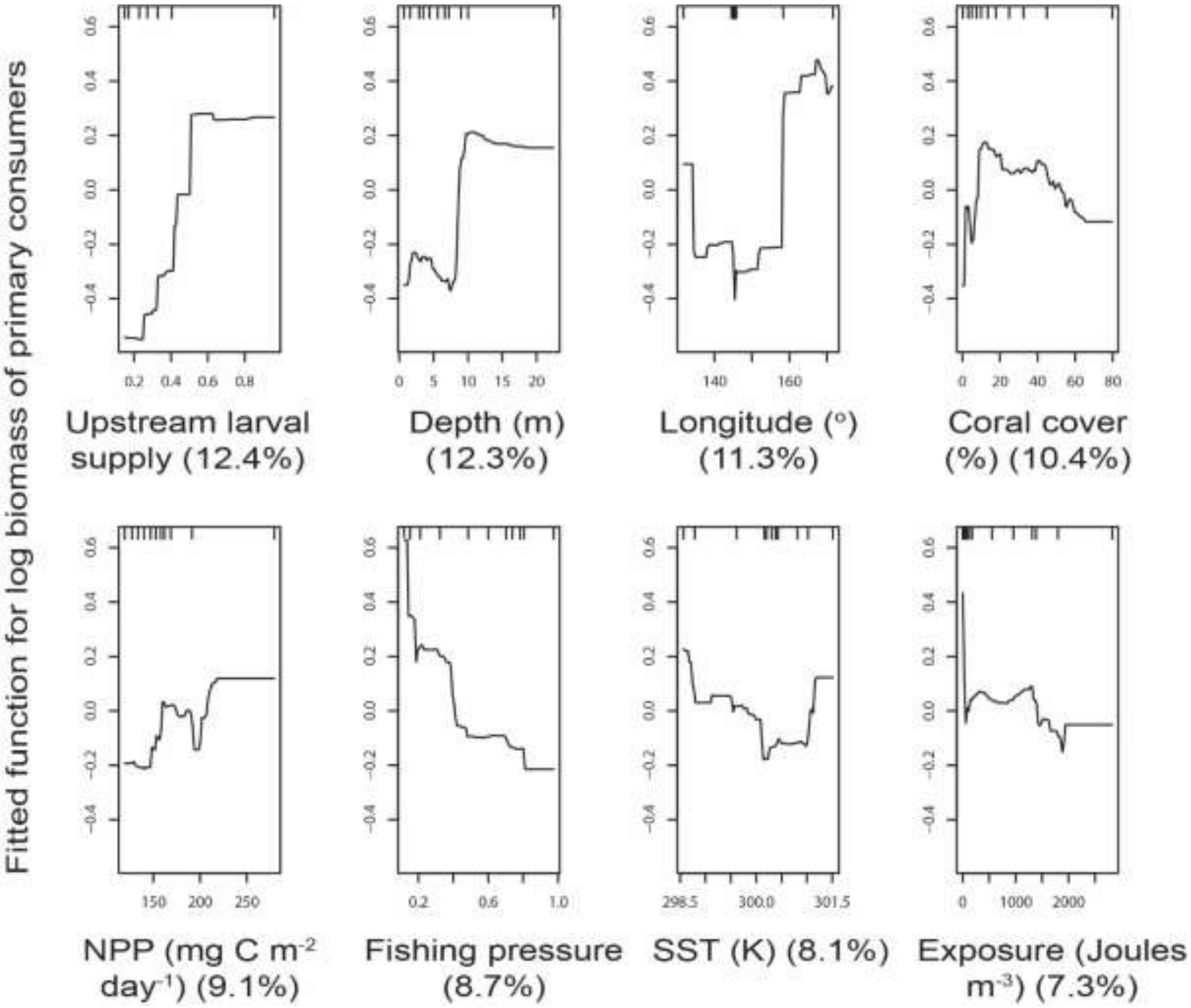
Fitted function for log biomass of primary consumers
-0.4
-0.2
0.0
0.2
0.4
0.6
0.2 0.4 0.6 0.8
Upstream larval supply (12.4%)
0 5 10 15 20
Depth (m) (12.3%)
140 160
Longitude (°) (11.3%)
0 20 40 60 80
Coral cover (%) (10.4%)
150 200 250
NPP (mg C m-2 day-1) (9.1%)
0.2 0.6 1.0
Fishing pressure (8.7%)
298.5 300.0 301.5
SST (K) (8.1%)
0 1000 2000
Exposure (Joules m-3) (7.3%)

FIGURE 4

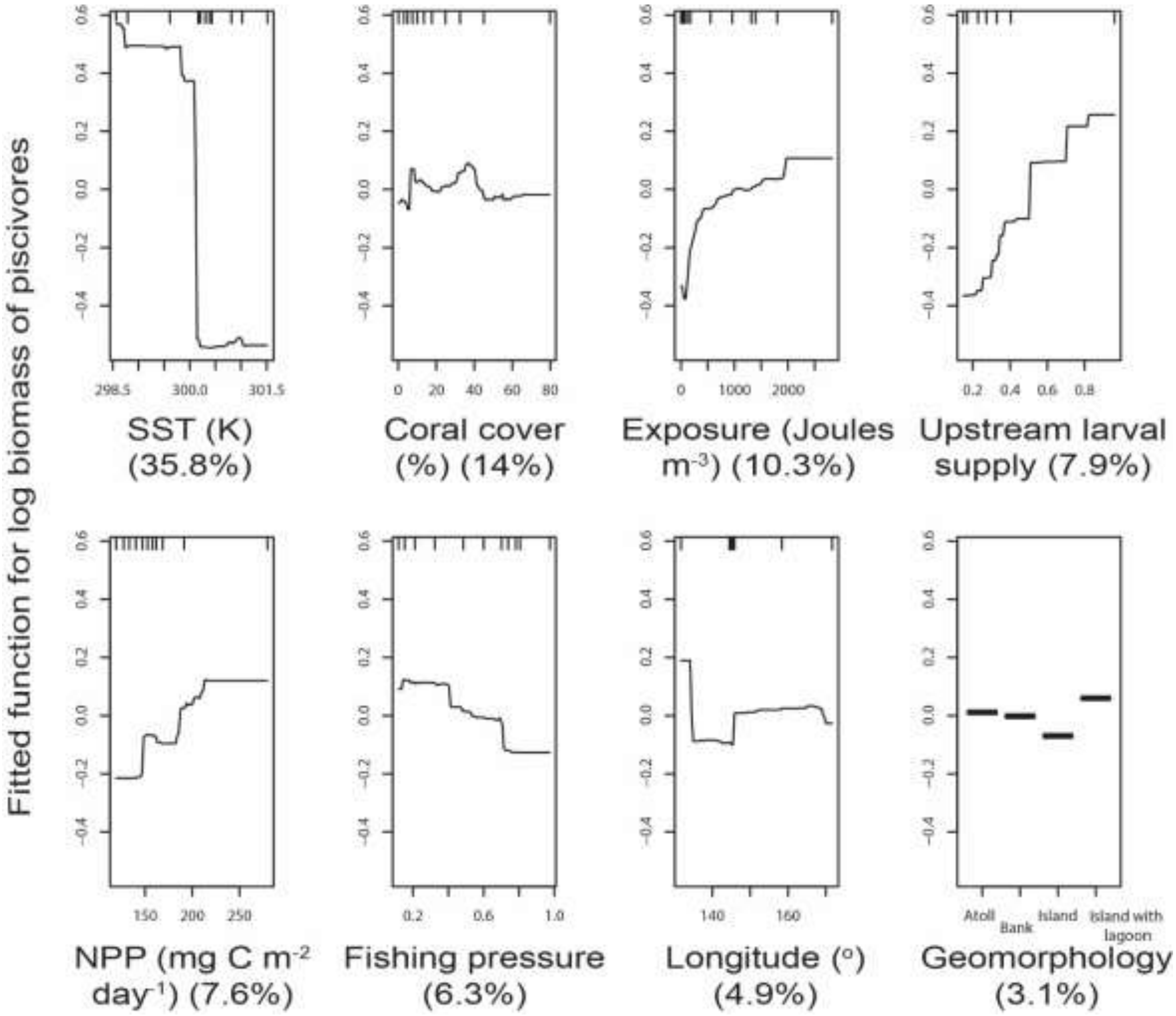
Fitted function for log biomass of piscivores
0.6
0.4
0.2
0.0
-0.2
-0.4
298.5
300.0
301.5
SST (K) (35.8%)
0
20
40
60
80
Coral cover (%) (14%)
0
1000
2000
Exposure (Joules m-3) (10.3%)
0.2
0.4
0.6
0.8
Upstream larval supply (7.9%)
150
200
250
NPP (mg C m-2 day-1) (7.6%)
0.2
0.6
1.0
Fishing pressure (6.3%)
140
160
Longitude (°) (4.9%)
Atoll
Bank
Island
Island with lagoon
Geomorphology (3.1%)

FIGURE 5

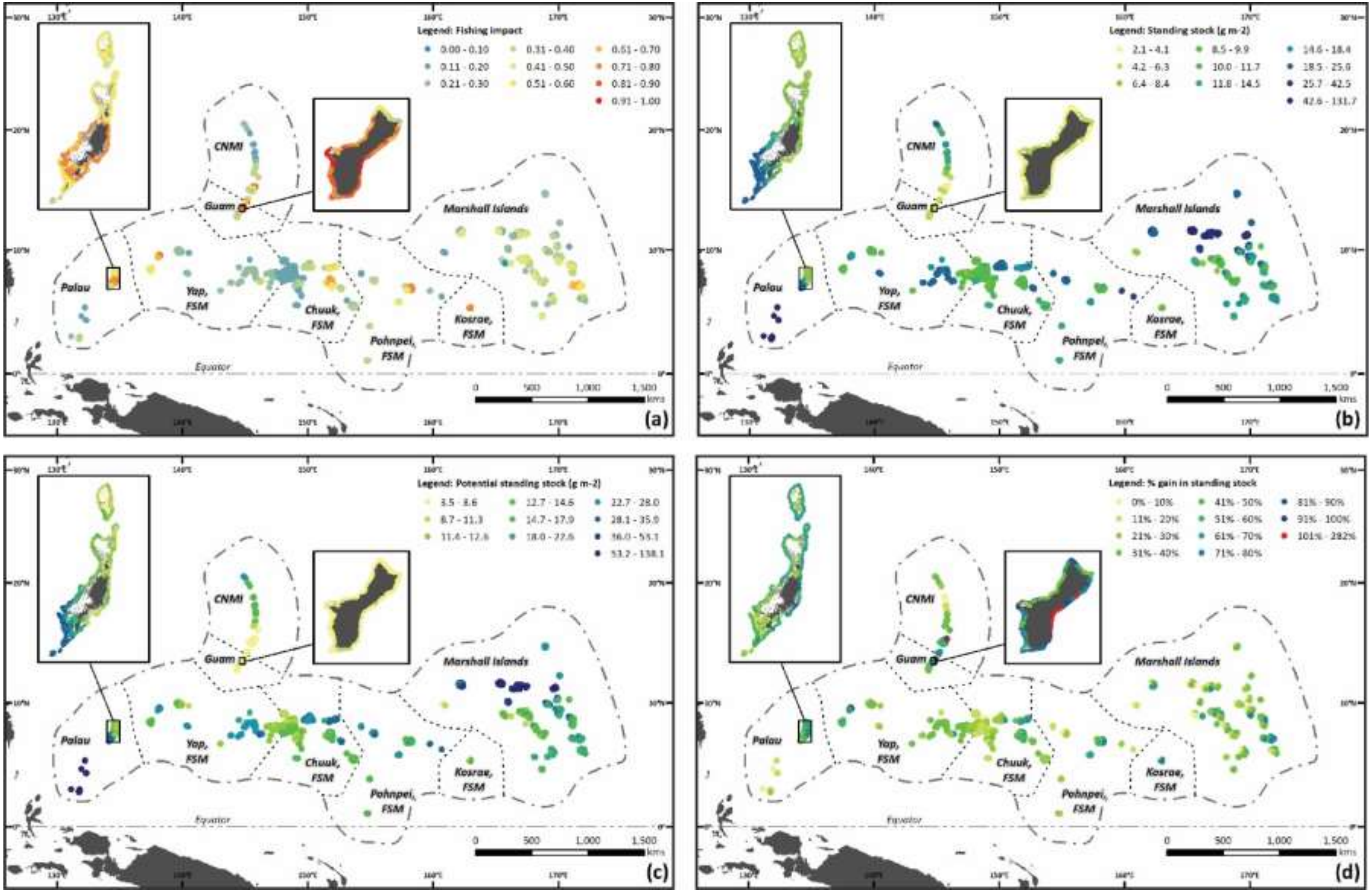
Legend: Fishing impact
● 0.00 - 0.10
● 0.11 - 0.20
● 0.21 - 0.30
● 0.31 - 0.40
● 0.41 - 0.50
● 0.51 - 0.60
● 0.61 - 0.70
● 0.71 - 0.80
● 0.81 - 0.90
● 0.91 - 1.00
CNMI
Guam
Marshall Islands
Palau
Yap, FSM
Chuuk, FSM
Pohnpei, FSM
Kosrae, FSM
Equator
0
500
1,000
1,500
kms
(a)
Legend: Standing stock (g m-2)
● 2.1 - 4.1
● 4.2 - 6.3
● 6.4 - 8.4
● 8.5 - 9.9
● 10.0 - 11.7
● 11.8 - 14.5
● 14.6 - 18.4
● 18.5 - 25.6
● 25.7 - 42.5
● 42.6 - 131.7
(b)
Legend: Potential standing stock (g m-2)
● 3.5 - 8.6
● 8.7 - 11.3
● 11.4 - 12.6
● 12.7 - 14.6
● 14.7 - 17.9
● 18.0 - 22.6
● 22.7 - 28.0
● 28.1 - 35.9
● 36.0 - 53.1
● 53.2 - 138.1
(c)
Legend: % gain in standing stock
● 0% - 10%
● 11% - 20%
● 21% - 30%
● 31% - 40%
● 41% - 50%
● 51% - 60%
● 61% - 70%
● 71% - 80%
● 81% - 90%
● 91% - 100%
● 101% - 282%
(d)
130°E
140°E
150°E
160°E
170°E
30°N
20°N
10°N
0°

FIGURE 6

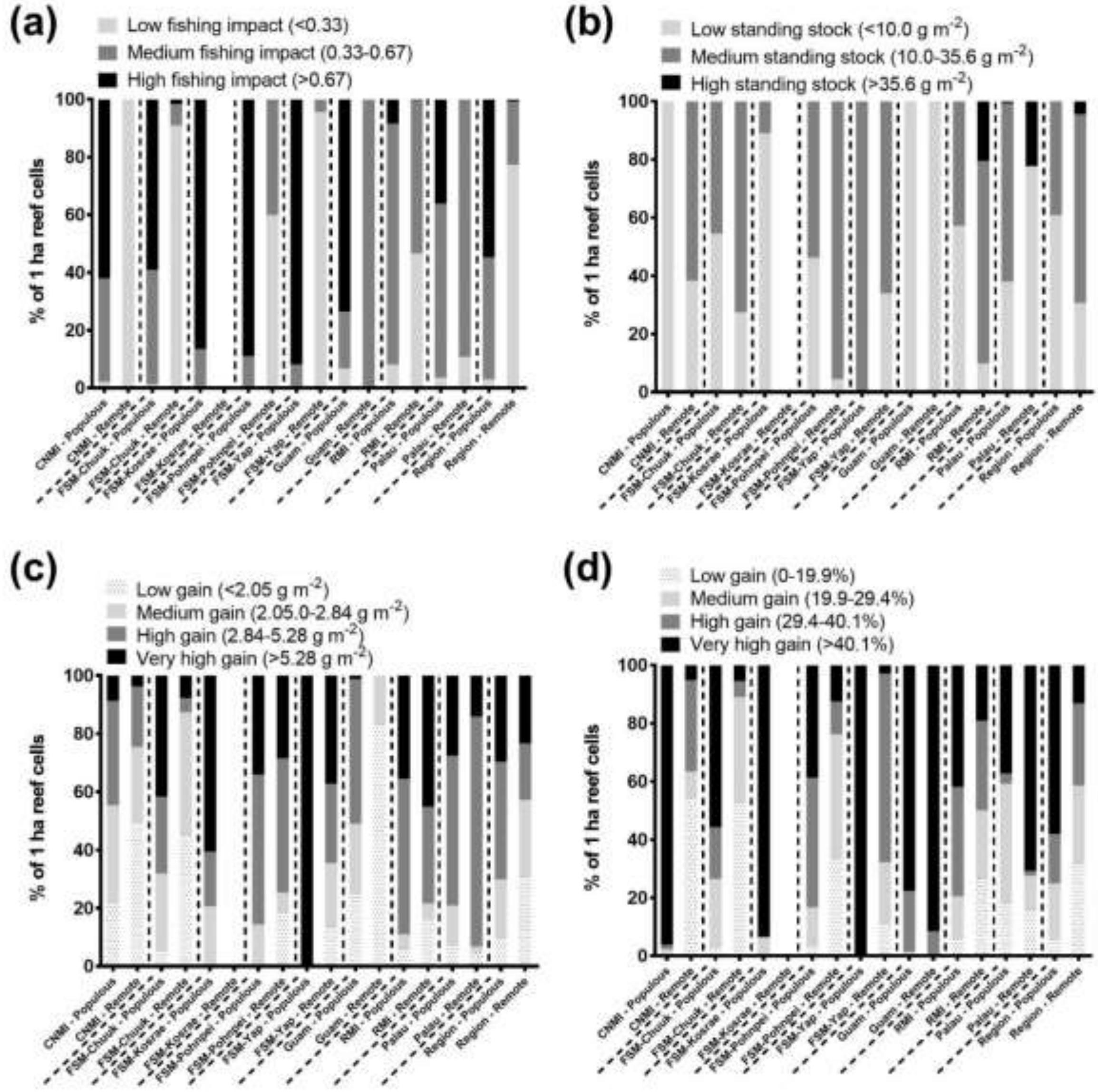
(a)
Low fishing impact (<0.33)
Medium fishing impact (0.33-0.67)
High fishing impact (>0.67)
(b)
Low standing stock (<10.0 g m-2)
Medium standing stock (10.0-35.6 g m-2)
High standing stock (>35.6 g m-2)
(c)
Low gain (<2.05 g m-2)
Medium gain (2.05.0-2.84 g m-2)
High gain (2.84-5.28 g m-2)
Very high gain (>5.28 g m-2)
(d)
Low gain (0-19.9%)
Medium gain (19.9-29.4%)
High gain (29.4-40.1%)
Very high gain (>40.1%)
% of 1 ha reef cells
0
20
40
60
80
100
CNMI - Populous
CNMI - Remote
FSM-Chuuk - Populous
FSM-Chuuk - Remote
FSM-Kosrae - Populous
FSM-Kosrae - Remote
FSM-Pohnpei - Populous
FSM-Pohnpei - Remote
FSM-Yap - Populous
FSM-Yap - Remote
Guam - Populous
Guam - Remote
RMI - Populous
RMI - Remote
Palau - Populous
Palau - Remote
Region - Populous
Region - Remote

FIGURE 7

A.R. Harborne, A.L. Green, N. Peterson, M. Beger, Y. Golbuu, P. Houk, M.D. Spalding, B.M. Taylor, E. Terk, E.A. Treml, S. Victor, L. Vigliola, I.D. Williams, N.H. Wolff, P. zu Ermgassen, and P.J. Mumby. Modelling and mapping regional-scale patterns of fishing impact and fish biomass to support coral-reef management in Micronesia.

APPENDIX S1 – DETAILS OF FISH SURVEY DATA

TABLE S1.1 Millennium Coral Reef Mapping Project (MCRMP) level 4 marine classes found in the study region. Each class may either be represented by models of fishing pressure and standing stock, or not parameterised by these models. In addition, only some habitat classes were considered in calculations of human population per unit area of fishable reef (i.e. a ‘fished reef’ habitat). wc = with constructions.

MCRM habitat	Modelled?	Fished reef?
Bay exposed fringing	Yes	Yes
Bridge	Yes	Yes
Channel	No	No
Deep drowned reef flat	Yes	Yes
Deep lagoon	No	No
Deep lagoon wc	No	No
Deep terrace	Yes	Yes
Deep terrace wc	Yes	Yes
Diffuse fringing	No	Yes
Drowned bank	Yes	Yes
Drowned inner slope	No	Yes
Drowned lagoon	No	No
Drowned pass	No	No
Drowned patch	Yes	Yes
Drowned rim	Yes	Yes
Enclosed basin	No	No
Enclosed lagoon	No	No
Enclosed lagoon or basin	No	No
Enclosed lagoon wc	No	Yes
Faro reef flat	No	No
Forereef	Yes	Yes
Forereef or terrace	Yes	Yes
Inner slope	No	Yes
Lagoon pinnacle	Yes	Yes
Pass	No	Yes
Pass reef flat	No	Yes
Pinnacle	Yes	Yes
Reef flat	No	Yes
Reticulated fringing	Yes	Yes
Ridge and fossil crest	No	Yes
Shallow lagoon	No	No
Shallow lagoon wc	No	No
Shallow lagoonal terrace	No	Yes
Shallow terrace	No	Yes
Shallow terrace wc	No	Yes
Shelf slope	No	Yes
Subtidal reef flat	No	Yes
Undetermined envelope	Yes	Yes
Uplifted reef flat	No	Yes

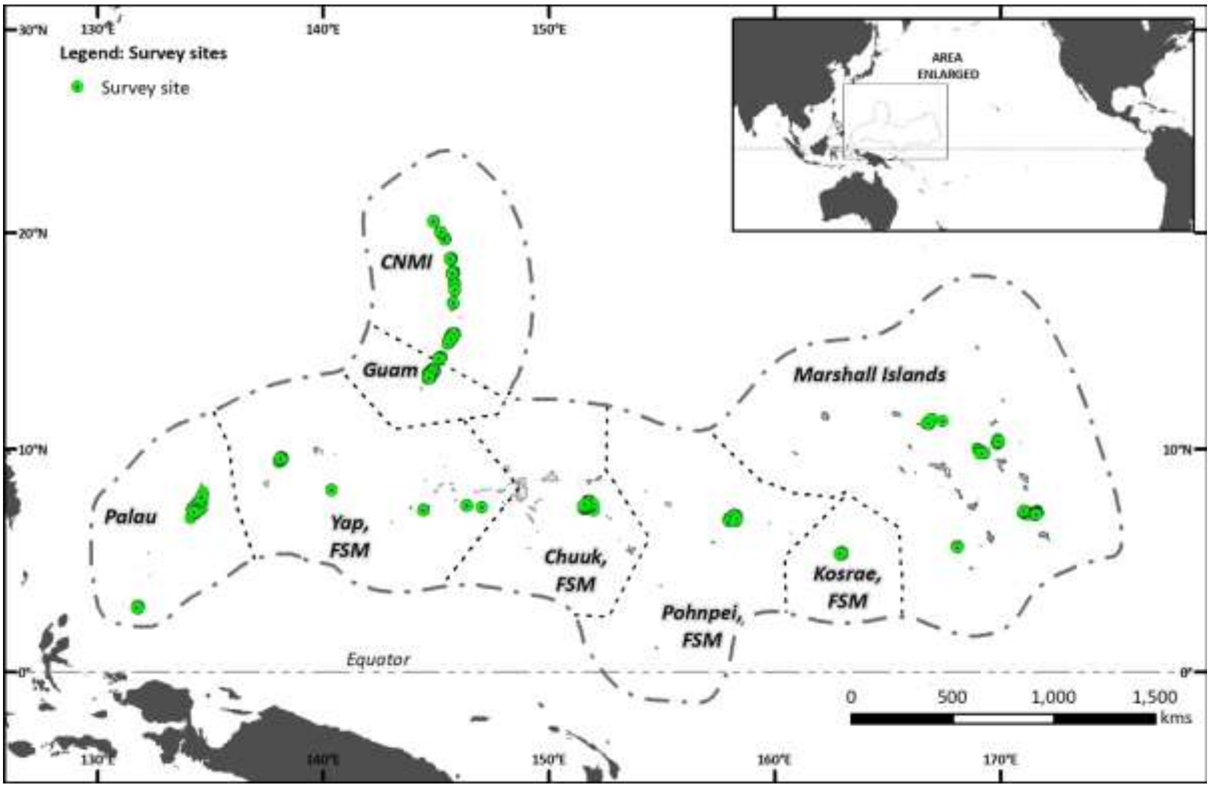

FIGURE S1.1 Location of survey sites used in the study.

TABLE S1.2 Summary of fish survey data sets available to the project, and whether they were used to model fishing pressure and / or standing stock. Numbers represent the number of sites used from each data set in each model. UVC = underwater visual census. CNMI = Commonwealth of the Northern Marianas, FSM = Federated States of Micronesia, RMI = Republic of the Marshall Islands.

Source	Sites from	Dates	Techniques used for fish and benthos	Species	Fishing model	Standing stock model
Peter Mumby	• Palau • Guam • Pohnpei	2009-2012	UVC belt transects (30x4m), photo quadrats	All species of parrotfish, surgeonfish, and rabbitfish	54	-
Maria Beger	• Marshall Islands (3 atolls)	2014	UVC belt transects (50x5m), visual estimation of coral	All non-cryptic species. 372 species from 39 families	15	14
Brett Taylor	• Guam • 7 islands in FSM	2011-2012	Video belt transects (5mx3 min), visual estimation of coral	143 taxa from 22 families	37	57
NOAA CRED	• Guam • 12 islands in CNMI	2011, 2014	Stationary point counts (15m diameter), visual estimation of coral	All non-cryptic species. >480 taxa from 53 families	297	414

Micronesia Challenge	- 4 islands in FSM - 3 islands in CNMI - 3 atolls in RMI	2011-2015	Stationary point counts (10m diameter), photo quadrats	157 taxa from 22 families	-	79
PICRC	- Palau	2014	UVC belt transects (50x5m), photo quadrats	Focused on 35 key species from 11 families	2	26
Alison Green	- Helen Reef (Palau)	2000	UVC belt transects (50x3m), video transects	All non-cryptic species. 245 species from 27 families	2	2
PROCFish	- Palau - 2 islands in FSM - 3 atolls in RMI	2006-2007	Distance-based UVC transects (50x10m), *in situ* quadrats	Most non-cryptic species. 313 species from 30 families	63	65
Total					470	657

TABLE S1.3 Details of the 19 key species used to model standing stock in Micronesia. Trophic group follows Sandin and Williams (2010). Vulnerability index taken from Abesamis et al. (2014) where available.

Family	Species	Common name	Trophic group	Vulnerability index
Acanthuridae	*Naso lituratus*	Orange-spine surgeonfish	Primary Consumer	Low - moderate
Acanthuridae	*Naso unicornis*	Blue-spine unicornfish	Primary Consumer	High
Carangidae	*Caranx melampygus*	Bluefin trevally	Piscivore	Moderate - high
Kyphosidae	*Kyphosus spp.*	Chub or drummer	Primary Consumer	-
Labridae	*Cheilinus undulatus*	Humphead wrasse	Secondary Consumer	High – very high
Lethrinidae	*Lethrinus obsoletus*	Orange-striped emperor	Secondary Consumer	-
Lethrinidae	*Lethrinus olivaceus*	Longface emperor	Piscivore	Moderate
Lutjanidae	*Lutjanus bohar*	Two-spot red snapper	Piscivore	High – very high
Lutjanidae	*Lutjanus gibbus*	Humpback red snapper	Secondary Consumer	-
Scaridae	*Cetoscarus bicolor*	Bicolour parrotfish	Primary Consumer	High – very high
Scaridae	*Chlorurus microrhinos*	Steephead parrotfish	Primary Consumer	Moderate
Scaridae	*Chlorurus sordidus*	Bullethead parrotfish	Primary Consumer	Low
Scaridae	*Hipposcarus longiceps*	Pacific longnose parrotfish	Primary Consumer	Low - moderate
Scaridae	*Scarus rubroviolaceus*	Redlip parrotfish	Primary Consumer	-
Serranidae	*Epinephelus fuscoguttatus*	Brown-marbled grouper	Piscivore	Moderate - high
Serranidae	*Epinephelus polyphekadion*	Camouflage grouper	Piscivore	-
Serranidae	*Plectropomus laevis*	Black-saddled coral grouper	Piscivore	High – very high
Siganidae	*Siganus argenteus*	Forktail rabbitfish	Primary Consumer	-

Siganidae	*Siganus punctatus*	Gold-spotted rabbitfish	Primary Consumer	-

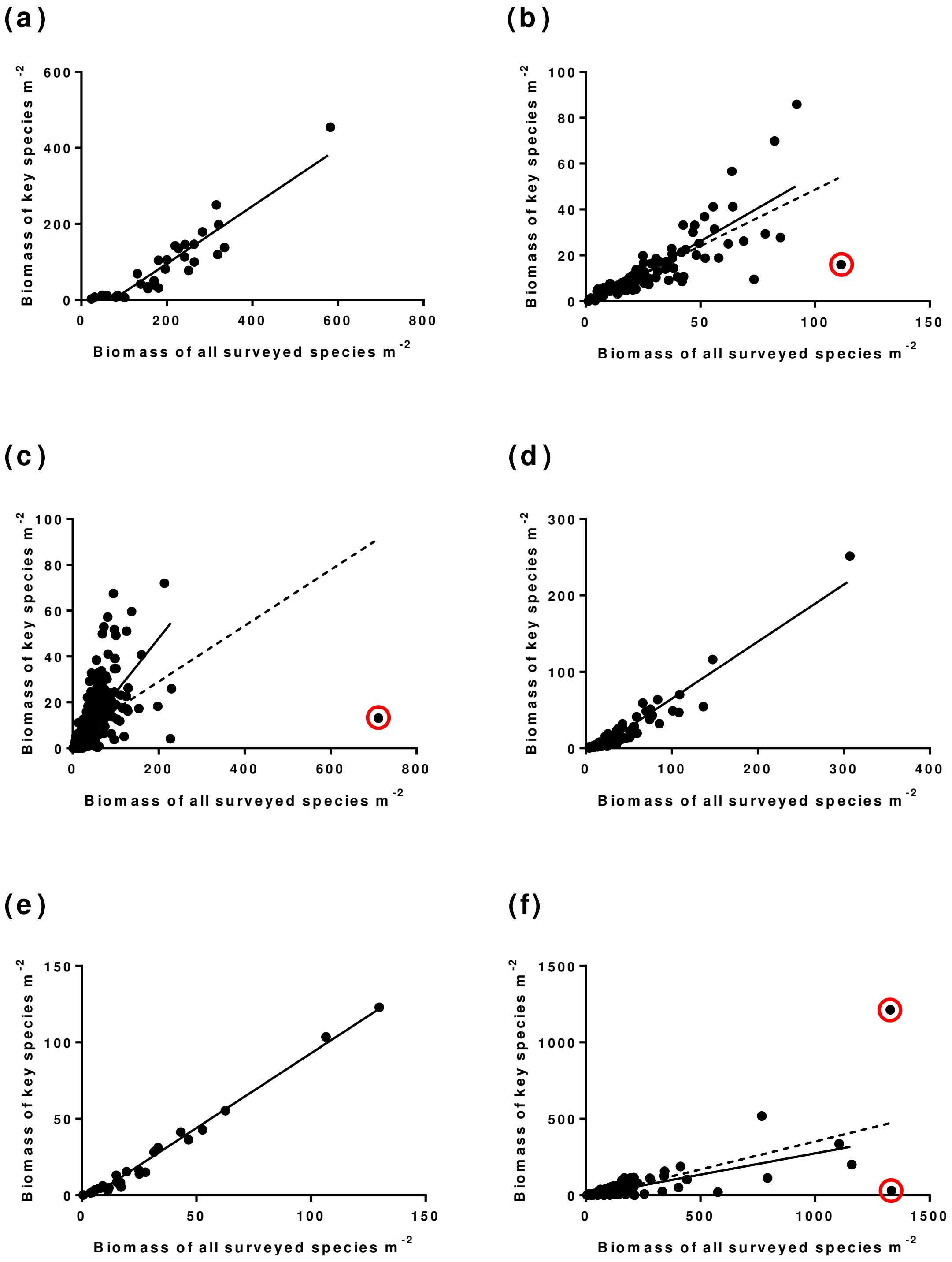

FIGURE S1.2 Scatter plots of site-level data comparing the biomass for all species recorded to the biomass for only the 19 species considered by the Phase 1 project. Data sets and Pearson correlation coefficients (solid line) are: (a) Maria Beger (0.925), (b) Brett Taylor (0.825), (c) NOAA CRED (0.697), (d) Micronesian Challenge (0.957), (e) PICRC (0.993), and (f) PROCFISH (0.777). Alison Green (0.913) not shown because of limited number of sites. Dotted lines represent correlations including outliers (red circles) where correlation coefficients are (b) 0.764, (c) 0.506, and (f) 0.694. Outliers are caused by large shoals of (b) *Platax orbicularis*, (c) *Caranx sexfasciatus*, and (f) *Bolbometopon muricatum* (lower) and *Lutjanus gibbus* (upper).

APPENDIX S2 - DETAILS OF PREDICTOR VARIABLES NOT COLLECTED *IN SITU*

Distance to pass

Level 4 of the Millennium Coral Reef Mapping Project (MCRMP) classification scheme (Andréfouët et al., 2006) includes a habitat class for pass, and so this variable was calculated as the Euclidean distance of the reef site to the nearest pass in the reef. To ensure that all distances were relevant to the behaviour of fishers distances were truncated at 20 km, which is slightly further than the average distance travelled by fishers in the region (~17 km; Sonia Bejarano, unpublished data). This truncation also ensured that there were no situations where large distances were returned because there was no pass present on a given island or atoll (i.e. no situations where meaningless distances were returned because the algorithm was measuring from a reef cell on one island or atoll to a pass on a different island or atoll).

Distance to port

This response variable was estimated as the Euclidean distance between each reef cell and the nearest major population centre (Koror on Palau, Apra Harbor on Guam, Rota Seaport and Tanapag Harbor in CNMI, Colonia on Yap, Moen on Chuuk, Kolonia on Pohnpei, Tafunsak on Kosrae, and Majouro in the RMI). We used Euclidean distance since it is unlikely that many of the small boats that make up a large proportion of Micronesian fisheries would take long marine detours to visit ports. Rather, they are likely to use a combination of boats and travel by road, and we assume that Euclidean distance is a reasonable proxy. This approach is consistent with other measures of distance to port that use a combination of across sea and across land distances (Brewer, Cinner, Fisher, Green, & Wilson, 2012; Brewer, Cinner, Green, & Pressey, 2013; Cinner, Graham, Huchery, & MacNeil, 2013).

Export

In some jurisdictions, the export of coral reef fishes can be an important driver of fishing pressure as coolers of coral reef fishes are exported by air for markets and off island family members (Grafeld, Oleson, Teneva, & Kittinger, 2017). The importance of these exports as drivers of fishing pressure depends on the current status of coral reef fish populations (i.e. if there are still enough fish to catch for export) and the access to airports. This variable was included in the fishing pressure model by developing a semi-quantitative scale for these exports using expert opinion, where every reef cell was ranked as 0, except for cells within 20 km of the main islands in some jurisdictions. These island were ranked as follows:

- Main islands in Pohnpei and Yap were ranked as 1 (low);
- Koror in Palau was ranked as 2 (medium); and
- Main island in Chuuk was ranked as 3 (high).

Consequently, this variable allows for reef cells close to these islands to potentially be more heavily fished than other reef cells because of the additional pressure of catch for export.

Geomorphology

Geomorphology was derived from levels 2 and 3 of the MCRMP classification scheme (Andréfouët et al., 2006). Level 2 distinguishes oceanic atolls, oceanic banks and ocean uplifted / filled atolls (low islands), and oceanic islands (high islands). The classification scheme does not distinguish among islands with and without lagoons, and those with lagoons (particularly Palau, Pohnpei, Chuuk, and Yap) were classified by hand. Level 3 was used to separate drowned atolls and those atolls with islands.

Habitat type

Although the majority of the sites modelled and mapped are from a single habitat class in the MCRM project classification scheme (forereef), some other habitats were included in the maps since the models were judged to be appropriate for extrapolation (Bay exposed fringing, Bridge, Deep drowned reef flat, Deep terrace, Drowned bank, Drowned patch, Drowned rim, Forereef or terrace, Lagoon pinnacle, Pinnacle, Reticulated fringing, Undetermined envelope).

Human density

Standardised, rasterized, global data sets of human populations are available online, and the Phase 1 project used data from SEDAC, the Socioeconomic Data and Applications Center (SEDAC), which is part of the Earth Observing System Data and Information System (EOSDIS) of NASA[1]. The project used the Global Rural-Urban Mapping Project (GRUMP) 2000 data layer, which provides estimated population sizes within at a resolution of 30 arc-seconds (~1km). Full details of the derivation of this data layer is provided in Balk et al. (2010), but it is generated using population counts and night-time light intensities. Defining the area included in assessing human populations affecting a survey site was informed by previous studies that have estimated populations within 5 km^2 (Stallings, 2009; Cinner, Graham, Huchery, & MacNeil, 2013), a radius of 15 km (Williams et al., 2008), and a radius of 25 km (Halpern et al., 2008; Mora et al., 2011). Furthermore, interviews with fisherfolk in Palau, Pohnpei, and Guam suggest that on average they travel ~17 km to fish (Sonia Bejarano, unpublished data). Therefore, the project considered human populations within 20 km of each fish survey site, and divided this figure by the area of reef within the same distance, resulting in a metric of human population pressure per km^2. In addition, we followed Williams et al. (2015) and calculated population pressure per km^2 of reef within 200 km as a metric of the potential for a reef to be fished by more distant populations that are increasingly using larger, faster boats that are able to fish more widely.

Larval supply

We used a biophysical model of larval supply throughout the area (see Mora et al., 2012 for a full description of the model). Briefly, patches of reef habitat were identified, and then 'virtual larvae' were released within a computer simulation of oceanic conditions. Larval release was at the midpoint of each season (i.e. 2 February, 5 May, 6 August, and 11 November) and across six years (2004–2009), for a total of 24 simulations. Virtual larvae were tracked for 100 days, a duration encompassing the majority of pelagic larval durations in tropical reef fishes, and where they 'settle' was recorded (either back to the same reef, to a different reef, or lost into oceanic water). These data generate a connectivity matrix, showing the proportion of larvae moving from each patch to every other patch. The connectivity matrix was used to quantify upstream larval supply following removal of self-recruiting arrivals at each patch (arrivals originating and settling at the same patch). This metric was calculated because local-retention patterns tend not to be reliable when extracted from biophysical models because they ignore all local processes (e.g. tides, local-scale eddies, and near-shore turbulence). The larval arrival metric for each modelled patch was assigned to every reef cell that was located within that patch.

Net primary productivity

Mean monthly net primary productivity from 2010-2014 at a resolution of ~350 km^2 was obtained from an online source[2]. Remotely sensed estimate of productivity of over reefs are confounded by bottom reflectance, so only data from pelagic areas around each reef were used. These areas were identified using the protocol described in Gove et al. (2013): productivity data was excluded where they intersected with any polygon delineated by the MCMP, and then the productivity value for each reef cell was derived as the value contained within the nearest, entirely pelagic data cell.

Protected status

Regional data layers of the extent of marine protected areas were available within the region, but included both well-enforced no-take reserves, areas with only limited regulations (e.g. no commercial fishing), and 'paper parks'. Therefore, expert opinion was used to refine this data layer and classify

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[1] http://sedac.ciesin.columbia.edu/

[2] http://www.science.oregonstate.edu/ocean.productivity/index.php

only no-take reserves as either ineffective (essentially comparable to areas open to fishing), partly effective (some enforcement of regulations), or effective (well enforced).

Sea surface temperature

Sea surface temperature data were obtained online from the Coral Reef Temperature Anomaly Database (CoRTAD)[3], and used data from 2008-2012 at a 4 km resolution. The metric of sea surface temperature followed Williams et al. (2015), namely the mean temperature from the coldest month of each year (i.e. the lower climatological mean) at each reef location (calculated from weekly means). The final metric was calculated as the mean temperature of the coldest month (which could potentially vary among years) over the five-year period from 2008-2012 (i.e. the mean of five temperatures, with one value from each year).

Socio-economic development

Socio-economic status could not be assessed for each island in the region, but was derived at a jurisdiction level using standardised data from online sources[4,5] (Table S3).

TABLE S2.4 The jurisdiction-scale, raw socio-economic data used in the Phase 1 project.

	CNMI	**Guam**	**FSM**	**Palau**	**RMI**
Population density (people per km^2 of land)	112.8103	297.3989	149.8803	46.32898	398.8453
Median age (years)	31.6	29.9	23.8	33	22.5
Annual population growth rate (%)	2.18	0.54	-0.46	0.38	1.66
Annual birth rate (per 1000 people)	18.32	16.82	20.54	11.05	25.6
Annual death rate (per 1000 people)	3.71	5.12	4.23	7.99	4.21
Urban population (%)	89.2	94.5	22.4	87.1	72.7
Life expectancy (years)	77.82	78.98	72.62	72.87	72.84
GDP (US$ million)	1232	4600	315	269	193
GDP growth rate (%)	4.5	0.6	0.1	8	0.5
GDP per capita ($)	13300	30500	3000	16300	3300
Unemployment rate (%)	11.2	8.4	16.2	4.2	36

Rather than use each variable separately, they were combined into a composite index using principle components analysis (PCA, Fig. S2.3). This analysis separated the jurisdictions with, for example, Palau, CNMI, and Guam having a higher median age, GDP, and life expectancy (negative scores on PC1) compared to FSM and RMI. Similarly, FSM and RMI have higher unemployment and population growth rates than the other three jurisdictions (positive scores on PC1). Finally, Palau is separated from CNMI and Guam by having a lower life expectancy (more positive values on PC2).

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[3] http://data.nodc.noaa.gov/cgi-bin/iso?id=gov.noaa.nodc:0126774

[4] http://databank.worldbank.org/data/reports.aspx?source=world-development-indicators

[5] https://www.cia.gov/library/publications/the-world-factbook/

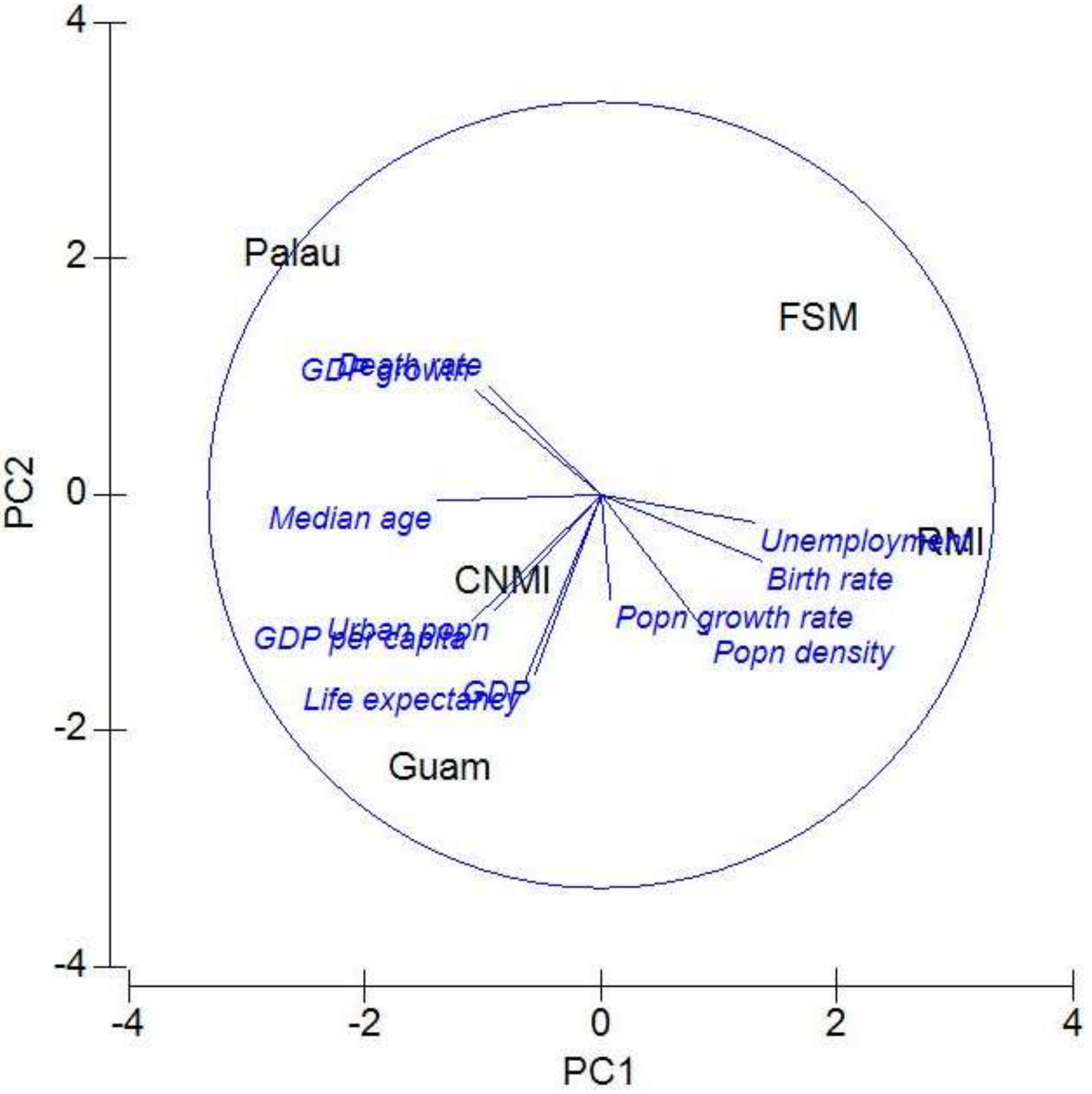

FIGURE S2.3 Position of each jurisdiction on the first two axes (PC1 and PC2) of a principle components analysis of the raw socio-economic data.

These first two axes were used as the two metrics of socio-economic development for reef cells. However, these values were only applied to reef cells within 20 km of the islands with major populations (Palau, Guam, Rota, Aguijan , Tinian, Saipan, Yap, Chuuk, Pohnpei, Kosrae, Majuro, and Kwajalein Atoll). The socio-economic situation at more remote islands with limited populations do not necessarily reflect the situation on these populous islands, and indeed these remote islands are more likely to be more socio-economically similar to each other than nearby population centres. Because no socio-economic data were available for these remote islands, values for these reefs cells were not included (‘missing data’).

Tourist pressure

Across the entire region, reliable tourist arrival data are only available at the jurisdiction level[6] (Table S4). These data were compared to total jurisdiction population predictions from the SEDAC data layer (see section on Human density) to generate a tourist to local population ratio. This ratio was then used to change the ‘Human density’ metrics at 20 and 200 km for each cell (i.e. Human density values were multiplied by 4.134 in CNMI and by 0.320 in FSM). This assumes that tourist numbers are distributed

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[6] http://data.worldbank.org/indicator/ST.INT.ARVL

around the jurisdiction in the same proportion as local populations, which seems likely as most tourists spend at least some time in the population centres. Consequently, this calculation leads to an estimate of the total number of tourists per km^2 of reef within 20 and 200 km of each reef cell.

TABLE S2.5 Total number of annual tourist arrivals into each jurisdiction, and the tourist to local population ratios.

Jurisdiction	2011 tourist arrivals	Local population	Tourist to population ratio
CNMI	336000	81275	4.134
FSM	35000	109411	0.320
Guam	1160000	152423	7.610
Palau	109000	19290	5.651
RMI	4600	52066	0.088

Wave exposure

Exposure was calculated using linear wave theory, which has successfully been used to predict habitat distribution and benthic beta-diversity on reefs (Harborne, Mumby, Żychaluk, Hedley, & Blackwell, 2006; Chollett, & Mumby, 2012). Full details of the method are described elsewhere (Ekebom, Laihonen, & Suominen, 2003), including their application to reefs (Harborne et al., 2006; Chollett, & Mumby, 2012), and are only described briefly here. Firstly, average weekly wind speed and direction for each ~25 km^2 cell across the region was obtained from QuikSCAT satellite scatterometer data (from 2005 to 2009), available online[7]. These data were then used to calculate mean wind speed in each 25 km^2 cell in each of eight directions (N, NE, E, SE, S, SW, W, and NW), and the proportion of time the wind blew from that direction. The fetch to the nearest land mass or reef crest in each of eight directions (N, NE, E, SE, S, SW, W, and NW) from each reef cell was then calculated using bespoke MATLAB code. The wave exposure in each direction was then calculated using fetch, mean wind speed and direction data, and linear wave exposure equations (Ekebom et al., 2003). An estimate of total wave exposure was calculated by summing the eight individual estimates of wave energy, weighted by the proportion of time the wind blows from each direction. Because of the lack of detailed bathymetric data needed to attenuate wave exposure with increasing water depth, surface wave exposure was used. However, this metric is likely to be a good estimate of the exposure experienced in each cell since this project focuses on shallow-water habitats.

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[7] http://www.ssmi.com/qscat/

APPENDIX S3 – ADDITIONAL ANALYTICAL RESULTS AND MAPS

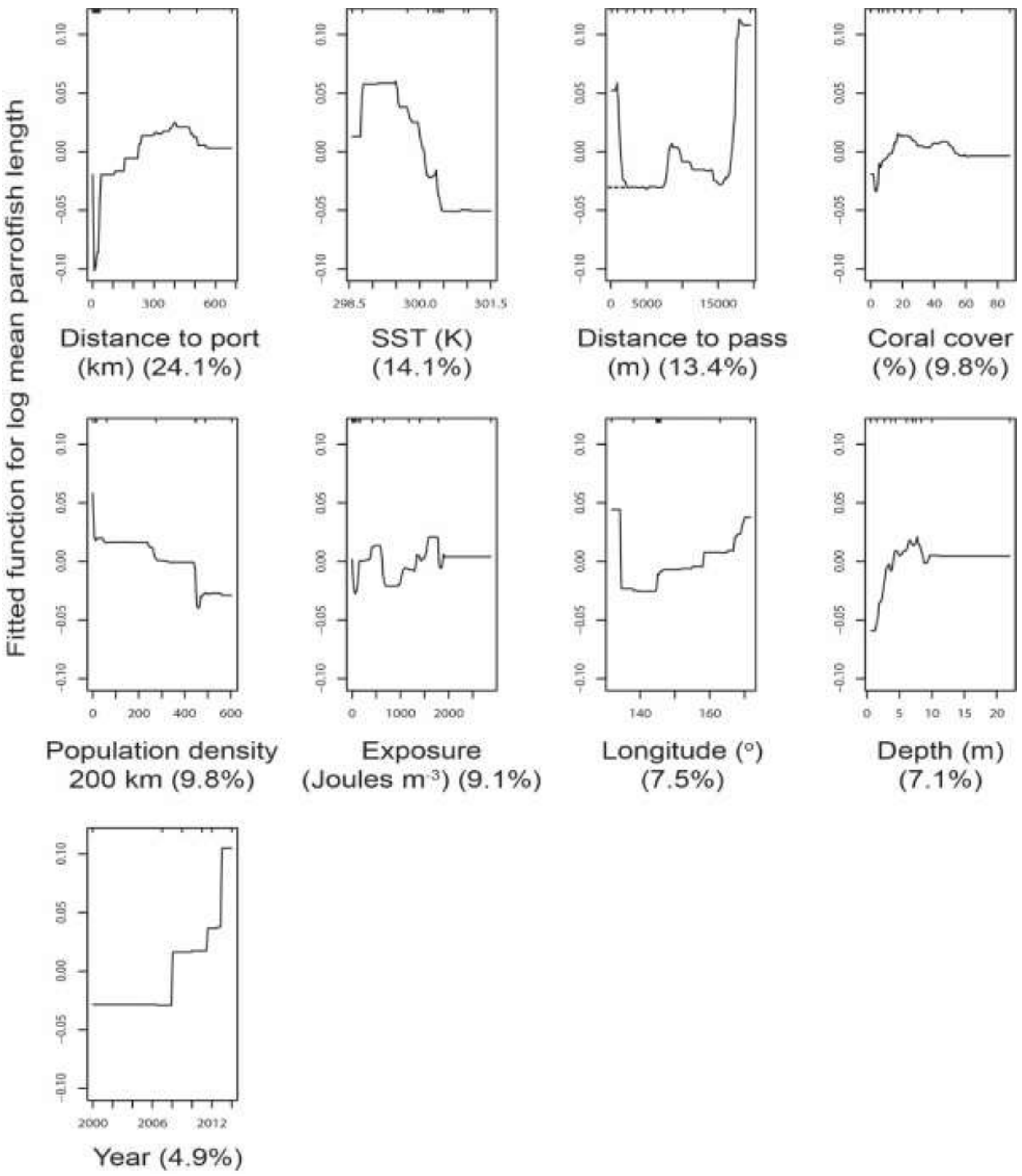

FIGURE S3.4 All partial dependence plots retained in the minimal boosted regression tree model of mean parrotfish length. Figures in parentheses represent percentage of explained deviance attributable to each variable. SST = sea surface temperature. Y axes centred to have zero mean over the data distribution (15 – 47.5 cm prior to transformation). Rug plots inside the top of plots show distribution of values, in deciles. For distance to pass, dotted line shows modification of fitted function used for fishing pressure predictions.

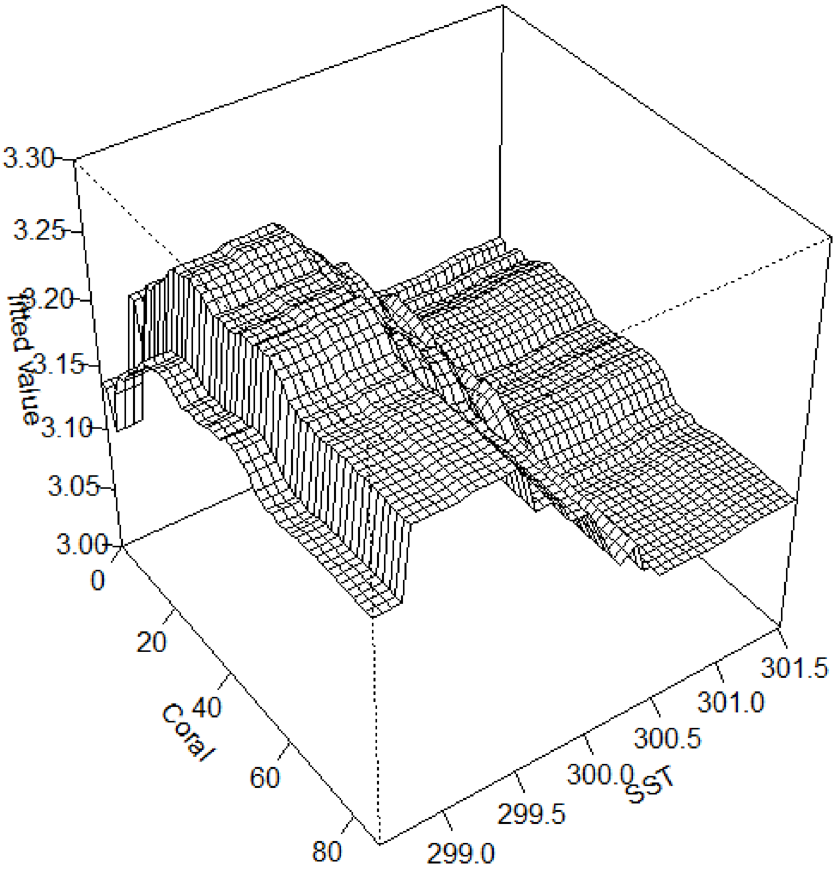

FIGURE S3.5 Three-dimensional partial dependence plot for the strongest interaction (coral cover and sea-surface temperature) in the model for fishing pressure (mean parrotfish size).

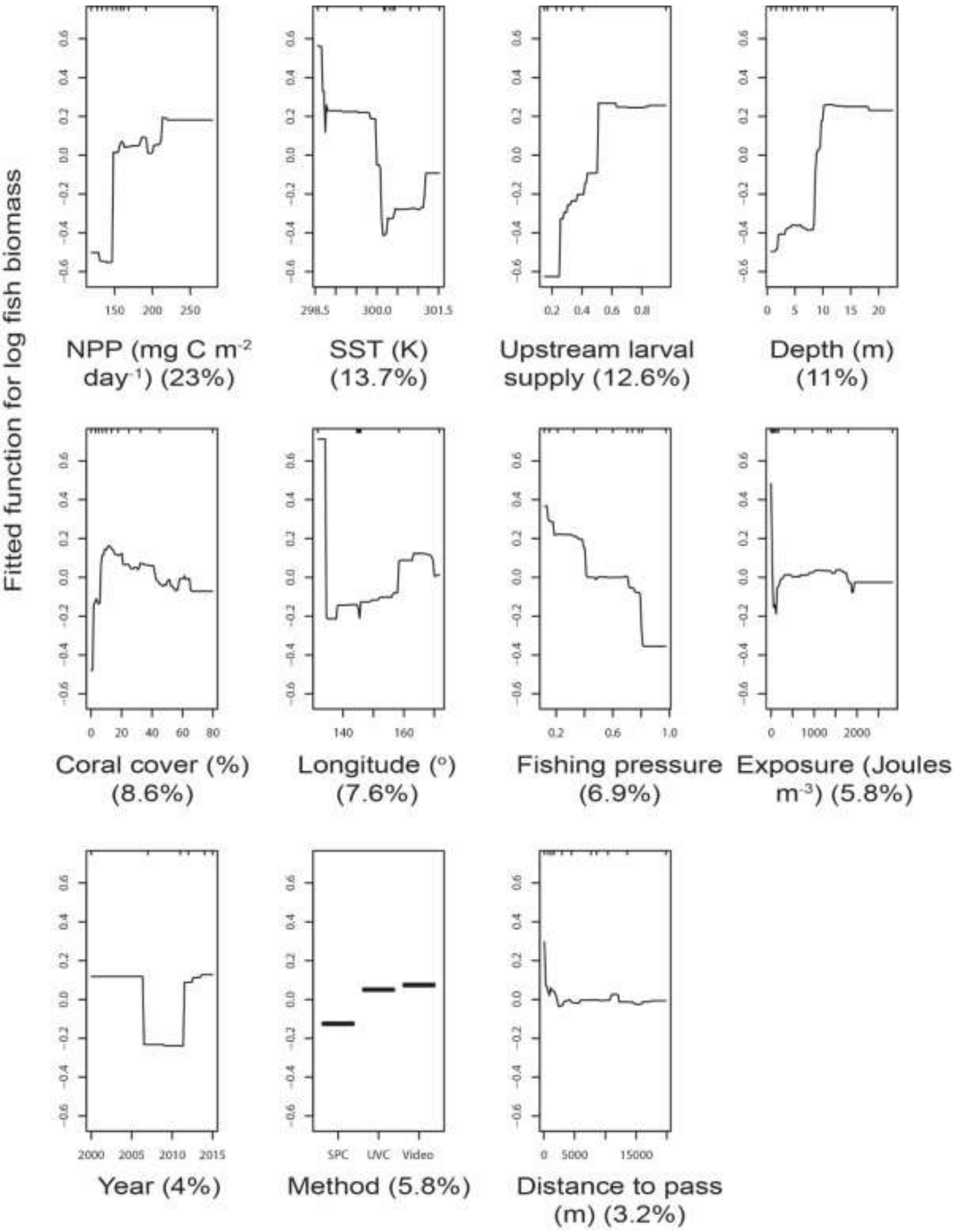

FIGURE S3.6 All partial dependence plots for variables retained in the minimal boosted regression tree model of total biomass of the 19 focal species. Figures in parentheses represent percentage of explained deviance attributable to each variable. SST = sea surface temperature; NPP = net primary productivity. Y axes centred to have zero mean over the data distribution (0 - 517.9 g m^{-2} prior to transformation). Rug plots inside the top of plots show distribution of values, in deciles.

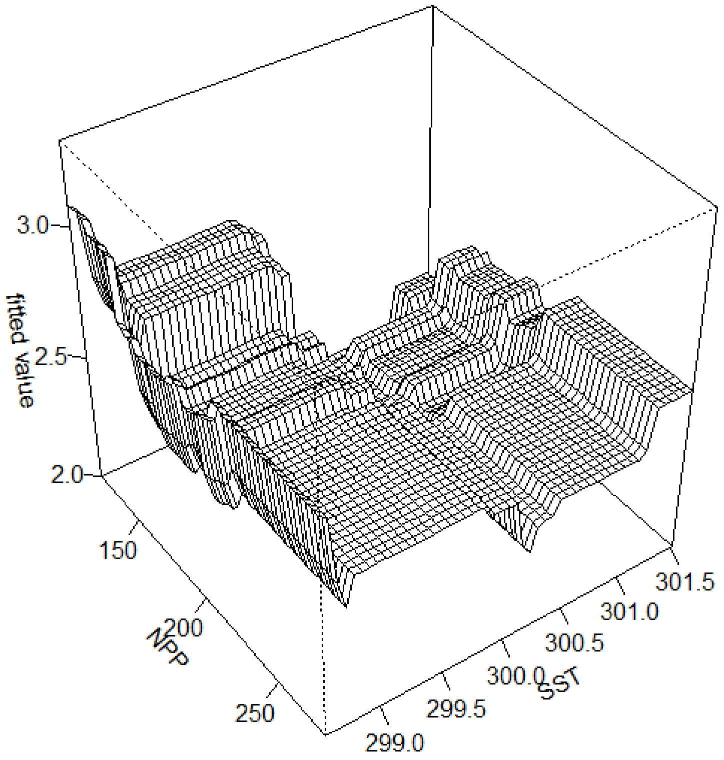

FIGURE S3.7 Three-dimensional partial dependence plot for the strongest interaction (net primary productivity and sea-surface temperature) in the model for total biomass of the 19 focal species.

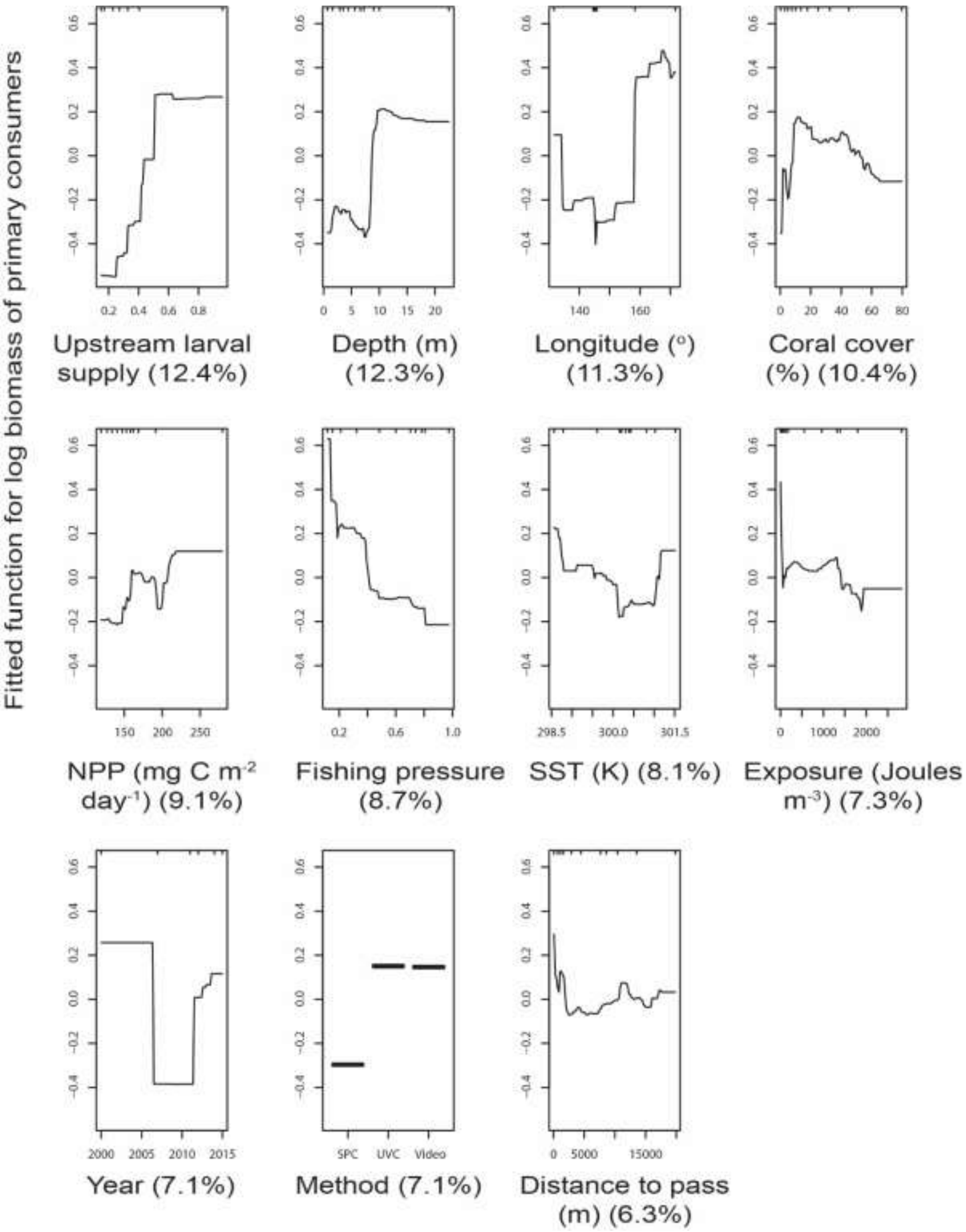

FIGURE S3.8 All partial dependence plots for variables retained in the minimal boosted regression tree model of total biomass of primary consumers. Figures in parentheses represent percentage of explained deviance attributable to each variable. SST = sea surface temperature; NPP = net primary productivity. Y axes centred to have zero mean over the data distribution (0 - 201.4 g m^{-2} prior to transformation). Rug plots inside the top of plots show distribution of values, in deciles.

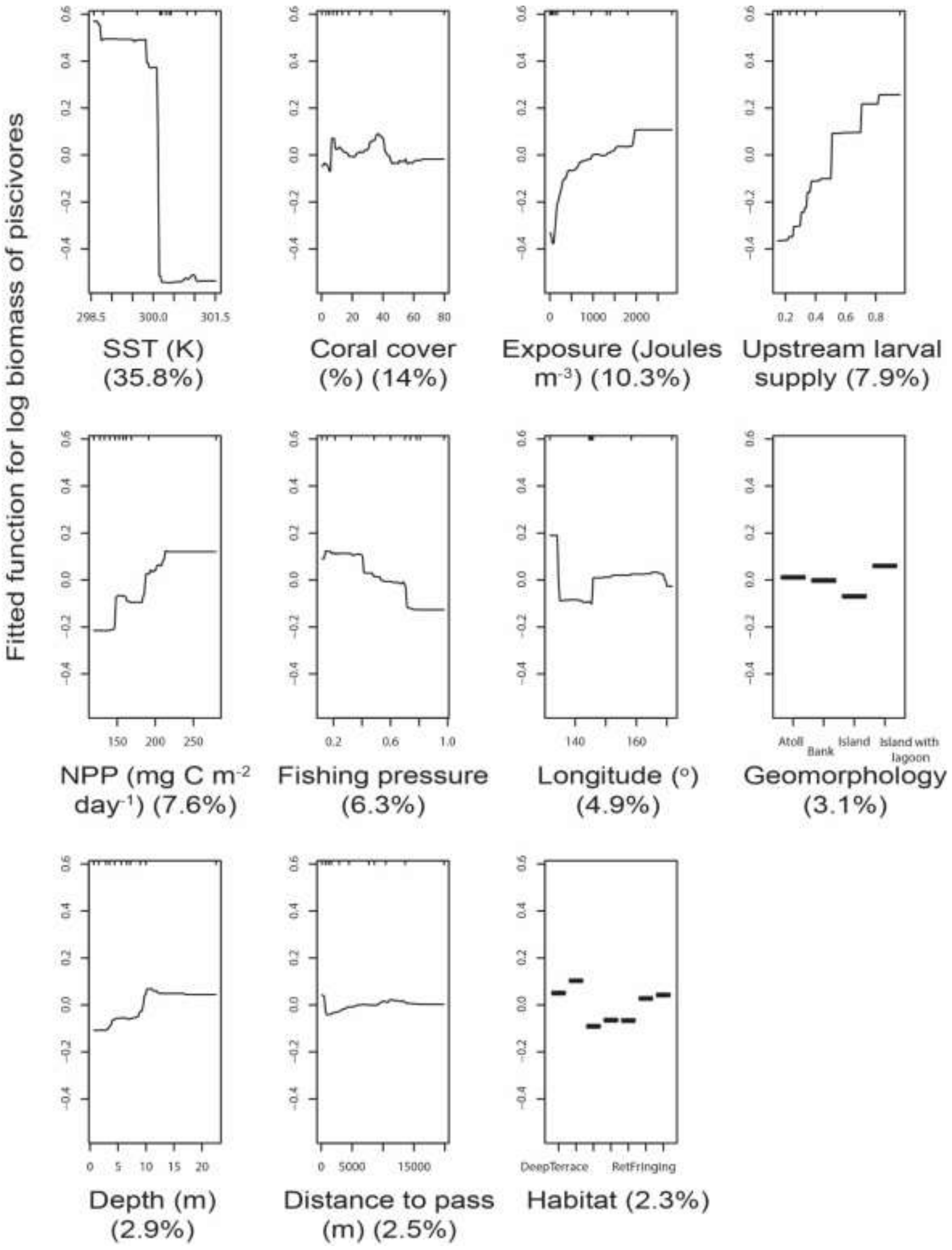

FIGURE S3.9 All partial dependence plots for the variables retained in the minimal boosted regression tree model of total biomass of piscivores. Figures in parentheses represent percentage of explained deviance attributable to each variable. SST = sea surface temperature; NPP = net primary productivity. Y axes centred to have zero mean over the data distribution (0 - 110.2 g m^{-2} prior to transformation). Rug plots inside the top of plots show distribution of values, in deciles.

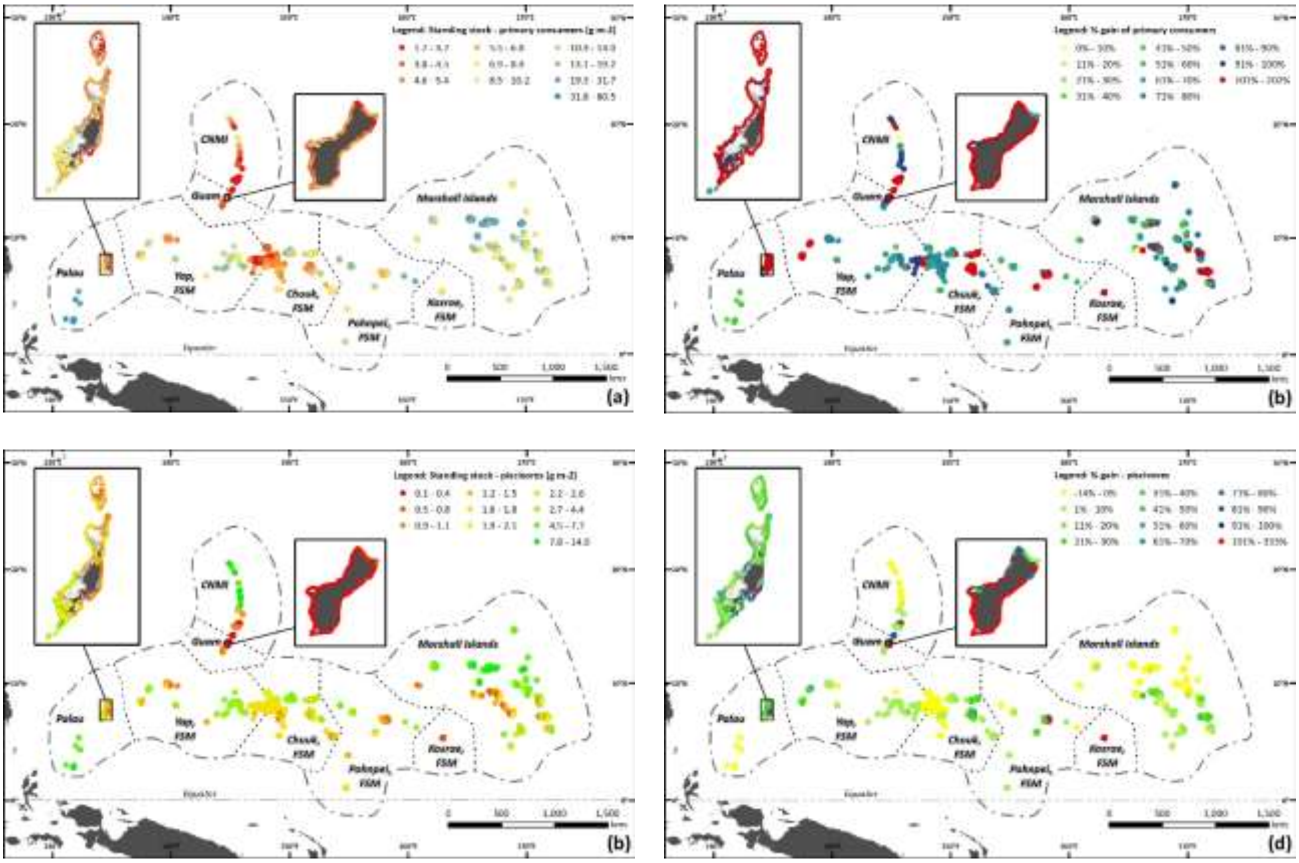

FIGURE S3.10 Regional maps of predicted current biomass and predicted potential percentage gain in biomass in the absence of fishing of (a, b) primary consumers and (c, d) piscivores among the19 focal fish species. Each panel includes larger-scale insets of Palau and Guam to show actual map resolution.

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