

**MARINE PROTECTION AND FOOD FISH RECOVERY
PATTERNS IN MICRONESIA**

BY

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Abstract

Micronesia's coral reefs host valuable but dwindling fisheries resources, which are important to local communities and are ecologically vital for reef stability and resilience. In recent decades, greater awareness of reef declines has helped foster strong and ongoing initiatives for protection of reefs throughout the region. Yet, quantitatively little is known about recovery in Micronesia, less still is known about the responses of important food-fishes within these isolated reefs. For reefs designated as protected areas, stability brings about new opportunities for food fish and communities to recover. With the increased extent of demand for reef fishes, identifying species responsive to protection can provide relevant evidence for optimizing protected reef networks, informing stakeholders, and guiding local and regional decision-making. Often the complexities of data analysis and differing methodologies prevent collective examination of valuable pockets of ecological data throughout Micronesia. Given today's rapidly and extensively-altered marine systems, simplifying the process of aligning and comparing regional data may help with broader contexts in modeling long-term reef fish populations.

This thesis study outlines a software-based methodological approach and robust analytical framework for evaluating change in marine communities, and presents results of these approaches on a typical fish dataset. In this study, food fishes present in marine protected areas were characterized and compared to nearby, fished reefs in a paired design. Results suggest that MPA food fish communities differed regionally, yet were driven by island and localized MPA-level differences in food fish community structure. Significant -yet collectively, marginal- differences in biomass occurred between MPAs and fished reefs throughout Micronesia, varying by jurisdiction, by individual reef, by species, and by functional group. Some MPAs showed no response, or showed negative responses, despite positive responses in specific functional or trophic

groups within these reefs. Yap showed exceptional levels of biomass, setting the standard for levels of biomass but with comparatively minimal differences between MPAs and fished reefs, Chuuk saw the greatest differences in MPAs across quantitative metrics, and Palau excelled predominantly when measuring response but had marginal absolute differences. Focal species and functional groups responded to the increased stability of MPAs in discordant ways, revealing novel complexities in species patterns. Overall, this study proposes evidence suggesting the need for complementary legislation protecting several important food fish species common on reefs throughout the region, and provides added perspective for further examination of marine protection in Micronesia and elsewhere.

Keywords: *marine protected area, food fish, coral reefs, regional marine policy, Micronesia*

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Academic statement can be logically understood as the formation -or continuation- of a valid and unifying thought process or methodology. I acknowledge all whom are cited in the subsequent pages of this thesis for their sound logic, and their contributions to my scientific understanding of the natural world. I also acknowledge the valuable advice and feedback from my committee, from colleagues, and from countless individuals who helped form my rationale.

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Many thanks to all who have suffered with me through my academic growth, particularly my family, and to all who helped in the pursuit of this achievement. In equal measures, I hope that this work serves to inspire others in search of scientific knowledge, and informs those seeking tools to minimize our pervasive human impact on the region's deteriorating coral reef systems.

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Introduction

Spanning Earth's equatorial oceans, one of the planet's most ecologically diverse and biologically productive ecosystems is the tropical shallow-water marine environment (Nelson 1999). Yet, strong evidence reveals extensive and dramatic reduction in marine diversity and richness (Babcock et al. 2010). More specifically, human activities negatively affect coral reef trophic diversity (De'ath & Fabricius 2010; Jackson 2008), functional capacity (Bellwood et al. 2004), and species distribution patterns (Golbuu et al. 2011a; Hughes et al. 2002). Of particular concern are shifting historical species baselines across many Pacific and Caribbean islands towards reduced trophic and functional potential on significant expanses of coral reefs (Mumby et al. 2006). Disturbances on reefs are well-documented, yet evidence suggest that relative contribution of key stressors remains predominantly site and context-specific, with strong human effects (Wolanski et al. 2003; Burkepile and Hay 2008; Rasher et al. 2012; Caveen et al. 2015). Despite evidence of fisheries depletion and reduced gains, Micronesia's sorely-undervalued and fully-exploited nearshore reef stocks remain in high demand (Houk et al. 2012; Rhodes et al. 2011).

Limited options for alternative livelihoods, improved technology, and overfishing of poorly-assessed stocks all contribute to the regional declines (Houk & Musburger 2013; Rhodes et al. 2011). Considerable political, socioeconomic, and scientific barriers arise when addressing these three issues. First, developing feasible alternative livelihoods requires contextually-relevant public policies alongside strong local and technical support systems (Richmond et al. 2007). Second, with increased income the learnt fisher will likely continue to maximize catch using

improved technology (Hardin 1968), unless greater human awareness (and collective-knowledge) of natural limitations helps depleted populations recover to sustainable levels requiring less effort for similar gains. Third, at the risk of disparaging the well-studied and empirically complex academic theories and scientific models proposed and confirmed elsewhere, rigorous assessment of reef-community feedback responses to protection are regionally limited, particularly for Micronesia. As new observational data is collected, what empirical methods can be utilized to efficiently display evidence of recovery (i.e., increased food-fish stock) or improved management (i.e., effective policy) across local, island, and regional scales of food-fishes? For the fisher, as with the manager, local perspective is the primary mode for selecting which species are of importance. Furthermore, if declines continue under current harvest levels, and with current (and highly variable) management initiatives in place (i.e., marine area protection, harvest moratoria, gear restrictions, etc.), which food-fish species will benefit most from protection (or vice versa)?

Managing public marine resources generally involves giving a resource the time and opportunity for recovery (i.e., restricting entry, managing harvest). One common method implemented in various forms throughout the tropics designates portions of coral-reefs or coastal marine areas as protected areas (hereafter, MPAs). Throughout the world, MPAs are acknowledged in significant recovery of heavily-targeted fishes (Russ et al. 2004; McClanahan et al. 2009), and can benefit migratory and long-range foraging fishes from diverse trophic levels (Green et al. 2014). Studies also demonstrate multi-species larval contributions to adjacent reefs, enhancing neighboring reefs open to human activities (Green et al. 2015; Harrison et al. 2012). Larger fish stocks in less-fished reefs reduced impacts from disturbance-related outbreaks of Crown-of-Thorn Starfish on reefs in Australia, Yap, and Fiji (Dulvy et al. 2004; Houk et al. 2012; Sweatman 2008), while high local

diversity helped ameliorate the impacts of coral disease in the Philippines (Raymundo et al. 2009). Overall, provided that restrictions are well-enforced (i.e., reduction of fishing in comparison to a neighboring reef), MPAs are a beneficial and natural means for the recovery of food-fishes.

Reef community structure in context

Coral-reefs operate from microscopic to oceanic contexts of ecosystem function and energetics (Hatcher 1988; Houk 2017). Complex biological and physical processes drive species abundance and reef community diversity patterns (Adam et al. 2011; Wolanski et al. 2003). Although hundreds of kilometers of ocean separate shallow-water communities, regional genetic connectivity exists for reefs across Micronesia (Davies et al. 2015), indicating that ocean-level hydrodynamic processes (e.g., equatorial and island currents) can provide spatial opportunity for a substantial diversity of dispersing species, while local climate cycles and availability of reef habitat (e.g., Pago Bay, Guam) regulate reef-level community structures and population dynamics. The insular nature of island reefs, and seasonal variability are strong drivers of fish population structures. Sea-surface temperature, island type, and human population measures are strong local drivers on islands (Heenan et al. 2016; Taylor et al. 2014). Ultimately, the typical reef fish community in Micronesia will vary across a diverse set of species and functional groups, which often have spatially-limited feeding ranges and partially-errant movement patterns (Green et al. 2014). This study assessed population variations of fishes targeted for commercial and subsistence consumption on individual MPAs across jurisdictions, and across the region-particularly for prominent or abundant species groups that serve important functional roles, which should vary minimally between neighboring reefs within islands. Functional groups are defined as related species with similar ecological roles (i.e., herbivore) and body sizes (i.e., small or large-bodied).

The biogeographic assortment and organization of fish species –on physically connected coral reef communities- can be characterized by considering fish species differences in territory and range (Green et al. 2014; Marshall et al. 2011), density-dependent factors such as competition and predation (Beukers & Jones 1997), site-specific factors such as habitat complexity and benthic rugosity (Harborne et al. 2012), and large-scale dispersal mechanisms (Hastings & Botsford 2003), which propel reef communities towards similar population structures across the region. Overall, although stochastic processes drive regional and island-wide assortment of fishes on Micronesian reef features (Kendall et al. 2016), populations are purported to be prominently self-seeding at the island scale (Wolanski & Kingsford, 2014), are heavily influenced by the collective influence of local fishing at the regional scale (Houk et al. 2012), and vary minimally by taxa that are assumed to be ancestrally (if not spatially) linked. A typical reef feature, such as Reey on the south western coast of Yap, hosts many species assemblages similar to those found on distant barrier reefs throughout the rest of Micronesia (e.g., Ileakl Beluu, Ngardmau Village, Palau; Kehpara, Enipein Village, Pohnpei; Woja, Majuro Atoll, Marshall Islands). One corollary line of rationale states that heavily-targeted reef species, all else equal, are collectively responding with similar direction and magnitude to disturbances (i.e., fishing) or lack, thereof (i.e., marine protected area).

Generally, reef resilience (the ability to recover from –or resist the effects of- chronic disturbance) is attributed to high species diversity and functional redundancy (Green et al. 2014). Chronic and intensive fishing can alter complex predator-prey relationships and functional diversities (Sebastian & McClanahan 2012). Overfishing of herbivorous species increases the competitive dominance of macroalgae over corals on reef substrates (Almany 2004; Golbuu et al. 2011b).

Herbivory rates and benthic grazing potential are important drivers of ecosystem function, often by effecting strong feedback on local and regional community patterns. Grazing by individuals and schooling fishes promotes benthic diversity on reefs dominated by corals and coralline algae (Hixon 1997; Hoey & Bellwood 2009; Mumby et al. 2013). Ultimately, species community structure is an important determinant of reef health across the region, while recovery trajectories are driven by socioeconomic, cultural, and commercial dimensions (Caveen et al. 2015; Lubchenco et al. 2003). Tenure systems, human population density, strong stakeholder involvement, and user compliance also predict local species recovery (Pollnac et al. 2010; Richmond et al. 2007; Russ et al. 2004). Thus, human self-restraint is possible through these lenses.

Micronesia's MPAs at a Glance

Micronesia is comprised of relatively small, geographically insular islands surrounded by highly productive nearshore reefs and intertidal beds. The region's terrestrial vertebrate fauna is species-destitute in comparison to larger land masses, with a handful of introductions from prehistoric human migrations (Wickler 2002), yet the five island jurisdictions in this study boast highly diverse marine fauna (Johannes 1978). Although geographically distant, with culturally diverse peoples (Wickler 2002), island communities throughout the region all traditionally perceived reefs as a resource of paramount importance to local livelihoods and identities (Johannes 1978). Reef activities were managed at the individual village or reef level, primarily by ranking or designated community members, who served as stewards of the reef system and oversaw harvest activities (Johannes 1981). Following western contact in the region, much of the traditional ways of managing reefs were lost, as the overwhelming effects of globalization destabilized previously-isolated socioeconomic structures. Adaptation of western governance eroded much of the local

stakeholder authority over reefs adjacent to villages and districts, and by the 20th century, long-standing traditional tenure systems had greatly diminished throughout the region (Johannes 1978).

As newly instituted forms of government had more pressing issues and transitions to contend with, legislation establishing site-level stakeholder authority (i.e., to declare and manage a reef area) were slow to materialize (Graham & Idechong 1998). Although publicly-owned fishing rights (e.g., offshore tuna fisheries) were well-defined and regulated under jurisdictional legislation by the turn of the millennium, reef tenure (i.e., traditional designation by village or leadership) over productive local reefs adjoining communities eluded judicial clarity throughout many districts within the island jurisdictions. In particular, site-level management (e.g. traditional closures, gear restrictions) often lack the legal footing needed to enforce regulations. In recent decades, greater awareness of reef declines has helped foster strong and ongoing initiatives for protection of reefs throughout the region, such as the Micronesia Challenge, a treaty, which sets clear targets for conservation in five member-countries. Still, evidence of fish recovery across the 4,000-km expanse remains sparse. More than a decade after the region's collective scientific and governing bodies reviewed and ratified the treaty, little is known about recovery in Micronesia, less still is published on responses of food-fish communities and taxonomic groups to protection.

While compiling metrics to evaluate ecosystem condition, Houk et al. (2015) reported that three (3) out of ten (10) MPAs in their region-wide assessment were meeting the Micronesia Challenge effective-conservation threshold scores. In Palau, five out of seven well-established MPAs were reported as successfully increasing biomass of food fishes (Friedlander et al. 2017). These studies asked two different questions. The former was a regional study based on an ecological “score”

derived from multiple datasets, designed for broad, regional analysis, yet lacking in samples of reference to MPAs. The latter was limited to a single island, yet provided robust measures of MPA-level sampling, with comparable replicates on fished reefs. With the revival of traditional stakeholder groups and organizations having regained authority to establish and enforce protected areas, resounding questions have emerged, regarding the precise nature of protection and recovery on reefs. Controlled in experimental design, or accounted for by large spatial scales crossing natural boundaries, local value systems, and environmental regimes consistently, ecological responses can provide insight into regional protection, and reveal the underlying limits of ‘and correlates between’ marine protection, fish community structure, and future recovery in the region. Using a robust and observationally-comparable data, this study posed three questions.

First, do food fish *communities* show a regionally-collective, significant increase to protection? As a management tool, MPAs remain a highly-debated form of resource management. Their popularity in Micronesia, both traditionally and currently, provides a cogent argument for evaluating the overall effectiveness –and limits- of this tool. Second, do heavily-targeted, reef-associated fish *species* or *groups* respond linearly to protection, and do they take on biogeographic (i.e., spatial scale and assortment of species community) characteristics (Micheli et al. 2004; Taylor et al. 2014)? Regional assessments require comparable data (Houk & van Woesik 2013), yet such datasets often differ in methodologies and study goals, which can limit broad-scale compilation, analysis, and interpretation of datasets (Kulbicki et al. 2010). Regional larval predictions exist (Kendall et al. 2016), yet, evidence describing biogeographic character in food-fish species or group response to protection is comparably less evident. Third, what proximal characters (e.g., size, habitat type, exposure, governance structure, etc.) are associated with

positive responses of fishes in MPAs? Frequently, recovery trajectories coincide less with scale (i.e., neighboring MPAs versus MPAs across a common eco-region), instead driven by local habitat constraints and management conditions (Allison et al. 1998; Fox & Bellwood 2008; Houk et al. 2015). Using a regional dataset, with high replication and comparable reference sites, this thesis outlines a set of statistical methods that were used to assess change in protected areas across Micronesia, provides results of tests assessing protection by characterizing food fish responses, and discusses some practical aspects of recovery on MPAs (and their management implications).

Methods

The dataset for this study originates from five jurisdictions across Micronesia, each culturally and socioeconomically distinct (Fig. 1). Beginning at the limits of the coral-triangle, and spanning 4,000 km eastward, these are: the Republic of Palau (ROP); Yap, Chuuk, and Pohnpei States (FSM); and the Republic of the Marshall Islands (RMI). A subset of MPA study sites were selected in each jurisdiction for detailed investigations. MPA sites were publically declared and actively managed by a resource agency or site-level stakeholder assembly. MPAs differed in ecology, size, governance structure, and management history. Overall, as outlined by the MC steering committee (2011), sites were determined by resource agencies as reflecting governance priorities and management efforts within each respective island jurisdiction. Three sites in each island (except four (4) in Palau) were surveyed based on information and recommendations from experts within jurisdictions (e.g., Yap Community Action Program, Conservation Society of Pohnpei, etc.).

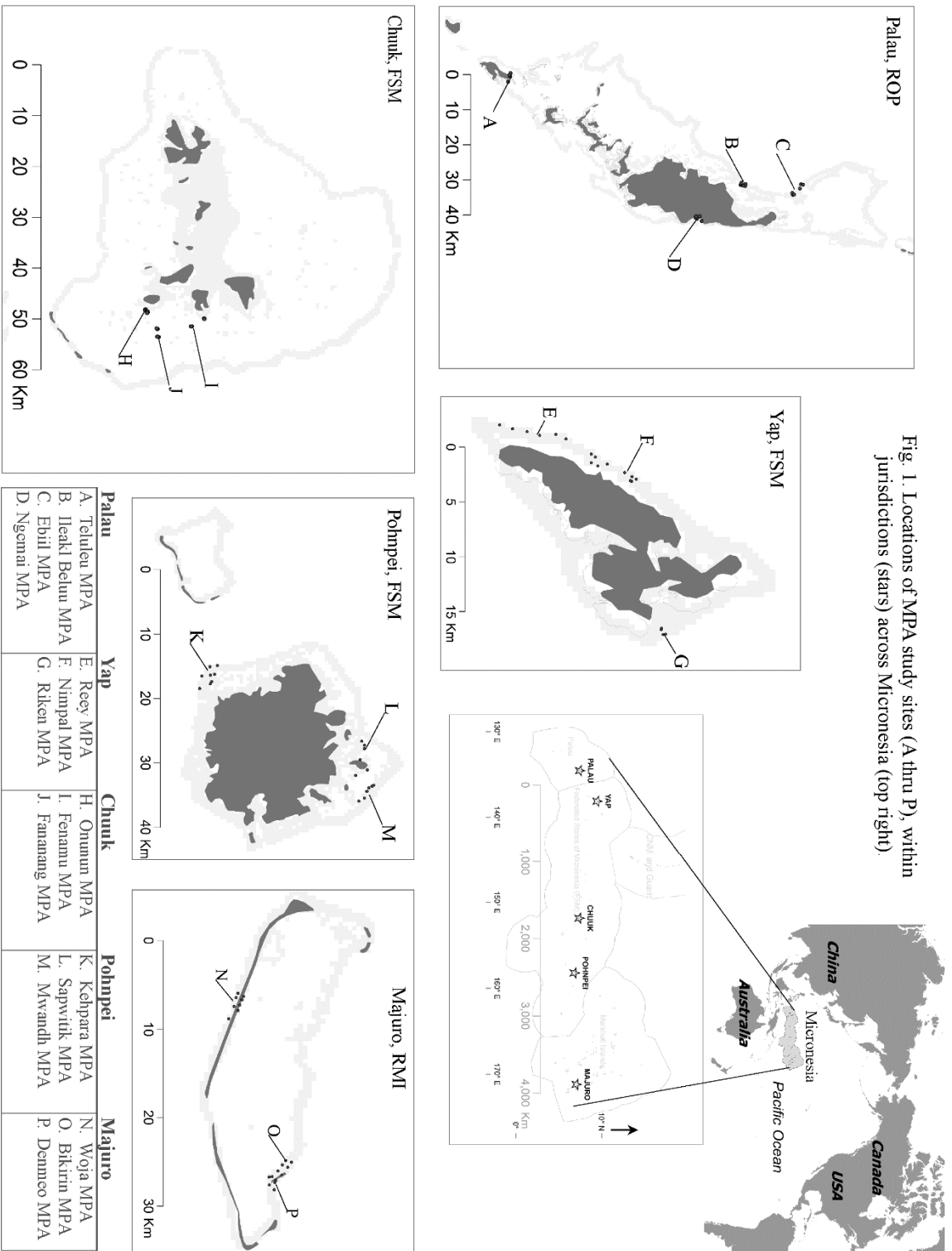


Fig. 1. Locations of MPA study sites (A thru P), within jurisdictions (stars) across Micronesia (top right).

Stakeholder agencies also guided selection of survey stations at each MPA. Technical briefs and data summaries for each jurisdiction in this study are publicly available at the Palau International Coral-reef Center (PICRC) academic repository, which describe site characters and outline preliminary test results. The present study expands on the fish survey results; first, by compiling jurisdiction-level datasets into a single, spatially-scalable and robustly-sampled set from across the region; and second, by conducting tests of statistical power and quantitative significance across geographic scales and between commonly-occurring taxa and ecologically-distinct subgroups.

Data Collection

Standardized measures and field survey protocols (MC 2011) were used to collect fish data, and samples were replicated as spatially-comparable belt transect pairs within stations (Fig. 2) at 16 MPAs and neighboring, fished reefs. Reef survey stations (Table SIV) consisted of five (5) concurrent 5 m x 50 m belt transects, which were surveyed at a rate of $0.5 \cdot \text{m sec}^{-1}$, along a depth of 10 m consistent with respect to the reef slope (except for Teluleu MPA, an intertidal seagrass bed with mean depth of 2 m). Each site had between two and five survey stations, which were placed haphazardly within logistical sampling limits. Placement of reference stations, and planning of surveys ensured repeated observations of individuals (i.e., spatial autocorrelation) was avoided. MPA-Reference pairs were considered comparable “spatial moments”, observations that were recorded by one surveyor, who identified and recorded the estimated size of individuals to the species level, based on a list of locally-harvested, diurnally-active food fishes. Three (3)

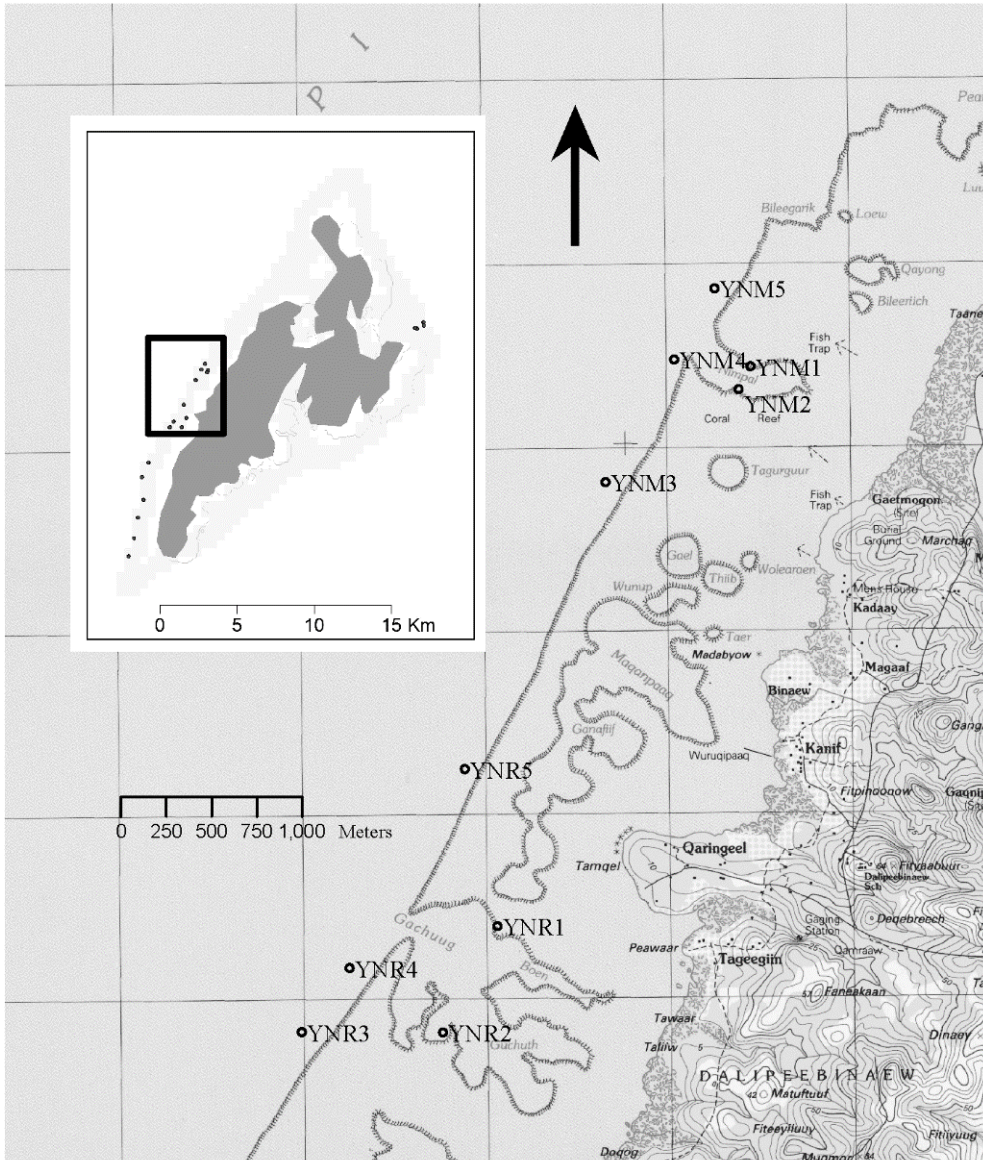


Fig 2. Locations of 5x50 m replicate stations at Nimpal MPA (YNM 1-5) and its comparable, fished reef (YNR 1-5) in Yap, FSM (inset).

experienced fish observers conducted surveys (JI – 62%, AM – 20%, and AB – 18% of sites, respectively) consistent within jurisdictions (i.e. all Chuuk MPAs) and between matched MPA-vs.-Reference pairs (M-vs.-R). For several species of parrotfishes, where identification could not be confirmed, members were named according to the next greater taxonomic unit (*Scarus sp.*). In total, visual census of 75 food fish species were recorded. Published species length-weight metrics were used to convert size to biomass, and used in conjunction with abundance for analyses.

Data analysis

Aims of this thesis study were twofold: first, to compile a set of robust software-based, parametric and non-parametric, heuristic tools for evaluating fish survey data; second, to apply this framework in assessing the aforementioned dataset. Windows-based versions of *R* (R Core Team 2016) and *Primer-E* (Clarke & Gorley 2009) served as platforms for handling data, performing calculations, and reproducing graphs. The *R* software contains a digitally open-sourced interface for the sharing of code-based, user-created computational and graphical ‘packages’. Packages were investigated for compatibility, efficiency, and flexibility. Compatibility was measured as the time needed to identify the structure, transform as needed, and conduct appropriate tests on datasets; efficiency was measured by the number of packages required to complete an analysis; flexibility was measured as the required number of steps to reproduce results on a typical dataset. Appendix I lists key portions of *R* code packages used, and sources for finding permanent data-access locations on the World Wide Web (i.e., *https*). The multi-variate approach utilized *Primer-E*, a digitally-licensed software program, to perform permutation-based analytical statistics and ordination of data summaries (Clarke & Gorley 2009). The utility of this software was in graphical reference and *post-hoc* exploration and characterization of species and functional group responses.

Hypothesis tests examined regional and local coral reef fish population character and structure by answering the following broader questions: 1) in Micronesia, are there significant differences between food fish community metrics (e.g., biomass, abundance) in MPAs compared to adjacent (fished) reefs, and if so, to what geographic extent?; 2) do these species (e.g., *Cetoscarus bicolor*, *Plectropomus areolatus*, etc.) or functional assemblage (e.g., large-bodied parrotfish, large-bodied

grouper, etc.) metrics vary across biogeographic scales, and –if so- by how much?; 3) what is successful recovery (i.e., positive difference in biomass), and what ecologically relevant scales of change can be inferred in a fish survey dataset? First, regional, island, and MPA-level differences between food fishes on protected reefs were compared to neighboring, fished areas across jurisdictions and MPAs (nested within). Then, difference coefficients representing this trajectory, herein *relative difference*, denoted using the symbol omega Ω , were calculated as a quantitative measure of change in total (or mean) species biomass or abundance. Effect sizes for a list of commonly-occurring species and prominent functional groups were determined, and used in hypothesis testing. Lastly, site characters (i.e. MPA size, habitat type, exposure, managing body) were assessed for contribution to differences in species and functional groups. Even with transformations applied as necessary (i.e., Box & Cox 1964), the raw dataset (and the majority of transformed subsets) failed to meet assumptions of normality. Graphical explorations of the data as frequency histograms and quantile-quantile plots revealed sensitivity of the Shapiro-Wilk test to outliers. Data were further treated by removal of rare and outlier species (i.e., standard deviation of *species A* biomass > mean of *species A* biomass), which excluded approximately 24% of observed individuals. The treated dataset was visually normal, yet, constrained by this alteration. Parametric tests, therefore, were used minimally and were limited to community-level analyses.

Absolute difference

Parametric (paired *t-test*) and non-parametric (Wilcoxon signed-rank test) methods were applied to the full dataset after investigations of normality (Shapiro & Wilk 1965) and homogeneity of variance (Levene 1960). In this study, the two hypothesis-driven approaches assert precise, yet distinct hypotheses, relating to differences between measurable quantities in a paired dataset (i.e.,

independent-but-comparable observations). A paired *t-test* assumes that data (i.e., biomass) are normally distributed with homogeneous variances, and computes a probability statistic with differences between actual values (i.e., between paired M-R transects). A null hypothesis would be that no statistical difference exists between the distribution of differences between transect pairs (i.e., M vs. R), the alternative accepted if differences otherwise did not fit a normal distribution curve (i.e., skewed). The Wilcoxon signed-rank test, on the other hand, makes no assumptions regarding sample or population distributions, relying instead on characteristics of the data (i.e., rank, frequency, etc.). Being distribution-free, the test is robust to non-normal and skewed sample distributions (Wilcoxon 1945). In this context, a null hypothesis would be that there is no stochastic difference between the two observations (M vs. R), the alternative accepted if statistically significant differences occurred. Used on the same data, the tests will produce differing results and interpretations. In the present context, the former approach assessed the probability that the mean difference between paired transects is equal to zero (no significant difference between M and R), while the latter determined the likelihood a randomly sample pair will have greater values (i.e., total biomass) in M, compared to R, or vice versa. Point estimates and confidence intervals for paired *t-tests* were derived using back-transformed means and standard deviations, while those for Wilcoxon tests were constructed with methods outlined by Rosenbaum (1993), using Hodges & Lehmann's calculations for estimating location shift (1963).

Effect size

Both approaches were also accompanied by calculations of effect size, which served to measure rigor for significance tests, determine recovery thresholds, and evaluate biogeographic differences in individual species and functional group biomass. Parametric tests utilized Cohen's *d* (Cohen

1988), the difference of mean values between MPA and paired Reference transects, divided by the pooled standard deviation of all paired transects. However, this method of estimating effect size has been shown to perform less optimally when parametric assumptions are violated (Hess & Kromrey 2004), a common occurrence with ecological surveying methods (i.e., fish census data). Stratified by jurisdiction and by MPA, effect sizes for non-parametric tests were derived using Cliff's *delta* δ (Cliff 1993), which is the difference between the number of sampled times (#) that total biomass observed within an MPA (M) transect is larger ($>$) than its Reference I transect, and its inverse ($\#M < R$), divided by the total number of pairs. These values, between -1 and 1, represent the degree of overlap between two sets of paired observations, going to zero when they completely overlap, and increasing (the likelihood that a sample pair will have greater transect biomass in M) or decreasing (it's inverse) when the two distributions are farther apart. δ were derived for all sample pairs (δ_{global}), for pairs within jurisdictions (δ_{island}), and for pairs within MPAs (δ_{mpa}). For all calculations, bootstrap procedures with bias-correction were applied in the construction of confidence intervals (Rogmann 2013; Ruscio & Mullen 2012).

Relative difference

To fully utilize the comparative sampling design, a straightforward computation of transect-level differences determined the relative differences (Chapman & Kramer 1999) of observed change in biomass, mean size, and abundance of fishes, with transect summaries as sampling units. Here, *relative differences* (Ω) were calculated as the difference between total biomass of each transect pair, divided by the sum of the pair ($M-R/M+R$). These values, between -1 and 1, represent the degree and direction of change at varying spatial scales discussed above. Not all species or groups were represented in all jurisdictions or MPAs, with minimal diversity (i.e., mostly zero values) at

the transect level ($\text{kg} \cdot 250 \text{ m}^{-2}$). Thus, two (2) data subsets were derived from the original dataset, one with transect-level differences in six (henceforth, focal) species (*Cetoscarus bicolor*, *Chlorurus microrhinos*, *Lutjanus bohar*, *Lutjanus gibbus*, *Naso lituratus*, and *Plectropomus areolatus*) and another of transect-level differences in five (henceforth, functional) groups (large-bodied groupers, large-bodied emperors, large-bodied parrotfishes, large-bodied snappers, and rabbitfishes), representing 50.6% and 70.3% of observed individuals, respectively.

Within each species or functional group, a negative value indicated greater biomass in R, while a positive value indicated greater biomass in M. Weighted trophic-level, functional group, and focal species averages of Ω were derived for all transect pairs (Ω_{global}), for pairs within jurisdictions (Ω_{island}), and for pairs within MPAs (Ω_{mpa}). In this analysis, the aim was to detect instances where an ecological metric (i.e., total biomass) was above (or below) zero, indicating positive (or negative) response to protection. Arbitrary thresholds were subjectively imposed on ranges, to extract notable and extreme values (i.e., between $-0.02 < \Omega > -0.04$, and $0.04 < \Omega > 0.02$). During graphical explorations of Ω (for greater ecological resolution) transects were summarized by station ($\text{kg} \cdot 1250 \text{ m}^{-2}$) and also by MPA ($\text{kg} \cdot 4375 \pm 1875 \text{ m}^{-2}$) utilizing distance-based (Euclidean) dissimilarity matrices of species and groups in multivariate ordination space. These visualizations helped illustrate the strength in response, while one-way PERMANOVAs helped determine if relative responses varied significantly between jurisdictions, or between MPAs within jurisdictions. Although summarizing spatial data increases the likelihood of detecting meaningful large-scale differences, it also reduces precision, confounding detection of community nuance.

Multi-variate analytical tests were conducted on absolute biomass and relative biomass akin to univariate mixed-model designs, except significance was assessed using a bootstrapping procedure (Anderson and Gourley 2009). Multiple regression tests examined site and jurisdictional factors using values derived from spatially explicit datasets and published information, testing for significant drivers (i.e., human demographics, governance types, site characters) of successful protection, with paired *t-test* and signed-rank test results as *a posteriori* baselines. Nested-multivariate permutational analyses of variance (PERMANOVAs) helped determine the spatial scales where variation occurred. PERMANOVAs of standardized (z) scores (calculated as the difference between a transect value and the mean of all transect values, divided by the standard deviation of all transect values) for all functional groups were used to assess change in composition due to status between jurisdictions, and between MPAs nested within jurisdictions.

To generate a regional biogeographic baseline of MPA response, global effect sizes (δ) and relative differences (Ω) were calculated for focal species, and for dominant functional assemblages; where δ was the likelihood of observing a larger individual in a random sample of M (or its inverse); and Ω was a quantitative proxy representing the relative degree of difference in total biomass between M and R transect pairs. In one set of comparisons, Ω were evaluated across space, where local (i.e., transect-level) responses were summarized by MPA, by island, and for all transect pairs. In this setting, a notable response occurred when $|\Omega_{\text{mpa}}| > |\Omega_{\text{island}}|$, or when $|\Omega_{\text{island}}| > |\Omega_{\text{global}}|$. Similar comparisons were made for focal species (e.g., $\Omega_{\text{Pareolatus}}$) and functional groups (e.g., $\Omega_{\text{LB group}})$ at the reef, island, and global levels. For example, an instance where $\Omega_{\text{Pareolatus}}$ or its functional group, $\Omega_{\text{LB group}}$ on Kehpara MPA was above Pohnpei's Ω_{island} value suggested a (potentially) notable MPA response. Additionally, Ω were calculated for all species, using weighted averages

of jurisdictions and MPAs. Thresholds for what constituted a notable species response were derived by imposing range limits (i.e., values below the first, and above the third quartile ranges). These thresholds are expected to change with the incorporation of other relevant datasets measuring recovery of these species. In this study, results are presented and discussed within the context of the dataset employed, serving only as baseline. For example, if the mean size of all individuals of the species *Naso lituratus* was smaller, while total biomass was simultaneously larger in MPAs (relative to comparable fished reefs), this would suggest a (potentially) notable – yet, tentative- ecological response. Instances where the opposite occurred (i.e., relatively larger individuals but less relative biomass in MPAs) were also identified as noteworthy responses to protection. The end goal was to provide a robust set of quantitative evidence and methodologies to help form and revise empirically-backed statements about MPA response of reef fish species, as well as assemble baseline recovery trends at the local, jurisdictional, and regional scale.

Results

Global responses

Both a shift towards greater total fish biomass (paired t -test, $t_{239} = 3.63$, $p < 0.001$), and a stochastic inequality (Wilcoxon signed-rank test, $V = 16895$, $p < 0.01$) were detected, collectively between all MPAs (M) and their corresponding, referenI(R) reefs. The former, which tested whether differences between transect pairs were within normal probability parameters, estimated a mean difference of $3.53 \text{ kg} \cdot 250 \text{ m}^{-2}$. The latter, which tested the degree to which transect pairs overlapped, estimated a positive shift in median location of biomass at $1.09 \text{ kg} \cdot 250 \text{ m}^{-2}$. However,

while significant differences existed when grouping data across the entire region, the effect size estimates were low for both parametric (Cohen $d_{global} = 0.25$, 95% CI [0.34, -0.02]) and non-parametric (Cliff $delta$ (δ_{global}) = 0.11, 95% CI [0.25, 0.05]) hypothesis tests.

Jurisdictional responses

Two (2) out of five (5) jurisdictions had significantly greater community biomass in MPAs based upon paired t -tests of absolute values (two-sided, $\alpha=0.05$). Significantly higher biomass was found in Yap State ($t_{49} = 2.17$, $p < 0.05$); and in Chuuk State ($t_{34} = 2.65$, $p < 0.01$) MPAs compared to nearby, fished reefs (Fig. 2a), while no significance was found elsewhere (Marshall Islands, $t_{49} = 0.26$, $p = 0.796$; Palau, $t_{54} = 1.31$, $p = 0.099$; Pohnpei, $t_{49} = 1.008$, $p = 0.318$). Effect sizes in Chuuk and Yap were greater than the regional Cohen d effect size estimate (0.25), while Yap showed the largest mean differences in biomass of MPAs (Table I). Wilcoxon signed-rank test detected significance stochastic shift only in Chuuk, $p < 0.001$, $V=523$, location shift = 2.3 kg \cdot 250 m⁻² (93.2 kg per hectare), with none detected in the remaining four jurisdictions (Fig. 2b). Non-parametric effect sizes matched parametric estimates, except for Palau and Yap (Table II).

In sum, despite Yap's larger fish biomass quantities (i.e., total fish biomass per transect), significance of stochastic shifts in MPA sites was most influenced in Chuuk. Mean relative differences (Ω) in total community biomass within jurisdictions were greatest for Palau and Chuuk (Table SI), while moderately large for Yap, and small for Pohnpei and the Marshalls (Fig. 2c), partially discordant with results of paired t tests and sign rank tests of absolute values, and suggested that Palau's MPAs were indeed showing positive community response, despite a lack of significant difference detected in neither parametric, nor in non-parametric test procedures.

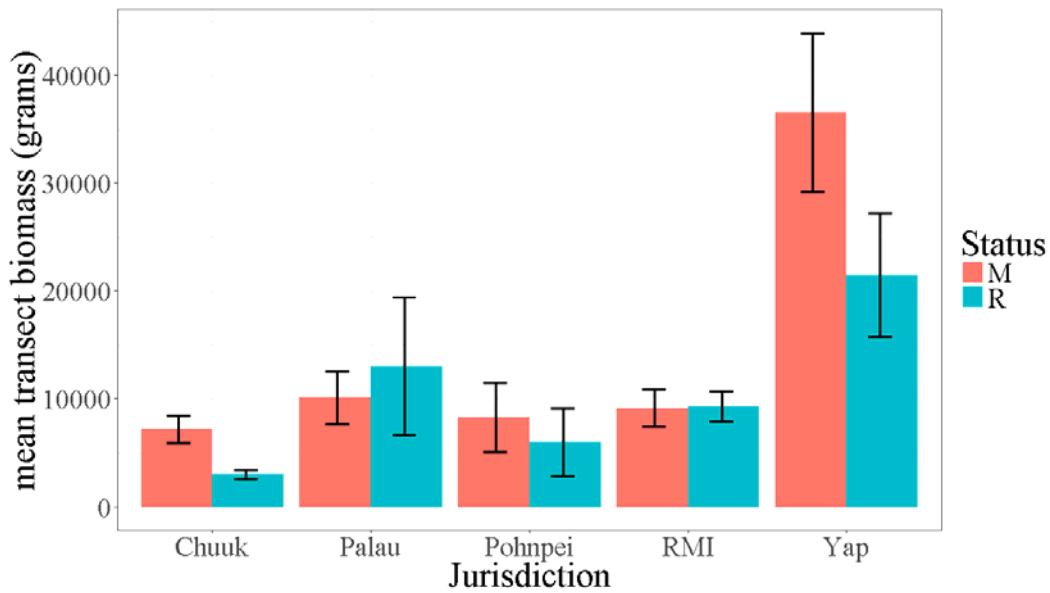


Fig. 2a, Bar plot comparing mean absolute values of biomass by jurisdictional MPA groups

Table I, jurisdictional gradient of parametric effect sizes (treated data, outliers removed) and mean differences of Box-Cox, back-transformed data (*), with unit confidence intervals (**)

<u>Jurisdiction</u>	<u>Cohen <i>d</i></u>	<u>Difference*</u>	<u>95% CI <i>u</i></u>	<u>95% CI <i>l</i></u>
Chuuk	0.626	4.18	6.862	1.497
Yap	0.323	15.09	29.051	1.123
Pohnpei	0.281	2.30	5.293	- 0.695
Palau	0.195	- 2.909	10.267	- 16.086
Marshalls	0.055	- 0.146	3.356	- 3.649

* units in $\text{kg} \cdot 250 \text{ m}^{-2}$

** (*u*) upper, (*l*) lower

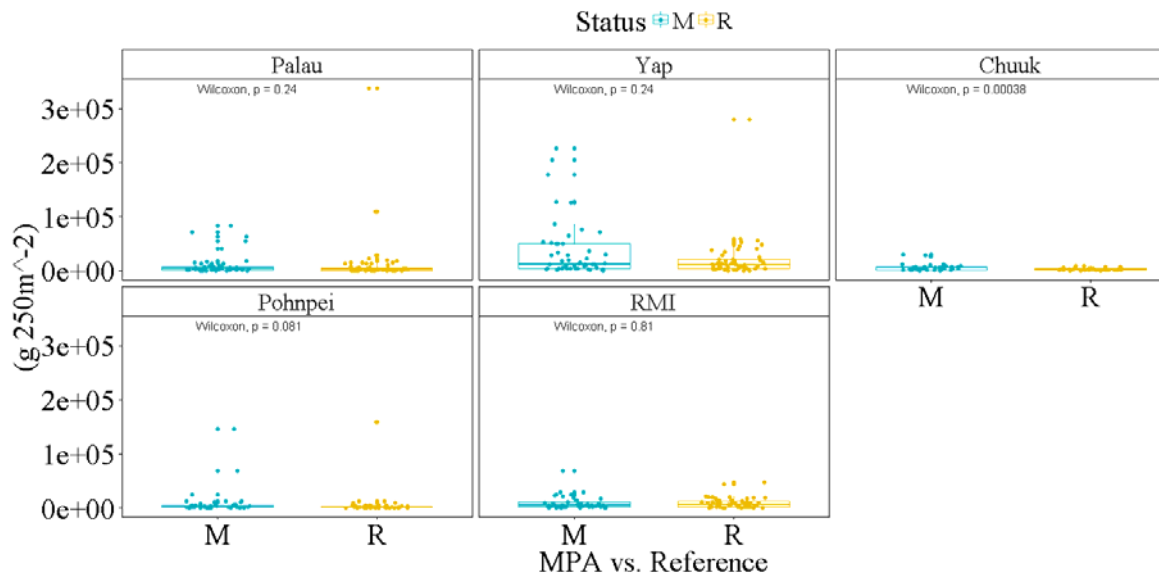


Fig. 2b, Dot plot comparing median absolute values of biomass by jurisdictional MPA groups

Table II, jurisdictional non-parametric effect sizes, and Hodges-Lehmann (H-L) estimates of shift in biomass (*), with bias-corrected confidence intervals (**)

Jurisdiction	Cliff delta δ	H-L*	95% CI <i>u</i>	95% C <i>l</i>
Chuuk	0.344	2.332	4.031	- 0.974
Palau	0.188	1.165	3.078	- 0.974
Pohnpei	0.186	0.652	1.651	- 0.633
Yap	0.155	6.543	20.116	- 3.197
Marshalls	- 0.054	- 0.239	2.833	- 2.813

* units in kg · 250 m⁻²

** (*u*) upper, (*l*) lower

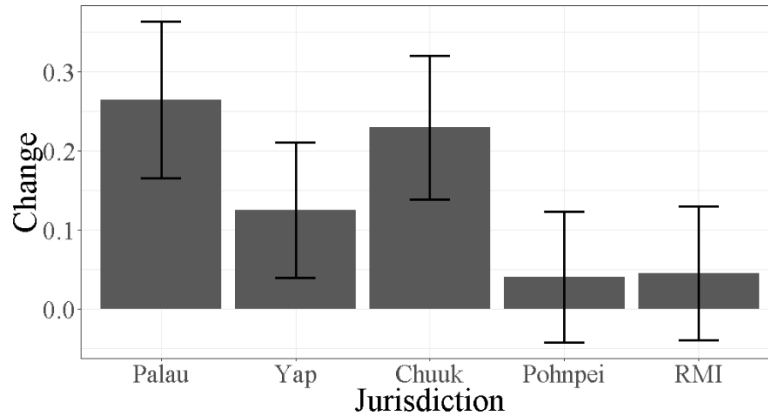


Fig. 2c, Bar plot of relative difference in total biomass by jurisdiction

Individual MPA responses

Mean-relative differences were positive in three of Palau’s MPAs (Fig. 2d), in Nimpal, Yap and Fonemu, Chuuk. No parametric tests -of absolute differences- were conducted at this level (due to limited statistical power). However, significant benefits of protection were observed in Fonemu, Chuuk ($p < 0.01$), Nimpal, Yap ($p < 0.03$), and Mwandh, Pohnpei ($p < 0.05$) under Wilcoxon sign-rank test with bootstrap assumptions, which were also the only three MPAs with location shifts bounded exclusively within positive confidence intervals (Table III). Tests suggested Fonemu was the “ideal” scenario, where community response was most detectable, despite an estimated shift in location of around half the shift seen in Nimpal. The largest range in location shifts both occurred in Yap, where shift estimates markedly increased (positively) in Nimpal, and (negatively) in Reey by 12.9 kg, and 4.2 kg \cdot 250 m², respectively. Also, in Yap, Riken showed the most dramatic location shift differences (i.e., H-L upper and lower confidence intervals) of all MPAs in this study.

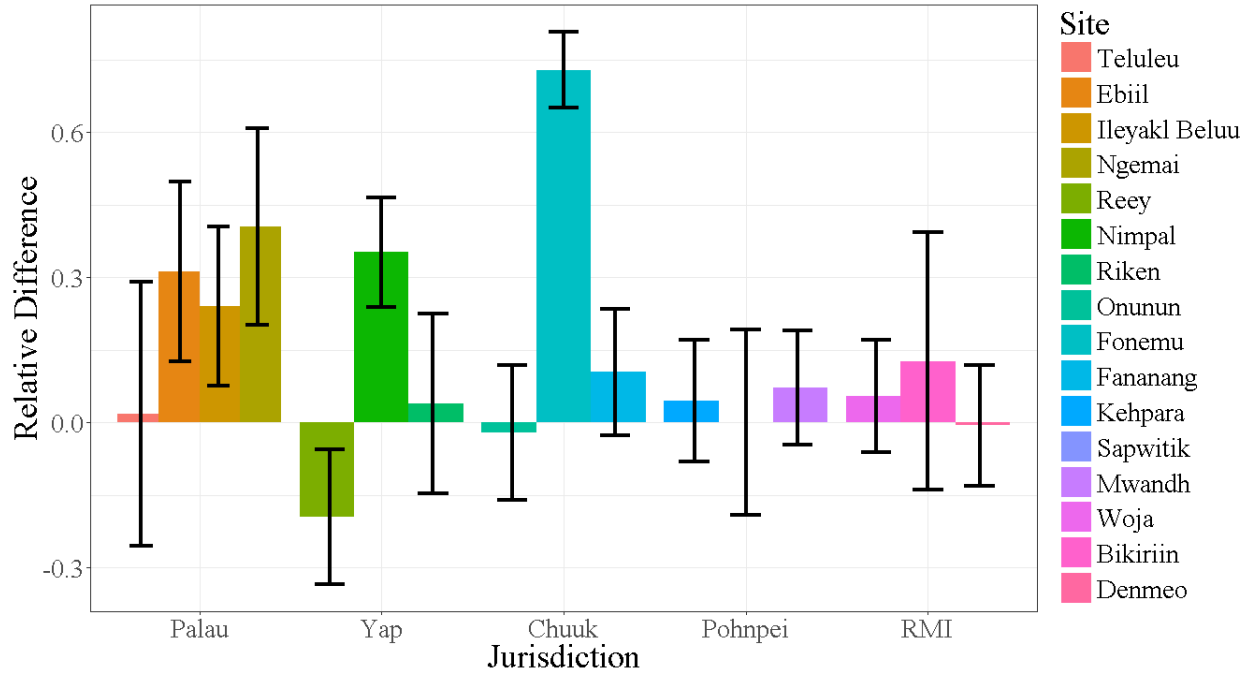


Figure 2d, Bar plot of relative difference in total biomass by MPA.

Table III, Wilcoxon sign rank test p-values, with Hodges-Lehmann estimates for shift in median location of biomass (*) and bias-corrected confidence intervals (**); zero (0) H-L indicates no location shift, while (-) indicates greater biomass outside MPA, and vice versa.

Site	p-value	H-L	95% CI(<i>u</i>)	95% CI(<i>l</i>)
Fonemu	0.002	6.8	16.9	4.0
Nimpal	0.026	12.9	31.8	0.9
Mwandh	0.041	1.6	4.3	0.0
Ngemai	0.169	2.0	4.7	- 0.5
Fananang	0.193	1.8	13.1	- 0.8
Sapwitik	0.359	0.5	1.5	- 0.5
Onunun	0.389	0.3	1.6	- 0.3
Denmeo	0.409	- 0.5	2.0	- 6.6
Woja	0.498	2.7	9.5	- 3.6
Ebiil	0.525	2.5	22.8	- 4.7
Reey	0.679	- 4.2	16.0	- 14.8
Kehpara	0.784	0.2	3.4	- 1.4
Teluleu	0.846	0.5	14.0	- 10.3
Bikiriin	0.922	- 0.9	6.9	- 9.6
Riken	0.922	0.6	56.8	- 23.7
Ileyakl Beluu	0.934	0.3	4.7	- 19.9

* units in $\text{kg} \cdot 250 \text{ m}^{-2}$

** (*u*) upper, (*l*) lower

Scaling effect size of MPA response

Cliff *delta* indicated eleven individual MPAs (e.g., δ_{Mwandh}) with larger effect sizes than their respective jurisdiction (e.g., δ_{Pohnpei}) (Table IV). When arbitrary thresholds were used to delineate between small ($|\delta| < 0.25$), moderate ($0.25 < |\delta| > 0.40$), and large ($0.40 > |\delta|$) effect sizes, eight

MPAs showed moderate or large effect sizes. These included two MPAs with moderate or large negative effect size (greater likelihood of observing larger overall biomass outside MPA).

Table IV, MPA-level effect size estimates (δ) of the likelihood of observing greater fish biomass inside (positive) or outside (-) an MPA, with bias-corrected confidence intervals

MPA	Cliff δ	95% C.I. <i>u</i>	95% C.I. <i>l</i>
Fonemu, Chuuk	1.00*	1.000	0.323
Ngemai, Palau	0.47*	0.806	- 0.104
Mwandh, Pohnpei	0.47*	0.806	- 0.104
Nimpal, Yap	0.44*	0.729	0.019
Ebiil, Palau	0.33*	0.727	- 0.225
Ileakl Beluu, Palau	0.33*	0.727	- 0.225
Teluleu, Palau	0.20	0.722	- 0.467
Fananang, Chuuk	0.20	0.722	- 0.467
Sapwitik, Pohnpei	0.20*	0.640	- 0.339
Bikiriin, Marshall Isl.	0.20*	0.722	- 0.467
Kehpara, Pohnpei	0.00	0.433	- 0.433
Onunun, Chuuk	- 0.07	0.446	- 0.547
Woja, Marshall Isl.	- 0.10	0.173	- 0.512
Riken, Yap	- 0.20*	0.467	- 0.722
Denmeo, Marshall Isl.	- 0.30*	0.350	- 0.661
Reey, Yap	- 0.47*	0.104	- 0.806

* |value| exceeds δ_{island}

Community function and focal species trends

Multivariate, functional-level differences (calculated as relative difference in biomass per transect unit) indicated spatially significant differences in recovery trajectories of functional assemblages due to protection (Table V). A comparison of response to protection found significant differences in permutation-based tests; first, between responses of functional groups across jurisdictions; and second, between responses of functional groups in MPAs nested within jurisdictions. Functional

groups with notable positive differences included large-bodied snappers (*Lutjanus bohar*, *Lutjanus monostigma*, etc.), which displayed the largest increase in size-class within MPAs, and large-bodied groupers (*Epinephelus fuscoguttatus*, *Plectropomus laevis*, etc.), which had the greatest levels of relative biomass in MPAs (Table VI). Large-bodied parrotfishes (*Cetoscarus bicolor*, *Chlorurus microrhinos*, etc.) showed minimal increases in both size and biomass. Rabbitfishes (*Signaus doliatus*, *Siganus puellus*, etc.) had larger body sizes within MPAs, yet had greater relative biomass in fished areas. In contrast, large-bodied emperors (*Lethrinus olivaceus*, *Monotaxis grandoculus*, etc.) were marginally smaller in MPAs, yet had positive -but minimal- differences in relative biomass. In sum, MPAs provided detectible effects to a number of functionally-important species groups, with observed instances of discord between size distribution and total biomass within these groups.

Table V, PERMANOVA results table of prominent *functional groups* in Micronesia

Source	df	SS	MS	Pseudo-F	P(perm)	Unique permutations
Ju*	4	22.803	5.7009	1.7614	0.016	997
Si(Ju)**	11	35.94	3.2673	1.4109	0.016	996
Res	224	518.74	2.3158			
Total	239	575.23				

*Jurisdiction, fixed

**MPA, nested, random

Table VI, Functional group effect size estimates (δ), with confidence intervals (*), of the likelihood a randomly-sampled individual from a Micronesian MPA will be larger (positive) or smaller (negative) than one sampled from a nearby, fished reef ($-1 < \delta < 1$), and transect-weighted *relative differences* ($-1 < \Omega < 1$) in MPA biomass, where a negative value indicates greater mean relative biomass on fished reefs, and vice versa.

Functional Group*	Cliff δ	95% CI <i>u</i>	95% CI <i>l</i>	Ω
LB Snappers	0.319	0.359	0.279	0.165
Rabbitfishes	0.234	0.302	0.163	- 0.136
LB Groupers	0.080	0.282	- 0.130	0.475
LB Parrotfishes	0.049	0.094	0.004	0.149
LB Emperors	- 0.061	0.040	- 0.161	0.052

* LB = Large-bodied

** (*u*) upper, (*l*) lower

Positive response in relative biomass (Ω) were detected in fifty-one (51) out of (74) fish species, with enhanced biomass due to greater abundances or larger body sizes in MPAs (Table SII). Notable positive response (i.e., relative differences within interquartile ranges) occurred in (29) of these species. The remaining twenty-two (22) species had differences outside of defined thresholds. For focal species, preliminary results showed strong jurisdictional (Plates I thru VI) differences in mean size, yet relative differences in weighted biomass did not differ between jurisdictions (Table VII), meaning, protection produced similar effects on these species across all jurisdictions, yet local recovery trajectories were highly variable within each island.

Regionally, within the present study's focal species (Table VIII), *Lutjanus bohar* (Plate V) and *Lutjanus gibbus* (Plate IV) were more often larger in MPAs, and although *L. bohar* showed moderate increases in relative biomass, *L. gibbus* did not strongly vary with this metric. *Naso lituratus* (Plate III) individuals were more likely to be smaller in MPAs, yet showed greater overall

relative biomass, while the opposite trend (larger individuals in MPAs, yet strong negative difference in relative biomass) occurred in a second focal species, *Cetoscarus bicolor* (Plate I). Overall, Palau had the fewest number, while the Marshall Islands had the greatest number of focal species with positive relative biomass outside MPAs (Table IX). *N. lituratus* and *P. areolatus* showed strong positive global responses, with the exception of Yap, where fished reefs had surprisingly greater overall biomass than MPAs for both species, and for most other focal species.

Table VII, PERMANOVA results table of focal *species* in Micronesia

Source	df	SS	MS	Pseudo-F	P(perm)	Unique permutations
Ju*	4	8.8148	2.2037	1.0977	0.36	996
Si(Ju)**	11	22.288	2.0262	1.4002	0.03	997
Res	224	324.15	1.4471			
Total	239	354.91				

*Jurisdiction, fixed

**MPA, nested, random

Table VIII, global effect size estimates (Cliff *delta* δ) of focal species, with confidence intervals (*), of the probability that a randomly-sampled individual from a protected reef in Micronesia will be larger (positive) or smaller (negative) than one sampled from a nearby, fished reef ($-1 < \delta < 1$); with global *relative differences* (Ω), the degree ($-1 < \Omega < 1$) to which a species differed in parametric MPA biomass, compared to fished reefs (per transect unit).

Focal Species	Cliff δ	95% CI u	95% CI l	Ω
<i>Lutjanus bohar</i>	0.313	0.539	0.046	0.316
<i>Lutjanus gibbus</i>	0.305	0.346	0.263	0.089
<i>Cetoscarus bicolor</i>	0.193	0.411	- 0.046	- 0.625
<i>Pletropomus areolatus</i>	0.156	0.445	- 0.163	0.443
<i>Chlorurus microrhinos</i>	0.041	0.142	- 0.061	0.107
<i>Naso lituratus</i>	- 0.077	0.020	- 0.017	0.455

* (*u*) upper, (*l*) lower

Table IX, Jurisdictional mean *relative difference* (Ω) in biomass of focal species, and jurisdictional values, longitudinally across Micronesia (from west, to east).

Focal Species	Ω_{global}	Ω_{Palau}	Ω_{Yap}	Ω_{Chuuk}	Ω_{Pohnpei}	$\Omega_{\text{Marshall Isl.}}$
<i>N lituratus</i>	0.09	0.08	- 0.14	0.19	0.13	0.18
<i>P areolatus</i>	0.06	0.12	- 0.01	0.13	0.05	0.01
<i>L bohar</i>	0.05	0.03	0.11	0.12	- 0.02	- 0.02
<i>L gibbus</i>	0.02	0.13	- 0.19	0.13	0.05	- 0.07
<i>C microrhinos</i>	0.02	0.08	0.04	- 0.03	0.03	- 0.07
<i>C bicolor</i>	- 0.05	- 0.05	0.01	- 0.13	- 0.03	- 0.04

Discussion

The preceding evidence revealed that marine protected areas across Micronesia did generate positive change in biomass and abundance of targeted food fish communities, varying by island, by MPA, by species or ecologically similar groups, and by effect sizes. Patterns of significant differences revealed both the limits of recovery on reef communities, and potential benefit from protection. Results also highlighted the isolation of management successes, and the complexity inherent of reef and species community population recovery. Combined analyses suggested that regional responses of food fish communities to marine protection were driven primarily by local success at one or a few sites per island. Recovery trajectories for a smaller set of key focal species (*Chlorurus microrhinos*, *Cetoscarus bicolor*, *Lutjanus bohar*, *Lutjanus gibbus*, *Naso lituratus*, and *Plectropomus areolatus*) showed no significant variation between-islands, yet showed significant

variation within-islands. Individual species and functional groups responded in discordant ways, revealing novel fish recovery patterns. The combined results suggested similar regional-level responses for most focal species, but not for groups with similar functional traits and body sizes. Responses in both functional groups and in focal species showed distinct positive or negative response to protection based upon analyses of relative differences. For instance, mean size and relative biomass were occasionally discordant (i.e., smaller individuals in MPA, yet greater overall biomass, or vice versa). Further analyses of these characters with long-term data may reveal new perspectives for understanding how entire assemblages respond to protection through time.

Implications of functional group and species responses

Multivariate analyses revealed that functional responses differed between islands, and between MPAs within their respective islands, meaning the *a priori* corollary -that group response to protection is similar- did not hold. In other words, effective protection of functional groups was not universal for any island nor reef type, and responses significantly differed. Two functional groups also showed inverted metrics (i.e., dissociation between mean-individual size and relative biomass). Large-bodied emperors (family Lethrinidae) were (more often) smaller in MPAs, while overall relative biomass was greater compared to fished reefs. Rabbitfishes (family Siganidae) responded oppositely, where individuals were more likely to be larger in MPAs, yet relative total biomass was significantly greater on fished reefs. The linear relationships between site factors and functional group biomass were minimal at best, likely due to the narrow margins –and required assumptions- imposed in order to increase overall statistical power (i.e., to precisely detect the effect of protection) and delineate thresholds (i.e., to determine potential biological and ecological scales of protection). Furthermore, although multivariate tests revealed differences in biomass of

functional groups, these groups consisted of broad species categories, which limited ecological inferences. No further assertions could be made for this dataset, as it included members of both rare and prolific taxa, worthy of further investigation, yet beyond the present study's scope.

In the six focal species, the highly-targeted snapper, *L. gibbus* was the most abundant species on reefs across the region (~24% of total individuals), yet the culturally-recognized, *Naso lituratus* (Ford et al. 2016) was the most prolific species, absent in only one MPA (Table SII). Recovery trajectories (positive vs. negative response) did not differ between islands, yet deeper investigations of relative responses revealed differences between MPAs within islands. Two predators, *Lutjanus bohar* and *L. gibbus* were more likely to be larger in MPAs, yet relative differences revealed these two species rarely exhibited the same trajectory on a single MPA, the former often being more abundant –or have larger size classes- than the latter (or vice versa). Two herbivorous species, *Naso lituratus* and *Cetoscarus bicolor*, showed discordance between absolute and relative metrics. The former species had greater overall biomass in MPAs, yet tended to have smaller individuals in MPAs, suggesting intraspecific altruism. The latter species, on the other hand, was more often larger but had less overall biomass in MPAs, suggesting population-level intraspecific competition. The regional scope at which these patterns are consistent may be evidence for localized, yet collectively-significant, species population traits emerging due to protection. In “altruistic” species, maximum size limits on harvest may protect larger, mature, and more fecund individuals occurring diurnally on fished reefs throughout jurisdictions (i.e., island-wide restrictions on taking and sale of individuals greater than published L50 reproductive baselines). For “competing” species that regionally displayed the opposite trends (e.g., *Cetoscarus bicolor*), there were simultaneously greater biomass outside, and fewer but larger individuals

inside MPAs. In this scenario, smaller individuals may be driven out of MPAs by larger conspecifics, and would collectively benefit instead from island-wide minimum size catch limits protecting juveniles, or banning certain gear types (e.g., small mesh-size nets), to ensure that displaced individuals reach maturity and contribute to the local reproductive gene pool.

Notable island and MPA responses

Houk et al. (2015) proposed an ecosystem-based framework for assessing marine communities across Micronesia and found that fishing pressure was the greatest driver of condition across the region. This study supported their argued stance, that community recovery is strongly limited by collective fishing pressure. There was also evidence that some islands had more heavily-exploited fish assemblage structures based on the overall absolute transect-values of biomass, size, and abundance observed throughout the region. Although Yap had the largest absolute biomass, for both MPAs and fished sites, and setting the standard for island-level reef biomass parameters, the island showed weak effect size and relative difference (low MPA success). In contrast, Chuuk MPAs had comparatively less biomass and abundance when examining absolute differences, yet significance tests and effect size were larger (high MPA success). Palau showed no significant absolute difference, and moderate effect size, yet when relative difference was used as a measure of success, the island showed the greatest –and most consistent- increases in biomass. Ultimately, Chuuk had pronounced differences in MPAs across all study metrics, while Palau excelled predominantly when measuring relative differences but had marginal absolute differences.

Conclusions

While regional, island, and individual MPA tests based upon total biomass showed community-level increases in fish biomass per transect-unit, spatial scales were not always ecologically or

biologically meaningful for functional groups or taxa. In other words, success (i.e., significant food-fish recovery) remains a highly relative term, invariably dependent on island-and-site-level taxonomic baselines, on habitats that support regionally-distributed coral reef fish species, and on locally-driven, stakeholder-initiated reef protection regimes. Species and groups that exhibit novel responses to protection would be appropriate starting points for identifying the scales at which regional-level and island-level initiatives complement localized protection.

Ultimately, any robust measure of change will also include effect size estimates alongside tests of significance. Effect size and relative difference provided two distinct measures of how MPAs performed, both approaches concluding that protection was altering species and group-level responses of fishes to both positive and negative degrees. However, these community-level biomass characters (i.e., between effect size and relative difference) did not hold at the island scale (Fig 1a & Table II), and only partially held at the scale of individual MPAs (hypothesized as dissociation between sample variability and sample size). Results also indicated there was partial accord between non-parametric absolute difference (Cliff delta) and mean relative (omega) values, these values are both robust and adaptable to assessing a wide range of ecological data.

The survey methods used in this study conform to minimum sampling standards of marine data collection, as agreed by the region's collective governing and scientific bodies. The statistical methodologies outlined are not limited to analysis of fish survey data, and should yield robust results for various other marine and terrestrial studies (with comparable references, or robust temporal baselines). Greater effort towards compiling and sharing data between jurisdictions and stakeholders should increase our understanding of species-level, assemblage-level, and

community-level response to protection. As more datasets accrue for the many small and increasingly mature MPAs in the region, the methodology outlined will dutifully provide robust assertions and baselines to absolute and relative change. Such inquiries provide new perspectives towards understanding reef-level, island-wide, and inter-island (stochastic) effects of protection.

Finally, while this study was performed on a spatially robust sample set, a second and equally relevant metric for examining coral reef community ecology, time (i.e., MPA maturity), is not specifically addressed. Additionally, various human drivers, particularly the differences in fishing activity conducted on reference reefs across sites (Cresswell et al. 2019), were not accounted for, as these are site-specific drivers that cannot be resolved under the present experimental design. However, the comparative survey design (complemented with robust sampling and reported effect size thresholds), provided acceptable levels of accuracy for characterizing specific differences in scales of protection. Nonetheless, these should be considered baseline measures, requiring further and repeated (i.e., temporal) verification. Replicate studies confirming (or refuting) the study's results will further refine our empirical understanding of the balance between human needs and sustained existence, diversity, and overall resilience of Micronesia's food fishes.

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Data access

The raw dataset used in this study is retained in the PICRC archives, publically accessible upon request to the Center's Research Department Head. Original datasets generated during this study can be accessed via direct download from *https* links below, which are digitally published archives, compatible with spreadsheet software applications (saved locally in working directory as comma-separated value, csv files), and are to be used and cited (including *https* links) as supplemental data for this thesis document (Appendix I). Omega coefficients (see Methods) are weighted by unique station (i.e., mean or total biomass of all transects within a station), these files can be used in conjunction with various package codes run in *R* environment to produce group and location-specific indices, where zero indicates no difference between sample means, while a larger (or smaller) value indicates positive (or negative) change in relative biomass.

DI, located at the stable *https* link, a spreadsheet showing community-level (i.e., pooled species) *relative differences* (see Methods) in total community biomass (reldiff_tb) and biomass treated by removal of outlier species, approximately 24% of data (reldiff_btb):

<https://docs.google.com/spreadsheets/d/e/2PACX->

[1vTRUzgmK53sYB2vpcwAGyQ2uVWwHYuaRpxpqs0ZtxAXXsy3vOt0mmgu3fccMuqw7w/pubhtml?gid=847130597&single=true](https://docs.google.com/spreadsheets/d/e/2PACX-1vTRUzgmK53sYB2vpcwAGyQ2uVWwHYuaRpxpqs0ZtxAXXsy3vOt0mmgu3fccMuqw7w/pubhtml?gid=847130597&single=true).

DII, located at the stable *https* link, a spreadsheet showing MPA-level (i.e., all food fish species) values of the relative difference between transect pairs (MPAs vs Reference), weighted by MPA:

<https://docs.google.com/spreadsheets/d/e/2PACX->

[1vTRUzgmK53sYB2vpcwAGyQ2uVWwHYuaRpxpqs0ZtxAXXsy3vOt0mmgu3fccMuqw7w/pub?gid=134073825&single=true&output=csv](https://docs.google.com/spreadsheets/d/e/2PACX-1vTRUzgmK53sYB2vpcwAGyQ2uVWwHYuaRpxpqs0ZtxAXXsy3vOt0mmgu3fccMuqw7w/pub?gid=134073825&single=true&output=csv)

DIII, located at the stable *https* link, a spreadsheet showing *relative differences* (e.g., Ω biomass, Ω Abundance) in community-level (i.e., all species) biomass and abundance, weighted by transect means, within stations at 16 study MPAs:

<https://docs.google.com/spreadsheets/d/e/2PACX->

[1vRp5LysilweaHF7BXtl30C_oJ5cF_ueiFFhAU0u0VQpRQvcHgnZoWYqKdJdLl4lYg/pub?gid=465591100&single=true&output=csv](https://docs.google.com/spreadsheets/d/e/2PACX-1vRp5LysilweaHF7BXtl30C_oJ5cF_ueiFFhAU0u0VQpRQvcHgnZoWYqKdJdLl4lYg/pub?gid=465591100&single=true&output=csv)

DIV, located at the stable *https* link, a spreadsheet with standardized (*z*) scores for (8) prominent functional groups and (3) major trophic groups, weighted by station means at (16) study MPAs:

<https://docs.google.com/spreadsheets/d/e/2PACX->

[1vQZmtCYHkWyMCRTdClSQQpFQippz81FVvYwkaPWPWqupLrQVCbRDtJ0ulq4Qo-GeF9U15EePl8a0cNl/pub?gid=1311382681&single=true&output=csv](https://docs.google.com/spreadsheets/d/e/2PACX-1vQZmtCYHkWyMCRTdClSQQpFQippz81FVvYwkaPWPWqupLrQVCbRDtJ0ulq4Qo-GeF9U15EePl8a0cNl/pub?gid=1311382681&single=true&output=csv)

DV, located at the stable *https* link below, a spreadsheet with omega (Ω) values for (8) prominent functional groups and (3) major trophic groups, weighted by transect means ($n=5$), within stations at (16) study MPAs:

<https://docs.google.com/spreadsheets/d/e/2PACX->

[1vQZmtCYHkWyMCRTdClSQQpFQippz81FVvYwkaPWPWqupLrQVCbRDtJ0ulq4Qo-GeF9U15EePl8a0cNl/pubhtml?gid=634793542&single=true](https://docs.google.com/spreadsheets/d/e/2PACX-1vQZmtCYHkWyMCRTdClSQQpFQippz81FVvYwkaPWPWqupLrQVCbRDtJ0ulq4Qo-GeF9U15EePl8a0cNl/pubhtml?gid=634793542&single=true)

DVI, located at the stable *https* link below, a spreadsheet with omega (Ω) values for (14) individual species and a group of (7) closely-related species in the family Scarinae. These global summaries are of total biomass (TOTB_{juris}), mean individual biomass (Mb_{juris}), and abundance (N_{juris}), weighted by transect, by station, finally by the means of the (5) jurisdictions in study*:

<https://docs.google.com/spreadsheets/d/e/2PACX-1vQtGH->

[Z52Bi6WYYM22G4tv8UmmbVdF19Qao2HJVAApVWzNgzV7rhWT3hyX4JPuapnuxxo-](https://docs.google.com/spreadsheets/d/e/2PACX-1vQtGH-Z52Bi6WYYM22G4tv8UmmbVdF19Qao2HJVAApVWzNgzV7rhWT3hyX4JPuapnuxxo-)

[ld7FrouAq/pub?gid=0&single=true&output=csv](https://docs.google.com/spreadsheets/d/e/2PACX-1vQtGH-Z52Bi6WYYM22G4tv8UmmbVdF19Qao2HJVAApVWzNgzV7rhWT3hyX4JPuapnuxxo-ld7FrouAq/pub?gid=0&single=true&output=csv)

*values of TOTB_{juris} are inverted, to be read as such (i.e., negative values are positive, and vice versa)

Supplemental information

Table SI, island-level parametric mean of relative differences (Ω) between transect pairs, with error values and 95% confidence intervals.

Jurisdiction	N	Ω	sd	se	ci
Palau	55	0.265	0.736	0.099	0.199
Chuuk	35	0.229	0.536	0.091	0.184
Yap	50	0.125	0.604	0.085	0.172
RMI	50	0.045	0.598	0.085	0.170
Pohnpei	50	0.040	0.584	0.083	0.166

Table SII, relative differences (Ω) in total biomass of focal species on Micronesian MPAs, summarized by MPA means; the basis for Euclidian matrix illustrations (Plates I thru VI); the full dataset (transect-level differences) was used for Permanova's (see Table VII).

MPA	<i>C bicolor</i>	<i>L gibbus</i>	<i>C microrhinos</i>	<i>L bohar</i>	<i>N lituratus</i>	<i>P areolatus</i>
Onunun	- 0.066	0.000	0.000	0.065	- 0.194	0.065
Ileyakl	- 0.066	0.249	0.271	- 0.066	0.200	0.265
Teluleu	0.000	0.337	0.000	0.000	0.000	0.000
Sapwitik	- 0.066	- 0.067	0.133	- 0.133	0.067	0.266
Bikiriin	0.000	- 0.100	0.000	- 0.002	0.000	0.307
Fananang	- 0.197	0.100	0.000	0.400	0.296	0.398
Fonemu	- 0.114	0.300	- 0.100	- 0.099	0.283	0.100
Ebiil	- 0.133	- 0.134	0.047	0.200	0.266	- 0.234
Ngemai	0.000	0.065	0.000	0.000	0.000	0.296
Kehpara	0.050	0.148	- 0.237	0.150	0.100	- 0.017
Mwandh	- 0.065	0.066	0.200	- 0.066	- 0.019	0.131
Denmeo	0.000	- 0.250	0.000	- 0.050	0.050	0.067
Woja	- 0.111	0.147	- 0.197	0.000	- 0.031	0.175
Riken	0.100	- 0.371	- 0.070	0.268	- 0.100	- 0.072
Nimpal	- 0.028	0.052	0.215	0.102	0.000	- 0.281
Reey	- 0.034	- 0.252	- 0.026	- 0.036	0.067	- 0.054

Table SIII, relative differences (Ω) in biomass, size, and abundance of target fish species in study MPAs, versus a paired reference, and fished reefs nearby. Horizontal line indicates inflection point.

Species	biomass	Species	size	Species	abundance
<i>Naso lituratus</i>	0.0853	<i>N lituratus</i>	0.0855	<i>N lituratus</i>	0.0412
<i>Cephalopholis argus</i>	0.0741	<i>C argus</i>	0.0663	<i>C argus</i>	0.0407
<i>Scarus sp.</i>	0.0642	<i>P areolatus</i>	0.0552	<i>P areolatus</i>	0.0376
<i>Plectropomus areolatus</i>	0.0614	<i>P barberinus</i>	0.0417	<i>P barberinus</i>	0.0351
<i>Lutjanus bohar</i>	0.0458	<i>L bohar</i>	0.0379	<i>L bohar</i>	0.0250
<i>Siganus punctatus</i>	0.0434	<i>S prasiognathos</i>	0.0347	<i>S prasiognathos</i>	0.0240
<i>Parupeneus barberinus</i>	0.0400	<i>S punctatus</i>	0.0332	<i>S punctatus</i>	0.0219
<i>Bolbometopon muricatum</i>	0.0362	<i>B muricatum</i>	0.0275	<i>C microrhinos</i>	0.0206
<i>Scarus psittacus</i>	0.0358	<i>E polyphekadion</i>	0.0254	<i>Scarus sp.</i>	0.0187
<i>Cheilinus undulatus</i>	0.0351	<i>P albobittatus</i>	0.0202	<i>B muricatum</i>	0.0173
<i>Epinephelus polyphekadion</i>	0.0260	<i>L harak</i>	0.0193	<i>L harak</i>	0.0166
<i>Lutjanus gibbus</i>	0.0242	<i>L obsoletus</i>	0.0193	<i>P albobittatus</i>	0.0146
<i>Lethrinus obsoletus</i>	0.0240	<i>C anchorago</i>	0.0192	<i>L obsoletus</i>	0.0143
<i>Choerodon anchorago</i>	0.0235	<i>L erythracanthus</i>	0.0183	<i>E polyphekadion</i>	0.0130
<i>Plectorhynchus albobittatus</i>	0.0208	<i>C undulatus</i>	0.0165	<i>A xanthopterus</i>	0.0115
<i>Lethrinus harak</i>	0.0193	<i>C carolinus</i>	0.0162	<i>C anchorago</i>	0.0102
<i>Lethrinus erythracanthus</i>	0.0187	<i>K bigibbus</i>	0.0160	<i>K cinerascens</i>	0.0097

<i>Kyphosus bigibbus</i>	0.0166	<i>Scarus sp.</i>	0.0153	<i>C undulatus</i>	0.0096
<i>Chlorurus microrhinos</i>	0.0147	<i>N unicornis</i>	0.0125	<i>K bigibbus</i>	0.0096
<i>Hipposcarus longiceps</i>	0.0136	<i>K cinerascens</i>	0.0121	<i>N unicornis</i>	0.0085
<i>Naso unicornis</i>	0.0131	<i>S ghobban</i>	0.0115	<i>H harid</i>	0.0074
<i>kyphosus cinerascens</i>	0.0125	<i>H harid</i>	0.0111	<i>K vaigiensis</i>	0.0069
<i>Siganus guttatus</i>	0.0111	<i>L rubrioperculatus</i>	0.0080	<i>L erythracanthus</i>	0.0063
<i>Kyphosus vaigiensis</i>	0.0104	<i>L fulvus</i>	0.0079	<i>Acanthurus sp.A</i>	0.0061
<i>Scarus ghobban</i>	0.0102	<i>C microrhinos</i>	0.0073	<i>S spinus</i>	0.0057
<i>Hipposcarus harid</i>	0.0099	<i>O cubicus</i>	0.0070	<i>B viridescens</i>	0.0055
<i>Lethrinus rubrioperculatus</i>	0.0083	<i>S spinus</i>	0.0069	<i>L gibbus</i>	0.0055
<i>Siganus spinus</i>	0.0081	<i>P chaetonoides</i>	0.0065	<i>S ghobban</i>	0.0040
<i>Ostracion cubicus</i>	0.0072	<i>S vulpinnis</i>	0.0063	<i>L rubrioperculatus</i>	0.0038
<i>Acanthurus blochii</i>	-0.0075	<i>E longispinis</i>	0.0060	<i>P chaetonoides</i>	0.0035
<i>Siganus randalli</i>	-0.0083	<i>A xanthopterus</i>	0.0059	<i>H longiceps</i>	0.0034
<i>Sphyraena barracuda</i>	-0.0083	<i>C melampygus</i>	0.0048	<i>S dimidiatus</i>	0.0034
<i>Siganus puellus</i>	-0.0148	<i>B viridescens</i>	0.0047	<i>L fulvus</i>	0.0032
<i>Parupeneus multifasciatus</i>	-0.0187	<i>V louti</i>	-0.0046	<i>L olivaceus</i>	-0.0032
<i>Chlorurus sordidus</i>	-0.0192	<i>S flavipectoralis</i>	-0.0047	<i>S barracuda</i>	-0.0035
<i>Siganus doliatus</i>	-0.0220	<i>S spiniferum</i>	-0.0048	<i>L xanthochilus</i>	-0.0035
<i>Scarus altipinnis</i>	-0.0279	<i>C sordidus</i>	-0.0049	<i>S puelloides</i>	-0.0042
<i>Siganus fuscescens</i>	-0.0295	<i>S rubroviolaceus</i>	-0.0049	<i>S randalli</i>	-0.0052
<i>Siganus argenteus</i>	-0.0399	<i>S puelloides</i>	-0.0053	<i>A blochii</i>	-0.0067
<i>Chlorurus bleekeri</i>	-0.0415	<i>L monostigma</i>	-0.0074	<i>L monostigma</i>	-0.0091
<i>Monotaxis grandoculis</i>	-0.0416	<i>S randalli</i>	-0.0080	<i>S altipinnis</i>	-0.0109
<i>Cetoscarus bicolor</i>	-0.0419	<i>S barracuda</i>	-0.0082	<i>P multifasciatus</i>	-0.0115
		<i>A blochii</i>	-0.0089	<i>S puellus</i>	-0.0117
		<i>S puellus</i>	-0.0098	<i>S doliatus</i>	-0.0159
		<i>P multifasciatus</i>	-0.0178	<i>M grandoculis</i>	-0.0185
		<i>H longiceps</i>	-0.0209	<i>C sordidus</i>	-0.0197
		<i>S doliatus</i>	-0.0221	<i>Cs bicolor</i>	-0.0207
		<i>S fuscescens</i>	-0.0251	<i>C bleekeri</i>	-0.0258
		<i>M grandoculis</i>	-0.0270	<i>S argenteus</i>	-0.0288
		<i>S altipinnis</i>	-0.0306	<i>S fuscescens</i>	-0.0297
		<i>C bleekeri</i>	-0.0394		

Table SIV, GPS coordinates of dive survey starting position for 16 MPA study Sites, where each row represents a Station code, and Transect codes for five consecutive (5 x 50 m) belts.

LAT	LONG	SITE	STATION	TRANSECTS				
7.541217	134.639183	Ngemai	BKR1	BKR1.1	BKR1.2	BKR1.3	BKR1.4	BKR1.5
7.536333	134.62725	Ngemai	BKR2	BKR2.1	BKR2.2	BKR2.3	BKR2.4	BKR2.5
7.525418	134.630398	Ngemai	BKR3	BKR3.1	BKR3.2	BKR3.3	BKR3.4	BKR3.5
7.535467	134.626733	Ngemai	BKM1	BKM1.1	BKM1.2	BKM1.3	BKM1.4	BKM1.5
7.529543	134.632423	Ngemai	BKM2	BKM2.1	BKM2.2	BKM2.3	BKM2.4	BKM2.5
7.5266	134.626833	Ngemai	BKM3	BKM3.1	BKM3.2	BKM3.3	BKM3.4	BKM3.5
7.652408	134.549462	Ileakl Beluu	BIM1	BIM1.1	BIM1.2	BIM1.3	BIM1.4	BIM1.5
7.653074	134.544122	Ileakl Beluu	BIM2	BIM2.1	BIM2.2	BIM2.3	BIM2.4	BIM2.5
7.646567	134.547967	Ileakl Beluu	BIM3	BIM3.1	BIM3.2	BIM3.3	BIM3.4	BIM3.5
7.640133	134.546833	Ileakl Beluu	BIR1	BIR1.1	BIR1.2	BIR1.3	BIR1.4	BIR1.5
7.641483	134.544133	Ileakl Beluu	BIR2	BIR2.1	BIR2.2	BIR2.3	BIR2.4	BIR2.5
7.643058	134.540828	Ileakl Beluu	BIR3	BIR3.1	BIR3.2	BIR3.3	BIR3.4	BIR3.5
7.77378	134.57143	Ebiil	BEM1	BEM1.1	BEM1.2	BEM1.3	BEM1.4	BEM1.5
7.7727	134.5671	Ebiil	BEM2	BEM2.1	BEM2.2	BEM2.3	BEM2.4	BEM2.5
7.776866667	134.57093	Ebiil	BEM3	BEM3.1	BEM3.2	BEM3.3	BEM3.4	BEM3.5
7.791827	134.555849	Ebiil	BER1	BER1.1	BER1.2	BER1.3	BER1.4	BER1.5
7.794867	134.545183	Ebiil	BER2	BER2.1	BER2.2	BER2.3	BER2.4	BER2.5
7.800166667	134.54602	Ebiil	BER3	BER3.1	BER3.2	BER3.3	BER3.4	BER3.5
7.051552	134.26975	Teluleu	BTM1	BTM1.1	BTM1.2	BTM1.3	BTM1.4	BTM1.5
7.051217	134.267891	Teluleu	BTM2	BTM2.1	BTM2.2	BTM2.3	BTM2.4	BTM2.5
7.050779	134.265741	Teluleu	BTM3	BTM3.1	BTM3.2	BTM3.3	BTM3.4	BTM3.5
7.0464	134.28192	Teluleu	BTR1	BTR1.1	BTR1.2	BTR1.3	BTR1.4	BTR1.5
7.052366667	134.26025	Teluleu	BTR2	BTR2.1	BTR2.2	BTR2.3	BTR2.4	BTR2.5
7.049406	134.265234	Teluleu	BTR3	BTR3.1	BTR3.2	BTR3.3	BTR3.4	BTR3.5
6.800433333	158.1247	Kehpara	PKM1	PKM1.1	PKM1.2	PKM1.3	PKM1.4	PKM1.5
6.794933	158.125983	Kehpara	PKM2	PKM2.1	PKM2.2	PKM2.3	PKM2.4	PKM2.5
6.794033333	158.11428	Kehpara	PKM3	PKM3.1	PKM3.2	PKM3.3	PKM3.4	PKM3.5
6.8045	158.11272	Kehpara	PKM4	PKM4.1	PKM4.2	PKM4.3	PKM4.4	PKM4.5
6.796567	158.134883	Kehpara	PKR1	PKR1.1	PKR1.2	PKR1.3	PKR1.4	PKR1.5
6.794783333	158.1386	Kehpara	PKR2	PKR2.1	PKR2.2	PKR2.3	PKR2.4	PKR2.5
6.783	158.127567	Kehpara	PKR3	PKR3.1	PKR3.2	PKR3.3	PKR3.4	PKR3.5
6.779783	158.14495	Kehpara	PKR4	PKR4.1	PKR4.2	PKR4.3	PKR4.4	PKR4.5
7.009083333	158.29735	Mwandh	PMM1	PMM1.1	PMM1.2	PMM1.3	PMM1.4	PMM1.5
7.012783333	158.28803	Mwandh	PMM2	PMM2.1	PMM2.2	PMM2.3	PMM2.4	PMM2.5
7.001283333	158.30175	Mwandh	PMM3	PMM3.1	PMM3.2	PMM3.3	PMM3.4	PMM3.5
7.015117	158.282983	Mwandh	PMR1	PMR1.1	PMR1.2	PMR1.3	PMR1.4	PMR1.5
7.022083	158.279433	Mwandh	PMR2	PMR2.1	PMR2.2	PMR2.3	PMR2.4	PMR2.5
7.01975	158.280817	Mwandh	PMR3	PMR3.1	PMR3.2	PMR3.3	PMR3.4	PMR3.5
7.009588889	158.22395	Sapwitik	PSM1	PSM1.1	PSM1.2	PSM1.3	PSM1.4	PSM1.5

7.005411111	158.2182	Sapwitik	PSM2	PSM2.1	PSM2.2	PSM2.3	PSM2.4	PSM2.5
7.009080556	158.22852	Sapwitik	PSM3	PSM3.1	PSM3.2	PSM3.3	PSM3.4	PSM3.5
7.01335	158.25829	Sapwitik	PSR1	PSR1.1	PSR1.2	PSR1.3	PSR1.4	PSR1.5
7.003383333	158.24397	Sapwitik	PSR2	PSR2.1	PSR2.2	PSR2.3	PSR2.4	PSR2.5
6.997069444	158.26584	Sapwitik	PSR3	PSR3.1	PSR3.2	PSR3.3	PSR3.4	PSR3.5
7.362463889	151.92199	Fenamam	CEM1	CEM1.1	CEM1.2	CEM1.3	CEM1.4	CEM1.5
7.361283333	151.92193	Fenamam	CEM2	CEM2.1	CEM2.2	CEM2.3	CEM2.4	CEM2.5
7.381591667	151.90777	Fenamam	CER1	CER1.1	CER1.2	CER1.3	CER1.4	CER1.5
7.382	151.90886	Fenamam	CER2	CER2.1	CER2.2	CER2.3	CER2.4	CER2.5
7.289930556	151.89186	Onunun	COM1	COM1.1	COM1.2	COM1.3	COM1.4	COM1.5
7.289772222	151.89408	Onunun	COM2	COM2.1	COM2.2	COM2.3	COM2.4	COM2.5
7.291861111	151.89528	Onunun	COM3	COM3.1	COM3.2	COM3.3	COM3.4	COM3.5
7.292491667	151.89509	Onunun	COR1	COR1.1	COR1.2	COR1.3	COR1.4	COR1.5
7.293213889	151.89687	Onunun	COR2	COR2.1	COR2.2	COR2.3	COR2.4	COR2.5
7.292502778	151.89863	Onunun	COR3	COR3.1	COR3.2	COR3.3	COR3.4	COR3.5
7.310577778	151.9408	Fananang	CAM1	CAM1.1	CAM1.2	CAM1.3	CAM1.4	CAM1.5
7.308594444	151.94014	Fananang	CAM2	CAM2.1	CAM2.2	CAM2.3	CAM2.4	CAM2.5
7.308472222	151.92664	Fananang	CAR1	CAR1.1	CAR1.2	CAR1.3	CAR1.4	CAR1.5
7.307308333	151.92542	Fananang	CAR2	CAR2.1	CAR2.2	CAR2.3	CAR2.4	CAR2.5
7.094269444	171.13201	Woja	RWM1	RWM1.1	RWM1.2	RWM1.3	RWM1.4	RWM1.5
7.092583333	171.13522	Woja	RWM2	RWM2.1	RWM2.2	RWM2.3	RWM2.4	RWM2.5
7.088702778	171.12871	Woja	RWM3	RWM3.1	RWM3.2	RWM3.3	RWM3.4	RWM3.5
7.08675	171.13306	Woja	RWM4	RWM4.1	RWM4.2	RWM4.3	RWM4.4	RWM4.5
7.090575	171.14066	Woja	RWR1	RWR1.1	RWR1.2	RWR1.3	RWR1.4	RWR1.5
7.088611111	171.14639	Woja	RWR2	RWR2.1	RWR2.2	RWR2.3	RWR2.4	RWR2.5
7.084530556	171.14213	Woja	RWR3	RWR3.1	RWR3.2	RWR3.3	RWR3.4	RWR3.5
7.07935	171.1547	Woja	RWR4	RWR4.1	RWR4.2	RWR4.3	RWR4.4	RWR4.5
7.139222222	171.30548	Bikirin	RBM1	RBM1.1	RBM1.2	RBM1.3	RBM1.4	RBM1.5
7.133897222	171.30299	Bikirin	RBM2	RBM2.1	RBM2.2	RBM2.3	RBM2.4	RBM2.5
7.143152778	171.30012	Bikirin	RBR1	RBR1.1	RBR1.2	RBR1.3	RBR1.4	RBR1.5
7.137027778	171.29852	Bikirin	RBR2	RBR2.1	RBR2.2	RBR2.3	RBR2.4	RBR2.5
7.127308333	171.31894	Denmeo	RDM1	RDM1.1	RDM1.2	RDM1.3	RDM1.4	RDM1.5
7.1263	171.32098	Denmeo	RDM2	RDM2.1	RDM2.2	RDM2.3	RDM2.4	RDM2.5
7.123286111	171.31498	Denmeo	RDM3	RDM3.1	RDM3.2	RDM3.3	RDM3.4	RDM3.5
7.120333	171.315517	Denmeo	RDM4	RDM4.1	RDM4.2	RDM4.3	RDM4.4	RDM4.5
7.13325	171.313267	Denmeo	RDR1	RDR1.1	RDR1.2	RDR1.3	RDR1.4	RDR1.5
7.125533	171.328317	Denmeo	RDR2	RDR2.1	RDR2.2	RDR2.3	RDR2.4	RDR2.5
7.129283	171.309267	Denmeo	RDR3	RDR3.1	RDR3.2	RDR3.3	RDR3.4	RDR3.5
7.120583	171.32353	Denmeo	RDR4	RDR4.1	RDR4.2	RDR4.3	RDR4.4	RDR4.5
9.5467	138.0827	Nimpal	YNM1	YNM1.1	YNM1.2	YNM1.3	YNM1.4	YNM1.5
9.545582	138.082125	Nimpal	YNM2	YNM2.1	YNM2.2	YNM2.3	YNM2.4	YNM2.5
9.541	138.075533	Nimpal	YNM3	YNM3.1	YNM3.2	YNM3.3	YNM3.4	YNM3.5
9.547033	138.078917	Nimpal	YNM4	YNM4.1	YNM4.2	YNM4.3	YNM4.4	YNM4.5

9.550533	138.080917	Nimpal	YNM5	YNM5.1	YNM5.2	YNM5.3	YNM5.4	YNM5.5
9.519083	138.070167	Nimpal	YNR1	YNR1.1	YNR1.2	YNR1.3	YNR1.4	YNR1.5
9.51385	138.06745	Nimpal	YNR2	YNR2.1	YNR2.2	YNR2.3	YNR2.4	YNR2.5
9.513867	138.060467	Nimpal	YNR3	YNR3.1	YNR3.2	YNR3.3	YNR3.4	YNR3.5
9.517033	138.062833	Nimpal	YNR4	YNR4.1	YNR4.2	YNR4.3	YNR4.4	YNR4.5
9.526817	138.06855	Nimpal	YNR5	YNR5.1	YNR5.2	YNR5.3	YNR5.4	YNR5.5
9.572533	138.20855	Riken	YKM1	YKM1.1	YKM1.2	YKM1.3	YKM1.4	YKM1.5
9.570783	138.2045	Riken	YKM2	YKM2.1	YKM2.2	YKM2.3	YKM2.4	YKM2.5
9.574467	138.2083	Riken	YKR1	YKR1.1	YKR1.2	YKR1.3	YKR1.4	YKR1.5
9.571117	138.203283	Riken	YKR2	YKR2.1	YKR2.2	YKR2.3	YKR2.4	YKR2.5
9.449644	138.039715	Reey	YYM1	YYM1.1	YYM1.2	YYM1.3	YYM1.4	YYM1.5
9.461467	138.042	Reey	YYM2	YYM2.1	YYM2.2	YYM2.3	YYM2.4	YYM2.5
9.47175	138.045033	Reey	YYM3	YYM3.1	YYM3.2	YYM3.3	YYM3.4	YYM3.5
9.484983	138.04425	Reey	YYR1	YYR1.1	YYR1.2	YYR1.3	YYR1.4	YYR1.5
9.493233	138.047967	Reey	YYR2	YYR2.1	YYR2.2	YYR2.3	YYR2.4	YYR2.5
9.439159	138.036414	Reey	YYR3	YYR3.1	YYR3.2	YYR3.3	YYR3.4	YYR3.5

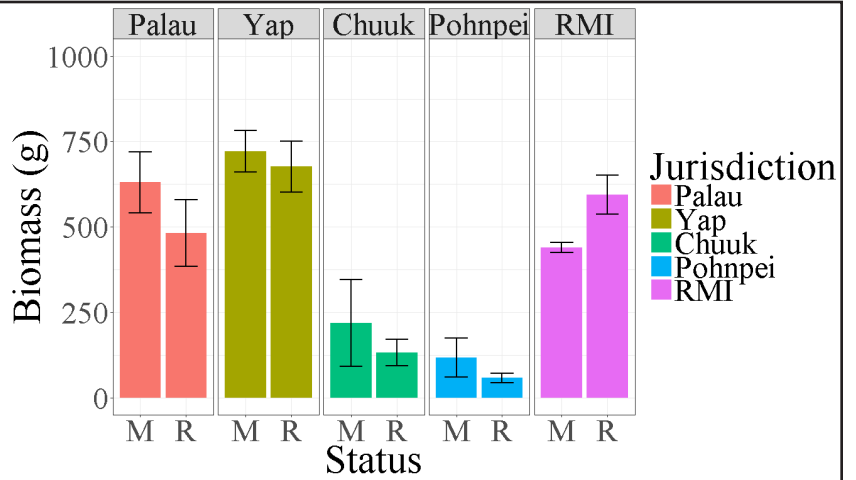
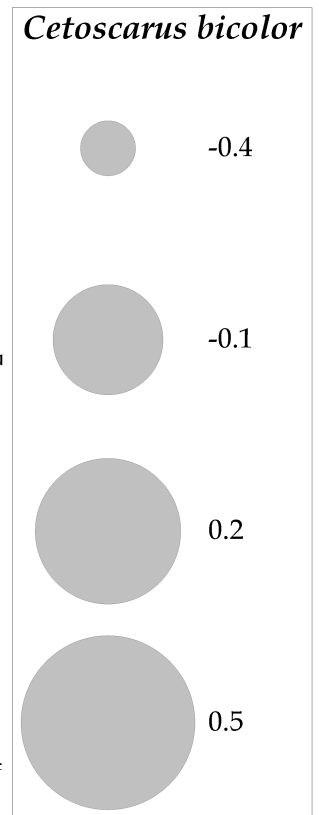
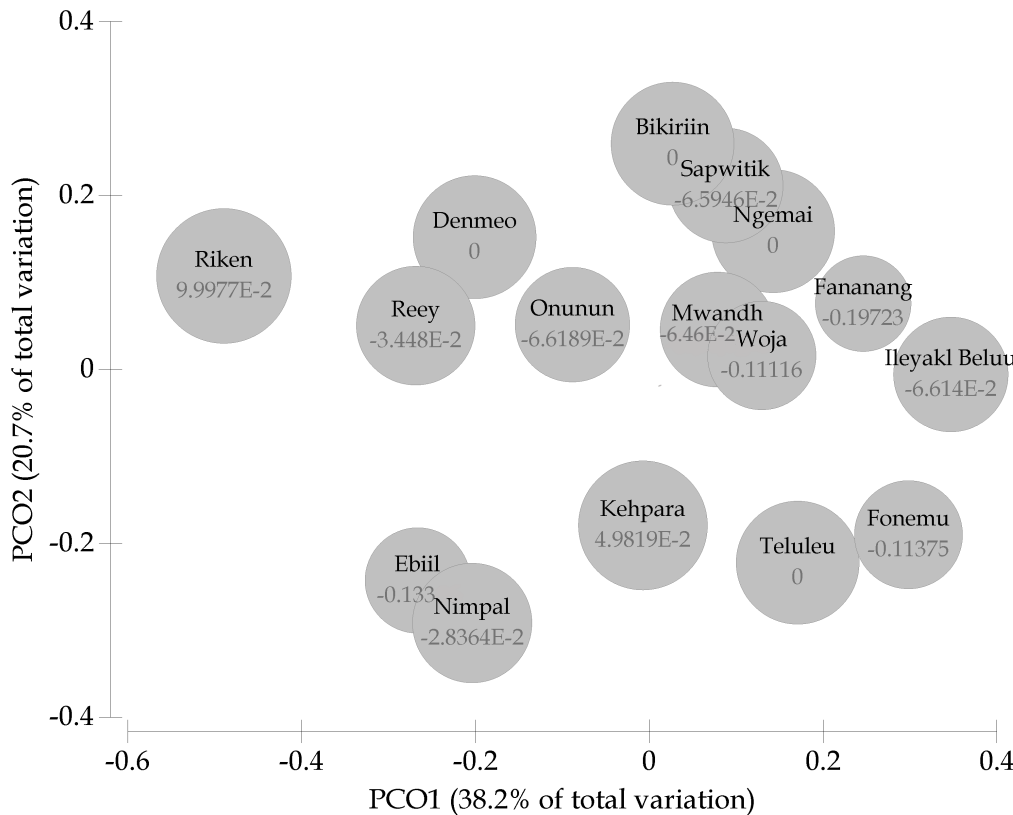
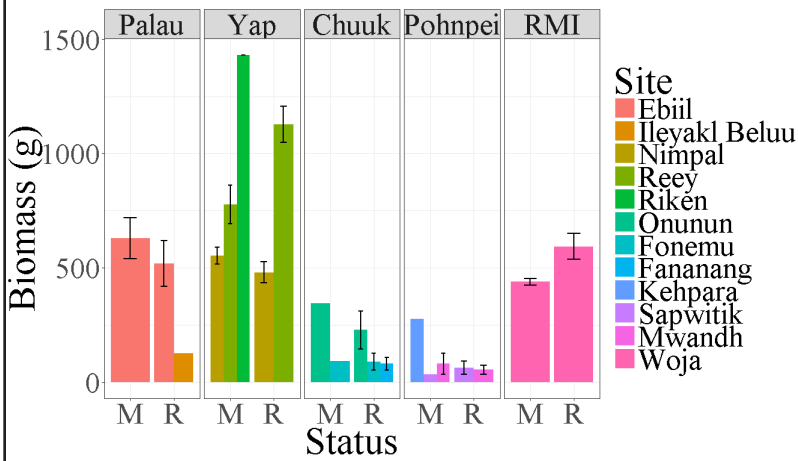


Plate I Plots of jurisdictions (above) and MPAs (left), with error bars (95% confidence) comparing mean *individual* biomass (g) of *Cetoscarus bicolor* (image) between protected (M) and adjacent, fished reefs (R). Ordination plot (below) shows relative differences in *total* biomass at each MPA (i.e., Fonemu -0.11375 = 11.375% less biomass in MPA).





Lino 2016

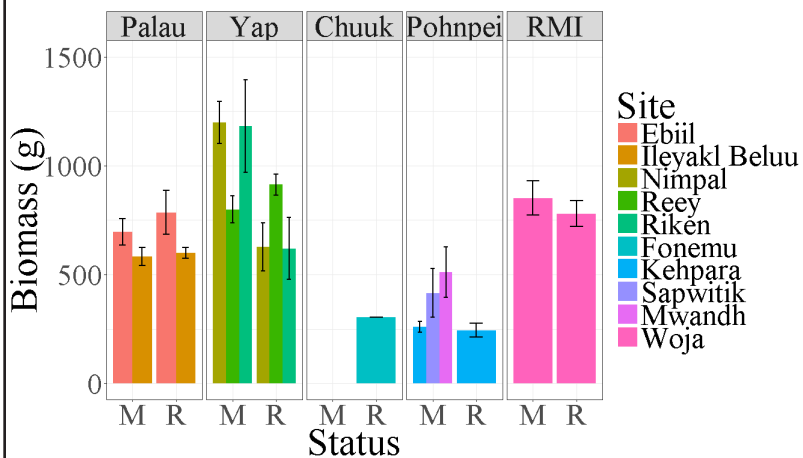
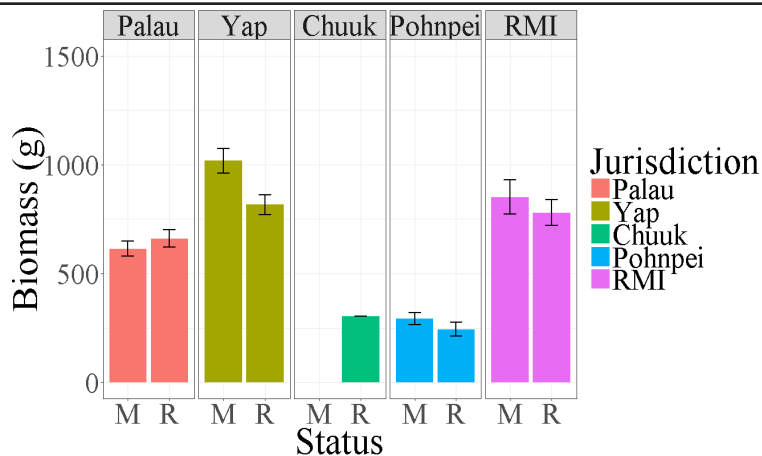
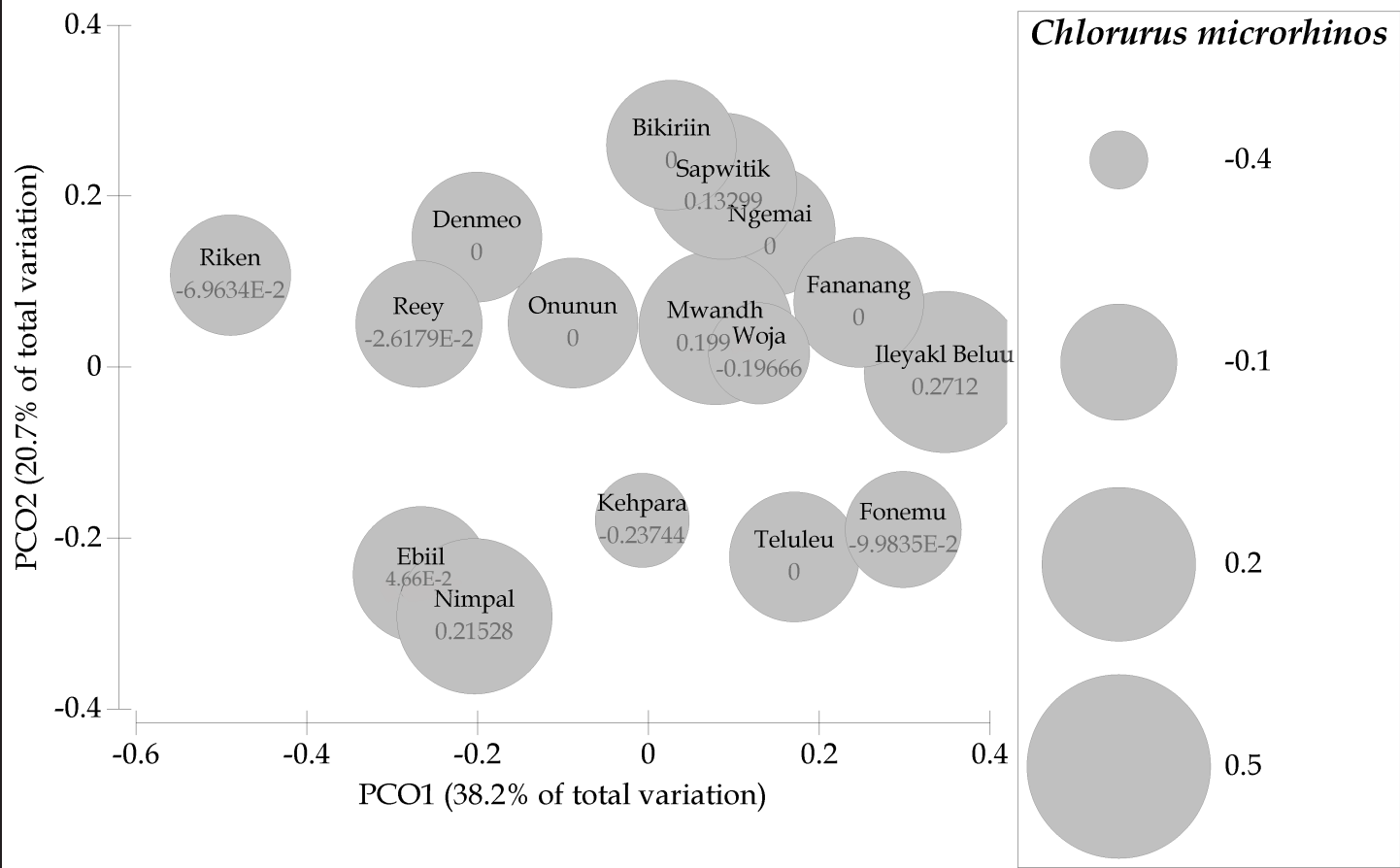


Plate II, Plots of Jurisdictions (above) and MPAs (left), with error bars (95% CI) comparing mean *individual* biomass (g) of *Chlorurus microrhinos* (image) between protected (M) and adjacent, fished reefs (R). Ordination plot (below) shows relative differences in *total* transect biomass at each MPA (i.e., Ileyakl Beluu 0.2712 = 27.12% greater total biomass, when compared to a nearby, fished reef).





Randall 2006

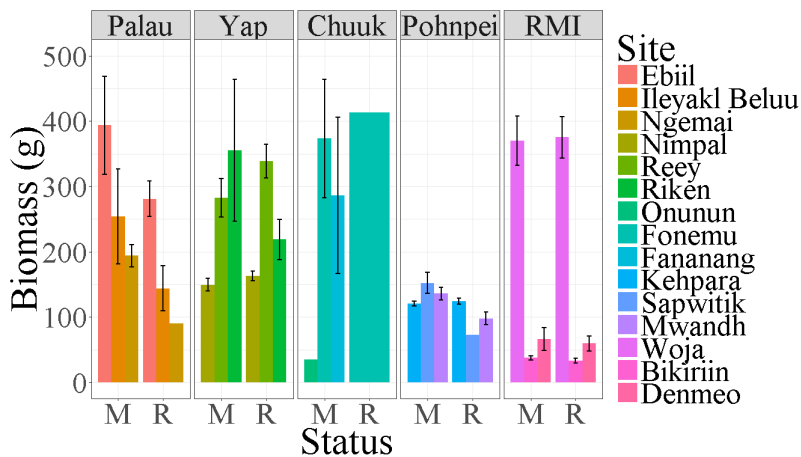
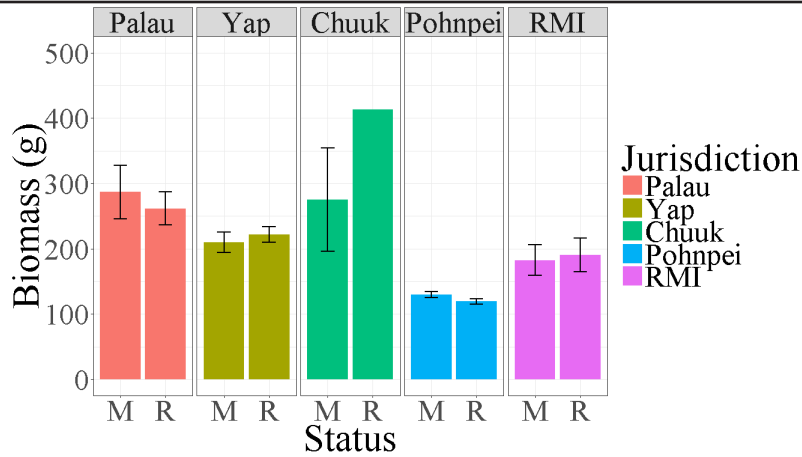
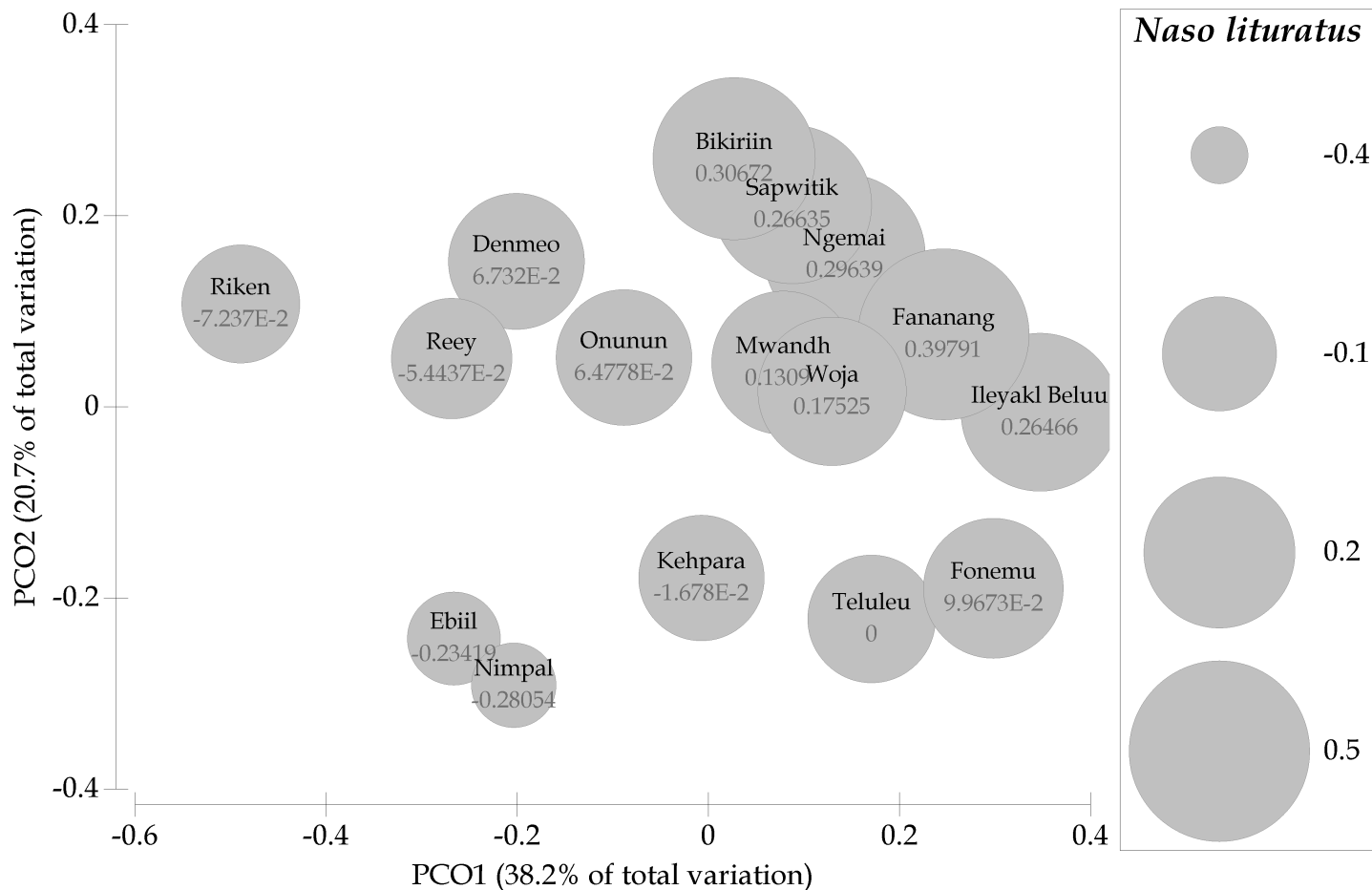


Plate III, Plots of jurisdictions (above) and MPAs (left), with error bars (95% CI) comparing mean *individual* biomass (g) of all *Naso lituratus* (image) between protected (M) and adjacent fished reefs (R). Ordination plot (below) shows relative differences in *total* transect biomass at each MPA (i.e., Nimpal $-0.28054 = 28.054\%$ less biomass in MPA, compared to a nearby, fished reef).





Bidet 2015

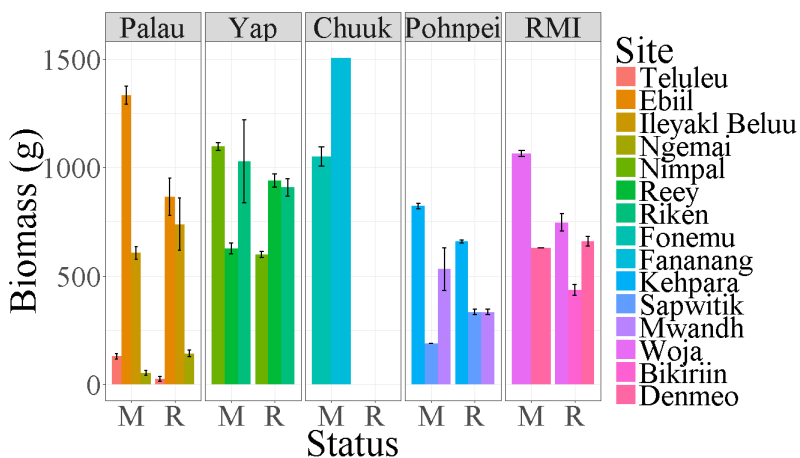
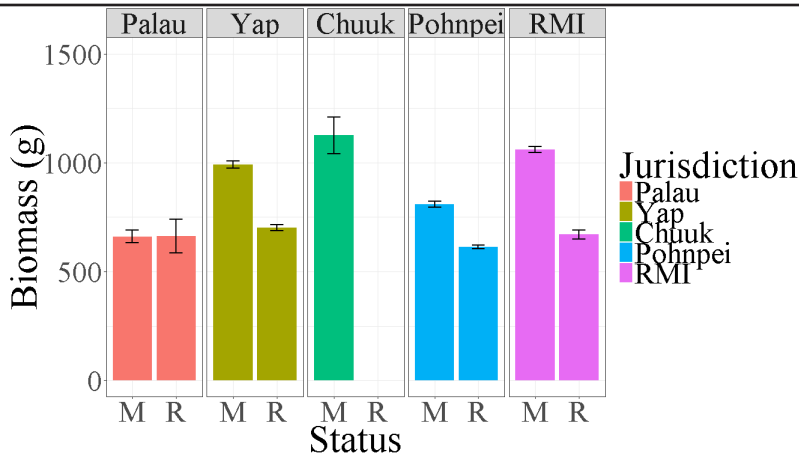
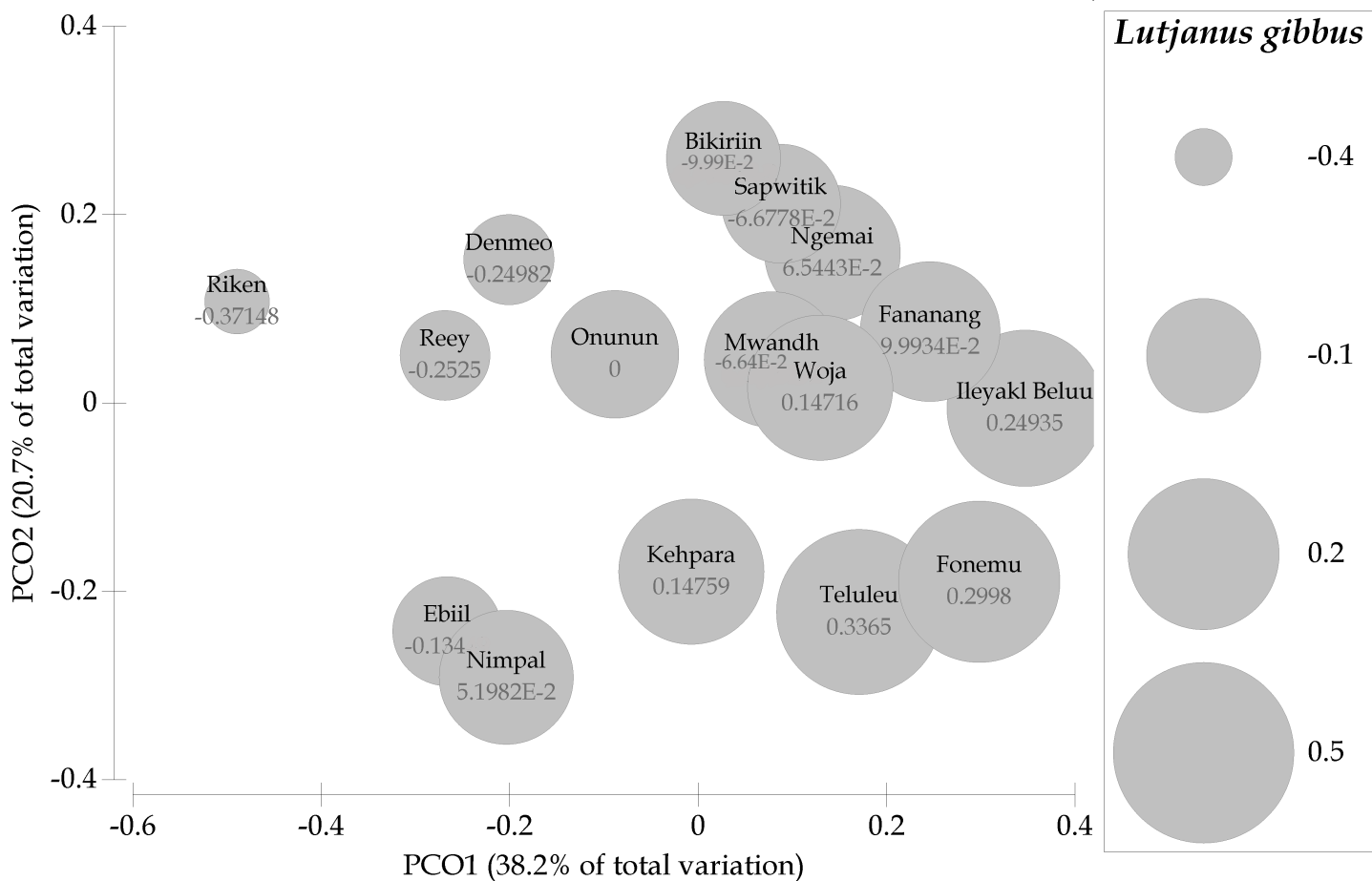


Plate IV Plots of Jurisdictions (above) and MPAs (left), with error bars (95% confidence) comparing mean *individual* biomass (g) of *Lutjanus gibbus* (image) between protected (M) and adjacent fished reefs (R). Ordination plot (below) shows relative differences in *total* transect biomass at each MPA (i.e., Kehpara 0.14759 = 14.759% more biomass in MPA, as compared to a fished reef nearby).



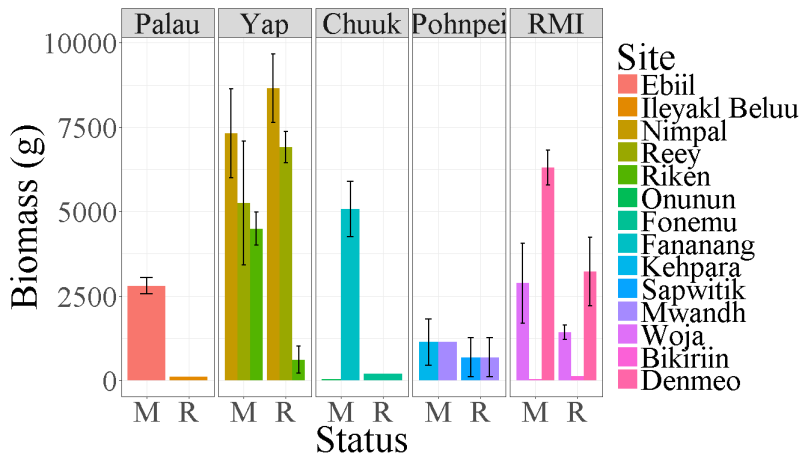
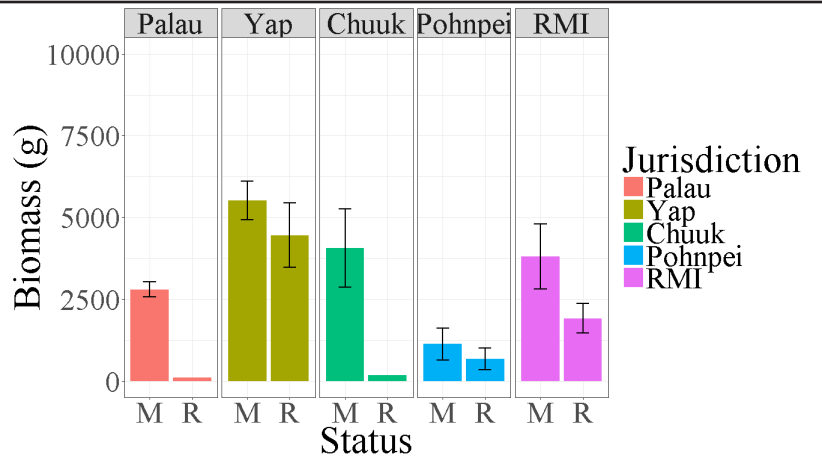
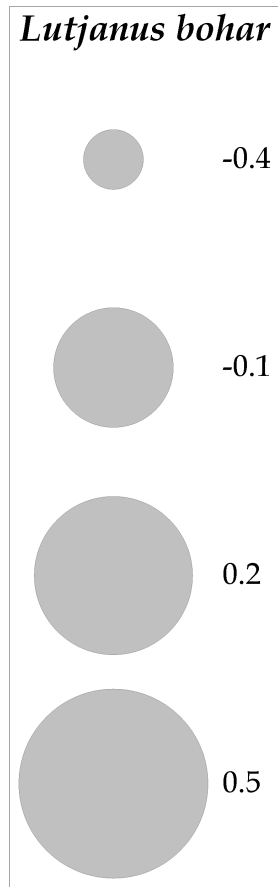
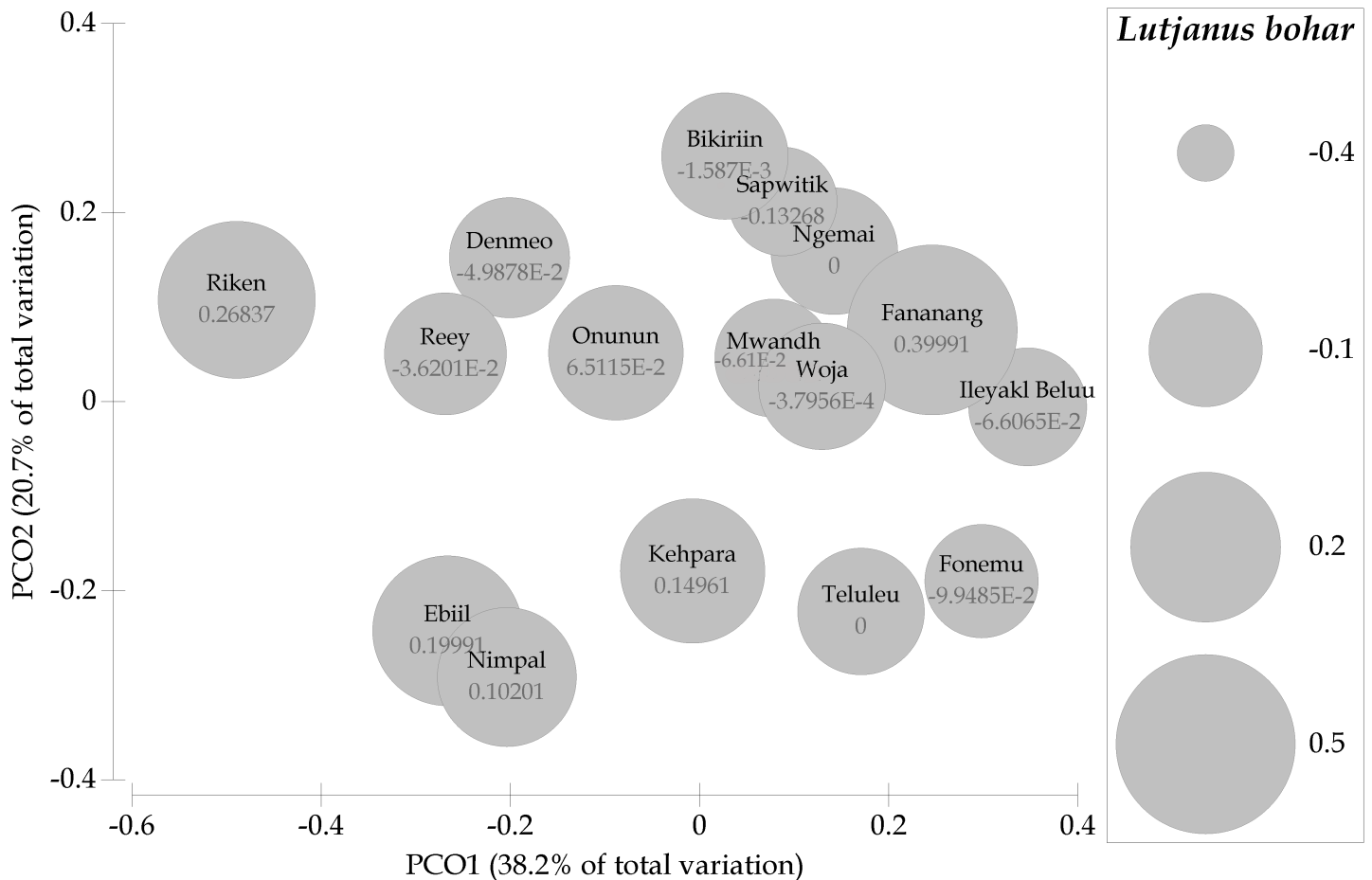


Plate V Plots of Jurisdictions (above) and MPAs (left), with error bars (95% confidence) comparing mean *individual* biomass (g) of *Lutjanus bohar* (image) between protected (M) and adjacent fished reefs (R). Ordination plot (below) shows relative differences in *total* transect biomass at each MPA (i.e., Riken 0.26837 = 26.837% more biomass in the MPA, compared to its Reference, fished reef).



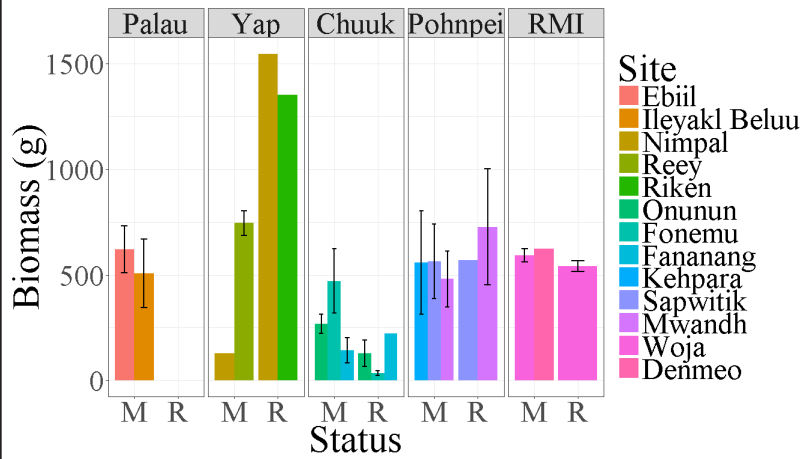
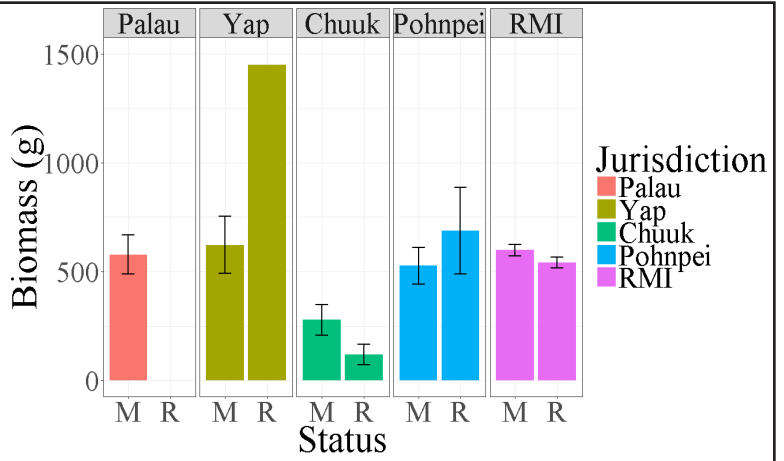


Plate VI Plots of Jurisdictions (above) and MPAs (left), with error bars (95% confidence) comparing mean *individual* biomass (g) of *Plectropomus areolatus* (image) between protected (M) and adjacent, fished reefs (R). Ordination plot (below) shows *total* biomass differences at each of 16 MPAs, where values denote relative differences (i.e., in Bikiriin and Ngemai, no magnitudinal difference was detected between MPA and its Reference).

