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The direct and indirect effects of predators on coral reef fish assemblages

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The direct and indirect effects of predators on coral reef fish assemblages

A dissertation submitted in partial satisfaction of the requirements for the degree
Doctor of Philosophy

in

Marine Biology

by

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The Dissertation of Brian Jon Zgliczynski is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

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2015

DEDICATION

I dedicate this dissertation to my family. I would not have become the man I am today without your love and support. To my Mom and Dad, thank you for taking me to the old Scripps Aquarium as a child, exposing me to the world, and encouraging me to pursue my dreams. To my sister Traci, thank you for being my childhood snorkel buddy, setting such a good example, and being my best friend. To my brother-in-law Trever, thank you for being the brother I always wanted, sharing my passion for the natural world, and being such a good man to my sister. To my niece and nephew Olivia and Cruz, thank you for always making me feel like a super hero and motivating me to truly care about the future of our oceans.

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ABSTRACT OF THE DISSERTATION

The direct and indirect effects of predators on coral reef fish assemblages

by

Brian Jon Zgliczynski

Doctor of Philosophy in Marine Biology

University of California, San Diego, 2015

Professor Stuart Sandin, Chair

The removal of apex predators is widely recognized to have broad ecological consequences for terrestrial and aquatic communities. In marine systems, the direct effects of fisheries exploitation include altering the community standing stock (biomass), species composition, and size-structure of the fish assemblage. Although the direct effects of fisheries exploitation are well documented, there is increasing evidence that the non-lethal effects of predation can also strongly influence the structure and function of ecological communities. In this dissertation I set out to increase our understanding of the effects of predators on coral reef fish assemblages by conducting a series of large-scale natural experiments across groups of Pacific islands spanning gradients of human population density and oceanographic productivity within four distinct geopolitical regions.

My dissertation research reveals striking evidence for the effects of fisheries exploitation and oceanographic productivity on coral reef fish assemblages in three key areas. First, I found strong evidence that the effects of fisheries exploitation are not restricted to large-bodied species from higher-trophic levels but are realized throughout the entire fish assemblage and across multiple trophic groups. Importantly, I show that multiple forms of fisheries exploitation may be present on coral reefs, indicating the complex nature of coral reef fisheries. Second, I show strong evidence of biophysical coupling with gradients of oceanographic productivity and alterations in predatory fish abundance on the body condition, growth rates, maximum size, and longevity of coral reef fishes. I also observe a breakdown of natural coupling at inhabited islands, suggesting that local human impacts are capable of homogenizing life history traits of fishes even when strong environmental gradients are present. Third, I show that the trophic structure of coral reef fish assemblages are more tightly linked to changes in oceanographic productivity than to predatory fish abundance. I observed trophic channeling, a process by which different basal sources of energy entering the system can remain isolated on coral reefs forming distinct pathways up through the food web to top-level carnivores. In summary, my dissertation provides important insight into the mechanisms that structure marine communities and the direct and indirect effects of removing predators from marine ecosystems.

Chapter 1.

THE IUCN RED LIST OF THREATENED SPECIES: AN ASSESSMENT OF CORAL REEF FISHES IN THE US PACIFIC ISLANDS

ABSTRACT

Widespread declines among many coral reef fisheries have led scientists and managers to become increasingly concerned over the extinction risk facing some species. To aid in assessing the extinction risks facing coral reef fishes, large-scale censuses of the abundance and distribution of individual species are critically important. We use fisheries independent data collected as part of the NOAA Pacific Reef Assessment and Monitoring Program from 2000 to 2009 to describe the range and density across the US Pacific of coral reef fishes included on The International Union for the Conservation of Nature's (IUCN) 2011 Red List of Threatened Species. Forty-five species, including sharks, rays, groupers, humphead wrasse (*Cheilinus undulatus*), and bumphead parrotfish (*Bolbometopon muricatum*), included on the IUCN List, were recorded in the US Pacific Islands. Most species were generally rare in the US Pacific with the exception of a few species, principally small groupers and reef sharks. The greatest diversity and densities of IUCN-listed fishes were recorded at remote and uninhabited islands of the Pacific Remote Island Areas (PRIA); in general, lower densities were observed at reefs of inhabited islands. Our findings complement IUCN assessment efforts, emphasize the efficacy of large-scale assessment and monitoring efforts in providing quantitative data on reef fish assemblages, and highlight the importance of protecting populations at

remote and uninhabited islands where some species included on the IUCN Red List of Threatened Species can be observed in abundance.

INTRODUCTION

Coral reefs are threatened by a host of human activities. Among these, fishing exerts significant and direct impacts on many coral reef fish assemblages (Jackson et al. 2001; Friedlander and DeMartini 2002; Sandin et al. 2008). Reef fishes have long supported subsistence and artisanal fisheries with the earliest record of fishing of coastal habitats traced back at least 35,000 years in the western Pacific (Allen et al. 1989). Today, coral reefs continue to support subsistence fisheries and millions of people depend directly on the harvested resources (Zeller et al. 2006). Financially, coral reef ecosystems support commercial fisheries estimated to be worth over $5 billion per year (Cesar et al. 2003).

Despite their importance, the complexity of coral reef fisheries provides many challenges for the development of management strategies aimed to maintain sustainable fisheries and other ecosystem services. Coral reef fisheries tend to exploit multiple species (Jennings and Polunin 1996a), with the primary targets oftentimes being large-bodied species such as sharks, groupers, snappers, jacks, parrotfishes, and wrasses (Roberts 1995; Jennings and Kaiser 1998; Pauly et al. 1998; Choat et al. 2006; DeMartini et al. 2008). Further, the life-history characteristics of many species render them particularly vulnerable to overexploitation. Many large-bodied species tend to be slow-growing, long-lived, have delayed reproductive development, and some form mass aggregations when they spawn (Choat et al. 2006; Tupper 2007; Sadovy de Mitcheson et al. 2008; Colin 2010). Large-bodied species play a critical role in structuring marine ecosystems (Bascompte et al. 2005; Estes et al. 2011), and severe reductions in their biomass have detrimental ecological and economic effects (Pauly et al. 1998; Jackson et al. 2001; Friedlander and DeMartini 2002; Myers and Worm 2003; Sandin et al. 2008). Therefore, knowing the distribution and relative abundance of these species is of critical importance to the development of effective management strategies.

In 1994 the International Union for Conservation of Nature (IUCN), aided by its Species Survival Commission (SSC), developed and adopted a standardized approach for assessing the extinction risk of species and biodiversity in both terrestrial and aquatic environments. Methods and criteria produced by the SSC were used by the IUCN to categorize Red-listed species (Baillie and Groombridge 1996). In general, assessment criteria incorporate estimates of current and historical population size and geographic range to assign species to one of 9 categories of risk. As of 2011 the ICUN Red List categories (in order of descending risk) are extinct, extinct in the wild, critically endangered, endangered, vulnerable, near threatened, least concern, data deficient, and not evaluated. The IUCN Red List of Threatened Species (hereafter IUCN List) has been widely adopted as the basis for identifying species at risk and developing programs to conserve biodiversity (Rodrigues et al. 2006; Mace et al. 2008). Although some assessment criteria used by the United States under the Endangered Species Act (ESA) are similar to those used by the IUCN, the listing process under the ESA incorporates additional criteria and listed species are afforded legal protection administered by either the US Fish and Wildlife Service and the National Oceanic and Atmospheric Administration (National Research Council 1995).

The purpose of this paper is to describe the geographic distribution and density across the US Pacific of shallow-water coral reef fishes included on the 2011 IUCN Red List (across all assessment categories identified above), including the two Indo-Pacific coral reef species identified by NOAA as Species of Concern. We use underwater visual survey data collected as part of the NOAA Pacific Reef Assessment and Monitoring Program (RAMP), a large-scale effort to monitor the status of coral reefs across much of the US Pacific. By design, NOAA Pacific RAMP allocates monitoring effort broadly across space (sampling over 40 islands at least once every two years), and thus lacks high replication at the within-island scale. As such, the ability to resolve temporal trends is limited to functional group assessments (e.g., total fish biomass) or to long-term changes (e.g., trends over decades), but the power of the sampling lies in the high replication at the island scale for each of these assessments. We provide information on the density of sharks, rays, groupers, the bumphead parrotfish (*Bolbometopon muricatum*) and the humphead wrasse (*Cheilinus undulatus*). Additionally, we compare densities of these species between inhabited and uninhabited US Pacific Islands.

MATERIALS AND METHODS

Study Area

Biennial surveys were conducted from 2000 to 2009 at 40 US Pacific Islands as part of the NOAA Pacific RAMP (Table 1.1, Figure. 1.1). Sites included islands under US jurisdiction within four geographic regions: American Samoa, the Hawaiian Archipelago, the Mariana Archipelago, and the Pacific Remote Island Areas (PRIA). These islands span much of the central and western Pacific and encompass 3363 km^2 of shallow-water (< 10 fathom) habitat (Rohmann et al. 2005). Islands are exposed to varying levels of anthropogenic disturbance, influenced by their degree of inhabitation and distance from population centers. Some islands, such as Oahu in the Hawaiian

Archipelago, Guam in the Mariana Archipelago, and Tutuila in American Samoa are densely populated islands with heavily exploited fisheries resources, while some other islands are remote, uninhabited, and relatively uninfluenced by direct human disturbances (Figure. 1.1). Islands were classified as either “inhabited” or “uninhabited,” based on their respective resident populations and level of fisheries management as described by Williams et al. (2011). In some instances, islands classified as uninhabited had or continue to have small resident populations of < 25 people, with two island atolls (Midway and Wake) having populations slightly higher during the survey period (Table 1.1). Although some islands classified as uninhabited had small resident populations, the level of fisheries exploitation at these islands was considered nonexistent, because residents of the island during the survey period were caretakers, contract staff, or field researchers, and fishing in surrounding shallow-water habitats was restricted or infrequent. Of the 40 islands and reefs included in this study, 15 islands were classified as inhabited and 25 as uninhabited.

Survey Methods

Two underwater survey techniques were used to estimate the density of diurnally active reef fishes. These included towed-diver survey (TDS) and belt transect (BLT) methodologies. All divers collecting data were trained in the identification and size-estimation of fishes following protocols outlined by NOAA Pacific RAMP (Richards et al 2011). Surveys were restricted to the upper forereef slope at depths shallower than 30 m with a majority of surveys conducted at depths of 12-15 m.

The TDS method consisted of a pair of SCUBA divers being towed ~ 60 m behind a small boat at a speed of ~ 1.5 kts and at depths typically between 10 and 20 m (Richards et al. 2011). Divers maneuvered towboards 1–3 m above the benthos, tallying all fishes ≥ 50-cm total length (TL) that enter a 10-m wide swath centered on the diver. Fish species were recorded to the finest recognizable taxonomic level (typically species) and size was estimated to the nearest 5 cm TL. Each TDS is 50 min in duration (10, 5-min segments) and covered an average of about 2.2 km of linear habitat (22,000 m^2 survey area). As such, the TDS method is spatially expansive and results in greater statistical power and higher frequency of encounter than more spatially constrained survey techniques when estimating the density and spatial distribution of rare, large-bodied reef fishes (Richards et al. 2011).

The BLT surveys consisted of a pair of divers conducting three 25-m strip transects, using protocols detailed elsewhere (Friedlander and DeMartini 2002; DeMartini et al. 2008, Friedlander et al. 2010). To summarize, individual fishes were identified to species and length (TL) was estimated to the nearest 5-cm size class. Fish abundance estimates were made by means of two passes for each 25-m transect. The pair of divers surveyed an 8-m width (200 m^2 area) for individuals ≥ 20 cm TL on an outward swim, and a 4-m width (100 m^2 area) for species < 20 cm TL on a return swim.

Data Analyses

Data from TDS and BLT methods were used to estimate size-specific numerical density for species of interest. Maximum body size of each species, based on published estimates and online sources, was used to determine which of these methods was appropriate for species-specific density estimates (Randall 2005, 2010; Froese and Pauly

2010). Fishes reaching a published maximum TL of 100 cm or greater were classified as large-bodied, and TDS data were used to estimate the density of these species. Fishes reaching a maximum TL < 100 cm were classified as smaller-bodied, and BLT data were used to estimate densities of these species. As such, larger-bodied species were assessed using a more spatially expansive method with densities reported as individuals km^{-2}, while smaller-bodied species were sampled using a more comprehensive but spatially constrained method with densities reported as individuals ha^{-1}. Detailed summaries of the mean and maximum size of each species using the results of TDS and BLT surveys are provided at the island level as a series of tables for each region in the Electronic Supplementary Material. To maintain sufficient statistical power, islands with a total survey effort of < 9 TDS or < 7 BLT were eliminated from the analyses.

Species included in this study were selected based on three factors: (1) inclusion on the 2011 IUCN Red List of Threatened Species (IUCN 2011), (2) biogeographic ranges encompassing the US Pacific Islands confirmed through RAMP surveys, and (3) inhabiting shallow-moderate (< 30 m) depth reef habitats. Web-based and published sources were used to identify the geographic ranges and ecological habitats of IUCN-listed species observed in the US Pacific Islands (Myers 1999; Randall 2005, 2010; Froese and Pauly 2010). A list of the 45 species meeting all three factors identified above is presented in Table 1.2.

Visual estimates of species density collected from TDS and BLT methods were non-normally distributed at both island and regional scales. For abundant species and species groups, region- (or island-) specific densities are presented as means with standard errors using all available survey data. However, for statistical comparisons of groups, transforming the data and applying parametric techniques to estimate population parameters, including explicit descriptions of variability, was not practical because of the rarity of many species and zero-inflated nature of the data. Additionally, survey effort for the TDS and BLT methods varied among islands throughout the survey period (Table 1.1), which complicated simple parametric comparisons of island mean densities. A statistical bootstrapping approach (Efron and Tibshirani 1986; Chernick 2008) was used to evaluate differences in the mean density of fishes between groups of inhabited and uninhabited islands within each region while accounting for the non-normality of the data and to standardize survey effort across islands. The bootstrapping analysis was based on island-specific survey data on density for each species combined over survey years. TDS data were used for large-bodied species and BLT data for smaller-bodied species. Each survey provided an estimate of mean density, and the number of density estimates varied among islands and survey methods (Table 1.1).

To create a bootstrap replicate, a sample of density estimates was drawn randomly with replacement for each island from the total pool of estimates for the island (Table 1.1). Bootstrap sample sizes were 9 surveys for TDS and 7 surveys for BLT. Within each region, island-specific bootstrap means were assigned to one of two habitation categories - inhabited and uninhabited islands. Within each region, the average bootstrap density was computed over all inhabited islands in the region, and similarly for the uninhabited islands, and the difference between the two averages was calculated.

The statistical resampling across all islands was completed 10,000 times, generating species-specific bootstrap statistical distributions of density within each region for each habitation stratum and the differences in average density between the habitation strata. In each case, 95% confidence intervals for mean density using the appropriate bootstrap distribution by calculating the 2.5 and 97.5 percentiles and setting them as the lower and upper 95% limits, respectively.

Regional differences in density for each species between inhabited or uninhabited island groups were determined by subtracting mean densities at inhabited islands from the mean densities of uninhabited island groups. Positive mean differences denoted that uninhabited island groups yielded a higher mean density of fishes while negative mean differences denoted that an uninhabited island group yielded a lower mean density of fishes than their inhabited counterparts. Significant differences in regional means were estimated by calculating the number of times that subsampled values differed between regional groups (either positive or negative), expressing the quantile range of the distribution of results (e.g., 0, 0.001, 0.01, 0.05, 0.25, 0.5, 0.75, 0.95, 0.99, 0.999, and 1.0 quantiles). If ≥ 95% of the distribution of data (positive or negative) fell within the quantile range, it was deemed significant and the corresponding level of significance was assigned (< 0.05, < 0.01, or < 0.001). Analyses were conducted using R version 2.8.1 (The R Foundation for Statistical Computing 2008).

RESULTS

IUCN-listed species in the US Pacific Islands

Forty-five species representing 11 families of fishes included on the IUCN List were observed during RAMP surveys (Table 1.2). Of the species observed, more than 25% (13 species) are categorized by the IUCN as endangered or vulnerable, the two highest extinction risk categories observed in this assessment. The humphead wrasse, scalloped hammerhead (*Sphyrna lewini*), and great hammerhead (*Sphyrna mokarran*) are the only three species observed during this study that are listed as endangered and are considered to face the greatest risk of extinction. The humphead wrasse is one of two Indo-Pacific coral reef fishes also listed as a NOAA Species of Concern.

Groupers (Serranidae) accounted for more than 60% (28 species) of the IUCN-listed species encountered during RAMP surveys. However, only 3 of the groupers observed are listed as vulnerable, the second highest risk of extinction. These include the giant grouper (*Epinephelus lanceolatus*), squaretail coral grouper (*Plectropomus areolatus*), and black saddled coral grouper (*P. laevis*). Three additional groupers observed during surveys are assigned to the near threatened category and considered to be close to qualifying or likely to qualify for one of the threatened categories in the near future. These include the camouflage grouper (*Epinephelus polyphekadion*), Hawaiian grouper (*Hyporthodus* [*Epinephelus*] *quernus*), and the leopard coral grouper (*Plectropomus leopardus*). The remaining 22 grouper species represent 49% of the IUCN-listed species encountered during RAMP surveys and are assigned to the least concern and data deficient categories.

Sharks and rays from the subclass Elasmobranchii accounted for the second greatest proportion (31%) of IUCN-listed species encountered during surveys. Of the 14 species of Elasmobranchs, nearly half (6 species) are requiem sharks (Carcharhinidae), with the lemon shark (*Negaprion acutidens*) being the only reef shark listed as vulnerable. The two species of hammerhead sharks are listed as endangered, and the remaining sharks and rays observed during surveys are listed as vulnerable (4 species) or near threatened (2 species). A complete list of all 45 IUCN-listed species observed during RAMP surveys is included in Table 1.2. Additionally, the results from the TDS and BLT surveys are summarized in a series of tables included in Electronic Supplementary Material identifying the mean and maximum size of each species observed at each island during this assessment.

Regional and island trends

At the regional level, the greatest number of IUCN-listed species (39 species) was observed in the PRIA, while the smallest number of species (12 species) was observed in the Hawaiian Archipelago. At the island level, the greatest number of IUCN-listed species was observed at Howland Island (PRIA) with 26 species, followed by Jarvis Island (25 species), Palmyra Atoll (24 species), and Baker Island (20 species), all located within the PRIA. Tutuila, the largest and most densely populated island in American Samoa, was the only non-PRIA island with more than 20 IUCN-listed species observed (21 species). Few species have ranges extending to all 4 geographic regions. These broad ranging species included gray reef sharks (*Carcharhinus amblyrhynchos*, near threatened), whitetip reef sharks (*Triaenodon obesus*, near threatened), spotted eagle rays (*Aetobatus narinari*, near threatened), and the peacock hind (*Cephalopholis argus*, least concern). The peacock hind's distribution includes the inhabited islands of the Hawaiian Archipelago following its deliberate introduction from the Society Islands in 1956 (Randall 1987).

Density of large-bodied species

Total mean density of large-bodied species varied greatly at the regional and island levels (Table 1.3). The greatest densities of IUCN-listed species were observed in the PRIA where the overall mean was 33 individuals km^{-2} (SE 21). In contrast, the lowest density of IUCN-listed species was observed in American Samoa, i.e., 2 individuals km^{-2} (SE 1). In the Hawaiian Archipelago and Mariana Archipelago IUCN-listed species were observed in densities less than a third of those in the PRIA with total mean density of IUCN-listed species being 7 individuals km^{-2} (SE 3) and 9 individuals km^{-2} (SE 5) observed respectively.

Considerable differences in the mean density of IUCN-listed species were observed between inhabited and uninhabited islands of the Hawaiian and Mariana Archipelagoes (Table 1.3). The mean density of IUCN-listed species (all species pooled) was fivefold greater at uninhabited islands within the two archipelagoes. Of the 11 IUCN-listed species observed in the Hawaiian Archipelago during TDS, 4 were recorded at significantly greater ($p < 0.01$) densities at uninhabited islands. Those were the gray reef shark, Galapagos shark (*Carcharhinus galapagensis*), whitetip reef shark, and Hawaiian grouper all of which are listed as near threatened.

In the Mariana Archipelago, 3 IUCN-listed species were observed in significantly greater ($p < 0.001$) densities at uninhabited islands: the tawny nurse shark (*Nebrius ferrugineus*, near threatened), gray reef shark, and whitetip reef shark. The humphead wrasse was the only IUCN-listed species and NOAA Species of Concern observed in significantly greater ($p < 0.05$) density at inhabited islands in the Mariana Archipelago with 14 individuals observed km^{-2} (95% CI: 5, 27) compared to 4 individuals observed km^{-2} (95% CI: 1, 9) at uninhabited islands within the archipelago. In American Samoa, no significant difference in the mean density of IUCN-listed species was observed between inhabited and uninhabited islands.

Density of high-risk, large-bodied species

In general, high-risk species listed as endangered or vulnerable were uncommon, with the exception of tawny nurse sharks, blotched fantail rays (*Taeniura meyeni*), scalloped hammerhead shark, and humphead wrasse (Figure 1.1). Tawny nurse sharks and blotched fantail rays were most frequently observed at uninhabited islands of the Mariana Archipelago, with a mean density of 0.16 individuals km^{-2} (95% CI: 0.10, 0.22) and 0.06 individuals km^{-2} (95% CI: 0.02, 0.12), respectively. Scalloped hammerhead sharks were rare throughout all islands but observed in the greatest density in the PRIA at 0.16 individuals km^{-2} (95% CI: 0, 0.46).

Humphead wrasse was the most widely distributed high-risk species that included all regions except the Hawaiian Archipelago. The greatest densities of humphead wrasse were observed in the PRIA, with a regional mean of 0.26 individuals observed km^{-2} (95% CI: 0.14, 0.42). Within the PRIA, the greatest density was recorded at Wake Atoll with 114 individuals observed km^{-2} (SE 15). Palmyra Atoll had the second greatest density with 63 individuals observed km^{-2} (SE 13). Humphead wrasse were also recorded at the southern islands of the Mariana Archipelago and throughout American Samoa. In the Mariana Archipelago, Rota Island had the greatest density of humphead wrasse with 40 individuals observed km^{-2} (SE 10). Humphead wrasse were also observed at all of the islands in American Samoa with the greatest density observed at Swains Island [29 individuals km^{-2} (SE 7)].

Bumphead parrotfish (vulnerable), one of two Indo-Pacific coral reef species listed as a NOAA Species of Concern, were rare or absent in the US Pacific Islands except for at Wake Atoll where their mean density was 297 individuals km^{-2} (SE 96). Bumphead Parrotfish were also observed at Palmyra Atoll but only at a fraction of what was observed at Wake Atoll, where a mean 5 fish km^{-2} (SE 4) was observed. Other sightings of the bumphead parrotfish included Pagan Island (Mariana Archipelago), with 2 individuals observed, and at Tau and Tutuila (American Samoa), where a single individual was observed at each location.

Density of small-bodied species

Small-bodied grouper species reaching a maximum TL of <100 cm accounted for a majority (23 species) of the IUCN-listed species encountered. The yellow-crowned butterflyfish (*Chaetodon flavocoronatus,* vulnerable) was the only other small-bodied included on the IUCN List and recorded in the US Pacific Islands. In general, small-bodied IUCN-listed species were rare, and mean densities varied at both the regional and island level. Most species were infrequently recorded while a few others were observed in great densities (Table 1.4).

At the regional level, the highest mean densities of IUCN-listed grouper species were observed in the PRIA with 28 individuals observed ha^{-1} (SE 12). Grouper densities in American Samoa and the Mariana Archipelago were a little more than half of those observed in the PRIA, with mean densities equal to 23 individuals ha^{-1} (SE 12) and 17 individuals ha^{-1} (SE 10), respectively.

Significant differences in the density of small-bodied grouper species were observed between inhabited and uninhabited islands (Table 1.4). In American Samoa, 5 of the 22 IUCN-listed grouper species recorded in the archipelago were observed in significantly greater densities at uninhabited islands. The yellow-edged lyretail grouper (*Variola louti*, least concern), was the only grouper species observed at significantly greater ($p < 0.05$) densities at inhabited islands with 5 individuals ha^{-1} (95% CI: 1, 12); no individuals were recorded at uninhabited islands within the archipelago. In the Mariana Archipelago, 6 of the 22 grouper species were recorded in higher densities at uninhabited islands; and no grouper species was more abundant at inhabited islands. In the Hawaiian Archipelago the nonnative peacock hind was observed at significantly greater ($p < 0.001$) densities at inhabited islands [22 individuals ha^{-1} (95% CI: 14, 32)], likely a persistent consequence of its deliberate introduction into the inhabited main islands (Randall 1987).

The darkfin hind (*Cephalopholis urodeta*, least concern) was the most abundant grouper species overall with the greatest densities (340 individuals ha^{-1}; 95% CI: 285, 399) observed at the uninhabited islands of the Mariana Archipelago. The peacock hind also was abundant in all survey regions, with the greatest densities observed at the uninhabited islands of American Samoa [110 individuals ha^{-1} (95% CI: 74, 147)]. The coral hind (*Cephalopholis miniata*, least concern) and the blacktip grouper (*Epinephelus fasciatus*, least concern) were abundant in the PRIA with 127 individuals ha^{-1} (95% CI: 91, 166) and 75 individuals ha^{-1} (95% CI: 26, 143), observed respectively. These same species were rare or not observed at the inhabited islands of the American Samoa and Mariana Archipelagoes.

Density of high-risk, small-bodied species

The camouflage grouper (*Epinephelus polyphekadion*) and the yellow-crowned butterflyfish were the only two small-bodied species listed as vulnerable*,* the second-highest risk category included in this study. Camouflage grouper were most abundant in the PRIA [1 individual ha^{-1} (95% CI: 0, 3). The yellow-crowned butterflyfish typically observed at depths greater than 30 m in the Mariana Archipelago was recorded at a single site and depth less than 30 m.

DISCUSSION

Overexploitation is generally considered the primary threat facing coral reef fishes (Friedlander and DeMartini 2002; Reynolds et al. 2002, 2005; Dulvy et al. 2003; DeMartini et al. 2008). Although there are no documented cases of global marine fish extinctions, marked declines have occurred in several species, some of which are considered to be extinct at local or regional scales (Dulvy et al. 2003). Growing concerns over the status of many species led the IUCN to evaluate the conservation status of 1326 species of marine fishes, 45 of which were recorded in the US Pacific Islands as part of the RAMP. Our aim was to complement IUCN evaluation efforts by providing the first large-scale assessment of IUCN-listed species in the tropical US Pacific Islands. Data included in this study are substantial, representing 9 years of survey effort, including 40 islands spanning a large portion of the tropical Pacific. From these efforts 3 key findings emerge: (1) the diversity and density of IUCN-listed species in the US Pacific Islands varied across individual islands and at a regional scale; (2) mean densities significantly differed between uninhabited and inhabited islands—densities were greater in uninhabited versus inhabited regions in 78% of 23 total cases for which data were available; and (3) IUCN-listed species were most diverse and abundant in the remote and uninhabited PRIA. Threats to these IUCN-listed species continue to include their limited distributions, popularity among fisheries, life-history characteristics, and remote regional occurrence (Morris et al. 2000; Sadovy et al. 2003; Donaldson and Dulvy 2004; Sadovy 2005; Sadovy and Domeier 2005).

Widely distributed species are thought to face reduced risks of extinction compared to species with restricted ranges (Hawkins et al. 2000). Large-scale exploitation reduces population densities of a species which can lead to localized extirpations and an overall range reduction (Roberts 1995). Species with clumped population distributions and/or species that form spawning aggregations at specific and predictable times and locations are more susceptible to large-scale exploitation. In the US Pacific islands, most IUCN-listed species have patchy distributions (Tables 1.3 and 1.4; Figure 1.1). These heterogeneous distribution patterns were not restricted to species facing the greatest extinction risk but applied to most species regardless of their IUCN List categorization. Species with low levels of abundance or disparate populations are less resistant and resilient to perturbations and have a diminished capacity to recolonize locally extirpated populations (Cooper and Mangel 1999). These findings suggest that nearly all IUCN-listed species recorded in the US Pacific Islands may be vulnerable to large-scale exploitation or perturbations and face a greater risk of local extinction compared to species with less clumped population distributions.

Most of the IUCN-listed fish species are targets for subsistence, recreational or commercial fisheries (Morris et al. 2000; Donaldson and Sadovy 2001; Sadovy et al.

2003; Donaldson and Dulvy 2004; Robbins et al. 2006). Some species such as bumphead parrotfish might be especially vulnerable because they also are considered trophy by-catch within multi-species fisheries thus leading to rapid and little documented rates of population decline (Dulvy et al. 2003; Dulvy and Polunin 2004). Sharks, groupers, humphead wrasse, and bumphead parrotfish accounted for more than 80% of the IUCN-listed species observed in the US Pacific islands during RAMP surveys. These species are important in structuring fish and benthic communities through their roles as influential competitors and predators on coral reefs (Roberts 1995; Bascompte et al. 2005; Estes et al. 2011). We did not observe most conspicuous large-bodied species of sharks and groupers except at remote and uninhabited islands (Tables 1.3 and 1.4; Figure 1.1). Large-bodied highly mobile species such as sharks showed the greatest differences in abundance between inhabited and uninhabited islands in the Hawaiian and Mariana Archipelagoes. Significant differences in the mean density of small-bodied grouper species were also observed, although less often. The reason for these differences in unknown, but the pattern has been documented in many marine ecosystems where fishing down large-bodied species has been followed by exploitation of smaller-bodied species (Roberts 1995; Jennings and Polunin 1996a, 1996b; Pauly et al. 1998; Friedlander and DeMartini 2002; DeMartini et al. 2008). Importantly, there were similarities in the density patterns of these species regardless of category of extinction risk – each the high-risk, low-risk, and data deficient species of concern identified by IUCN showed vulnerability to exploitation as evidenced by regional comparisons of density between inhabited and uninhabited islands (Tables 1.3 and 1.4).

Furthermore, we documented only 3 instances where greater densities of IUCN-listed species were observed at inhabited islands. These differences were most likely attributed to: (1) persistent results of deliberate introductions of the species to inhabited islands, as is the case for the peacock grouper in the Hawaiian Archipelago (Randall 1987), (2) lack of suitable juvenile habitat (e.g., lagoons with branching coral and macroalgae) for humphead wrasse at uninhabited islands of the Mariana Archipelago (Tupper 2007), and (3) lack of suitable adult habitat (e.g., reef passes or lagoons) for the yellow-edged lyretail grouper at uninhabited islands in American Samoa (Randall and Brock 1960; Myers 1999). Despite some species-specific differences, the life-history characteristics common among a majority of the IUCN-listed species recorded during surveys make them particularly vulnerable to overexploitation. These characteristics include slow growth, long life span, late sexual maturation, group spawning, low replenishment rates, and low natural abundance (Reynolds et al. 2002; Sadovy and Cheung 2003; Tupper 2007; Sadovy de Mitcheson et al. 2008). These life-history characteristics, combined with the Pacific-wide declines of many of these species, reinforce the importance of large-scale assessments and conservation efforts.

Underwater visual census (UVC) methods are common tools used to characterize coral reef fish assemblages (Friedlander and DeMartini 2002; DeMartini et al. 2008; Sandin et al. 2008; Williams et al. 2011). Although these methods do not provide age-based demographic data used in modern stock assessments, they provide quantitative estimates of species density, size structure, and frequency of occurrence. A key advantage of UVC methods is that they are fishery independent and nondestructive. This is especially important when assessing species affected by overexploitation or while working in protected areas.

Recent conservation efforts in the tropical Pacific have formally protected many of the uninhabited islands of the US Pacific, including Papahānaumokuākea (Northwestern Hawaiian Islands), Pacific Remote Islands, Marianas Trench (including many of the uninhabited islands of the Mariana Archipelago), and Rose Atoll Marine National Monuments. Such management measures should afford many of species of concern with a refuge from fishing in perpetuity. Further, the remote, uninhabited islands provide an opportunity to estimate baselines and are among the few remaining “pristine” systems where IUCN-listed species can be observed in abundance. As such, these reefs provide an unprecedented opportunity for scientists and managers to examine ecosystem function and the ecology of IUCN-listed species in the absence of direct human-caused disturbances. The knowledge gained by studying these undisturbed systems can be used to identify spawning aggregations, essential fish habitat, fish behavior, and other ecological processes that can be applied to the development recovery strategies and ecosystem-based management plans, including those for sustainable fisheries in inhabited islands.

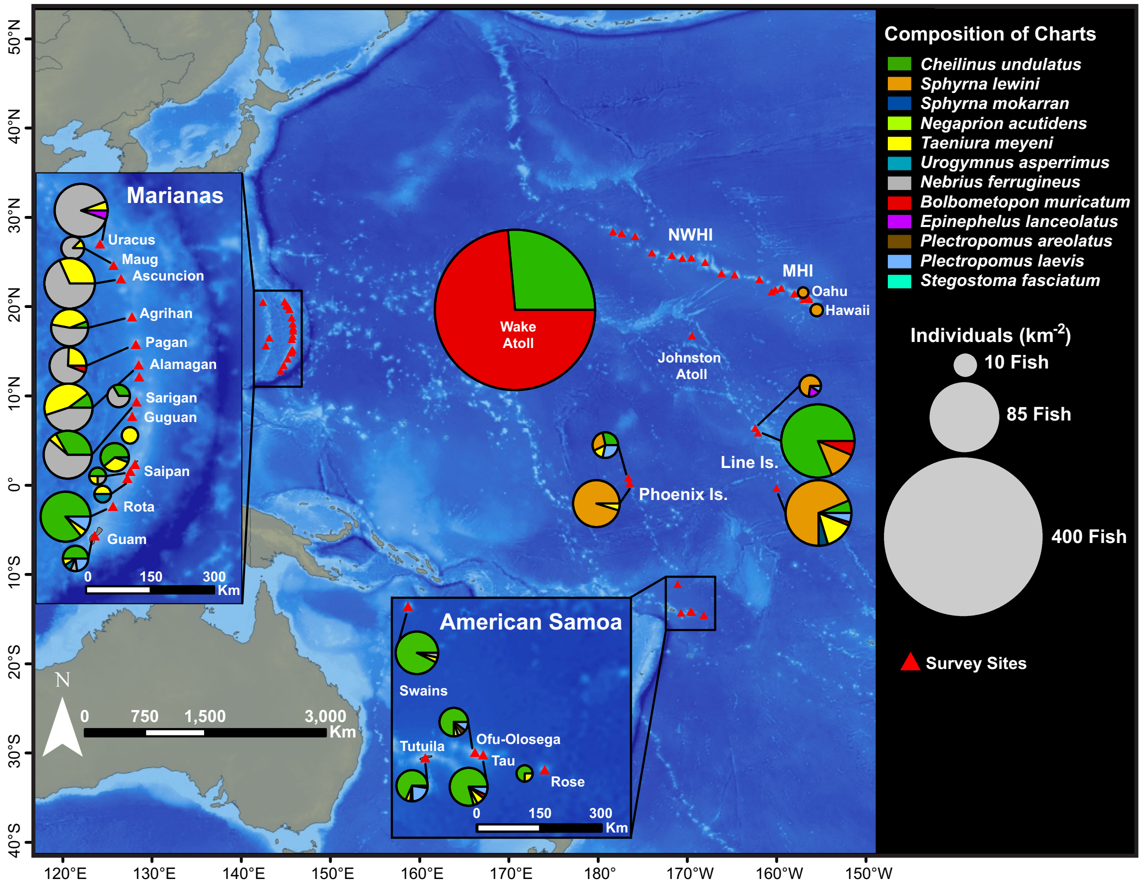

Figure 1.1. Chart of the US Pacific Islands identifying islands surveyed as part of the NOAA Pacific Reef Assessment and Monitoring Program (RAMP). Figure identifies the total mean density of IUCN Red-listed species facing the greatest threat of extinction (2011 IUCN Red List Categories: endangered and threatened). Data are based on towed-diver surveys conducted from 2000 to 2009. Mean densities of fishes are indicated by pie diagrams; the size of individual pies is proportional to the number of individuals observed km^{-2}.

Table 1.1. Sampling effort for surveys conducted as part of the NOAA Pacific Reef Assessment and Monitoring Program from 2000 to 2009. Uninhabited islands within each region are shaded, TDS: towed-diver surveys, and BLT: belt transect surveys. Uninhabited islands within each region are shaded. Abbreviations are as follows: TDS: towed-diver surveys, BLT: belt transect surveys.

Region	Island/Reef	Reef Area (km^2)[a]	Cruise visits	Number of TDS (Area surveyed, km^2)	Number of BLT (Area surveyed, ha)
American Samoa	Ofu & Olosega	3.6	4	62 (1.3)	34 (1.0 / 2.0)
	Tau	3.8	4	50 (1.2)	33 (0.9 / 1.9)
	Tutuila	35.8	4	122 (2.6)	72 (2.1 / 4.3)
	Rose	7.9	4	60 (1.0)	36 (1.0 / 2.1)
	Swains	2.4	4	42 (0.8)	28 (0.8 / 1.6)
	American Samoa Total			336 (6.9)	203 (6.1 / 12.2)
Hawaiian Archipelago	Hawaii	193.7	3	74 (1.5)	60 (1.8 / 3.6)
	Kauai	178.8	3	56 (1.1)	28 (0.8 / 1.6)
	Lanai	46.3	3	33 (0.8)	18 (0.5 / 1.0)
	Maui	164.6	3	65 (1.4)	35 (1.0 / 2.1)
	Molokai	161.6	3	24 (0.6)	13 (0.3 / 0.7)
	Niihau-Lehua	6.7	3	47 (1.0)	26 (0.7 / 1.5)
	Oahu	374.8	3	40 (0.8)	19 (0.5 / 1.1)
	French Frigate	469.4	8	62 (1.3)	31 (0.9 / 1.8)
	Kure	90.2	6	49 (0.9)	29 (0.8 / 1.7)
	Laysan	26.4	6	31 (0.5)	23 (0.6 / 1.3)
	Lisianski	215.6	6	71 (1.3)	44 (1.3 / 2.6)
	Maro	217.5	7	82 (1.5)	48 (1.4 / 2.8)
	Midway	85.4	5	47 (0.9)	21 (0.6 / 1.2)
	Necker	9.1	4	12 (0.2)	9 (0.2 / 0.5)
	Pearl & Hermes	374.5	7	78 (1.6)	32 (0.9 / 1.9)
	Hawaiian Archipelago Total			771 (15.5)	436 (13.1 / 26.2)
Mariana Archipelago	Guam	91.3	4	84 (1.8)	39 (1.1 / 2.3)
	Rota	12.1	4	44 (0.9)	23 (0.6 / 1.3)
	Saipan	56.8	4	59 (1.2)	30 (0.9 / 1.8)
	Tinian	14.7	4	37 (0.8)	19 (0.5 / 1.1)
	Aguijan	2.6	4	18 (0.4)	8 (0.2 / 0.4)
	Agrihan	8.6	4	34 (0.7)	18 (0.5 / 1.0)
	Alamagan	3.2	4	24 (0.5)	11 (0.3 / 0.6)
	Asuncion	0.5	4	21 (0.4)	15 (0.4 / 0.9)
	Farallon de Pajaros	0.8	4	19 (0.4)	13 (0.3 / 0.7)
	Guguan	1.1	4	18 (0.3)	11 (0.3 / 0.6)
	Maug	2.1	4	44 (0.8)	34 (1.0 / 2.0)
	Pagan	11.1	4	69 (1.3)	33 (0.9 / 1.9)
	Sarigan	1.9	4	22 (0.4)	12 (0.3 / 0.7)
	Mariana Archipelago Total			493 (9.8)	266 (8.0 / 16.0)
Pacific Remote Island Areas (PRIAs)	Baker	5.2	5	29 (0.5)	29 (0.8 / 1.7)
	Howland	3	5	30 (0.7)	26 (0.7 / 1.5)
	Jarvis	3	5	43 (0.8)	29 (0.8 / 1.7)
	Johnston	150.1	2	35 (0.5)	7 (0.2 / 0.4)
	Kingman	20.9	5	53 (0.8)	13 (0.3 / 0.7)
	Palmyra	47.2	5	64 (1.2)	39 (1.1 / 2.3)
	Wake	22.9	3	51 (1.0)	36 (1.0 / 2.1)
	PRIAs Total			305 (5.4)	179 (5.4 / 10.8)

Table 1.2. Fish species included on the 2011 IUCN Red List of Threatened Species observed in the US Pacific Islands during belt transect (BLT) and towed-diver surveys (TDS) completed on a biennial or annual basis from 2000-2009.

		Ecological Information[a]					IUCN Assessment[b]		
Family	Species	Max Length (cm TL)	Depth Range (m)	Habitat[c]	Observed Region[d]	Published Range[d]	Status[e]	Year	Trend
Ginglymostomatidae	*Nebrius ferrugineus*	320	1-70	RA	A, M, P	A, M, P	VU	2003	decreasing
Stegostomatidae	*Stegostoma fasciatum*	235	1-63	RA	A	A, M, P	VU	2003	decreasing
Carcharhinidae	*Carcharhinus amblyrhynchos*	255	0-1000	RA, O	A, H, M, P	A, H, M, P	NT	2005	unknown
	C. galapagensis	370	0-286	RA	A, H, P	A, H, P	NT	2003	unknown
	C. melanopterus	200	20-75	RA	A, M, P	A, H, M, P	NT	2005	decreasing
	Galeocerdo cuvier	750	0-371	B, O	H, P	A, H, M, P	NT	2005	unknown
	Negaprion acutidens	380	0-92	RA	A	A, M, P	VU	2003	decreasing
	Triaenodon obesus	213	1-330	RA	A, H, M, P	A, H, M, P	NT	2005	unknown
Sphyrnidae	*Sphyrna lewini*	430	0-512	PO, O	H,P	A, H, M, P	EN	2007	unknown
	S. mokarran	610	1-300	PO, O	P	A, H, M, P	EN	2007	decreasing
Dasyatidae	*Taeniura meyeni*	330	0-500	RA	A, M, P	A, M, P	VU	2006	unknown
	Urogymnus asperrimus	147		RA	M	M	VU	2005	unknown
Myliobatidae	*Aetobatus narinari*	330	1-80	RA	A, H, M, P	A, H, M, P	NT	2006	decreasing
Mobulidae	*Manta alfredi*	910[f]	0-120	RA, O	H,P	A, H, M, P	VU	2011	unknown
Serranidae	*Aethaloperca rogaa*	60	1-60	RA	M ,P	M	DD	2008	unknown
	Anyperodon leucogrammicus	65	1-80	RA	A	A, M, P	LC	2008	unknown
	Cephalopholis argus	60	1-40	RA	A, H, M, P	A, H, M, P	LC	2008	stable
	C. leopardus	24	1-40	RA	A, M, P	A, M, P	LC	2008	unknown
	C. miniata	45	2-150	RA	A, M, P	A, M, P	LC	2008	decreasing
	C. sexmaculata	50	6-150	RA	A, M, P	A, M, P	LC	2008	decreasing
	C. sonnerati	57	10-150	RA	M	A, M, P	LC	2008	stable
	C. spiloparaea	30	15-108	RA	A, P	A, M, P	LC	2008	unknown
	C. urodeta	28	1-60	RA	A, M, P	A, M, P	LC	2008	unknown
	Epinephelus fasciatus	40	4-160	RA	A, M, P	A, M, P	LC	2008	decreasing
	E. hexagonatus	27.5	0-30	RA	A, M, P	A, M, P	LC	2008	stable
	E. howlandi	55	1-37	RA	A, M, P	A, M, P	LC	2008	unknown
	E. lanceolatus	270	4-100	RA	M, P	A, H, M, P	VU	2006	decreasing
	E. macrospilos	51	1-30	RA	P	A, P	LC	2008	unknown
	E. maculatus	60.5	2-100	RA	A, M	A, M, P	LC	2008	decreasing
	E. melanostigma	35	0-30	RA	A, M, P	A, M, P	DD	2008	unknown
	E. merra	31	0-50	RA	A, M, P	A, M, P	LC	2008	stable
	E. polyphekadion	90	1-46	RA, O	A, M, P	A, M, P	NT	2006	decreasing
	E. retouti	50	20-220	RA	P	A, M, P	DD	2008	unknown
	E. spilotoceps	35	0-30	RA	A, P	A, P	LC	2008	unknown
	E. tauvina	75	1-300	RA, O	A, M, P	A, M, P	DD	2008	unknown
	Gracila albomarginata	40	6-120	RA	A, M, P	A, M, P	DD	2008	unknown
	Hyporthodus quernus	122	20-380	B	H	H	NT	2004	unknown
	Plectropomus areolatus	73	1-20	RA	A	A, M, P	VU	2008	decreasing
	P. laevis	125	4-100	RA	A, M, P	A, M, P	VU	2008	decreasing
	P. leopardus	120	3-100	RA, O	A	M	NT	2004	decreasing
	Variola albimarginata	65	4-200	RA	A, M	A, M	LC	2008	decreasing
	V. louti	83	3-250	RA	A, M, P	A, M, P	LC	2008	stable
Chaetodontidae	*Chaetodon flavocoronatus*	12	36-75	RA	M	M	VU	1996	needs updating
Labridae	*Cheilinus undulatus*[g]	229	1-100	RA	A, M, P	A, M, P	EN	2004	decreasing
Scaridae	*Bolbometopon muricatum*[g]	130	1-30	RA	A, M, P	A, M, P	VU	2007	decreasing

[a] FishBase served as the source for Ecological information

[b] IUCN assessment information is based on the 2011 IUCN Red List of Threatened Species

[c] B = Benthopelagic, O = Oceanodromous, PO = Pelagic-oceanic, RA = Reef-associated

[d] A = American Samoa, H = Hawaiian Archipelago, M = Mariana Archipelago, P = Pacific Remote Island Areas

[e] NT = Near Threatened, VU = Vulnerable, EN = Endangered, DD =Data Deficient; LC = Least Concern

[f] Disk Width

[g] NOAA Species of Concern

Table 1.3. Summary results of towed-diver surveys using a resampling approach (n = 10,000) to evaluate differences (between inhabited and uninhabited regions) in mean densities (individuals km^{-2}) of large-bodied fishes (> 50 cm TL) included on the IUCN Red List of Threatened Species observed in the US Pacific Islands from 2000 to 2009.

			American Samoa			Hawaiian Archipelago			Mariana Archipelago			PRIAs
Status[a]	Family	Species	Inhabited		Uninhabited	Inhabited		Uninhabited	Inhabited		Uninhabited	Uninhabited
EN	Sphyrnidae	*Sphyrna lewini*	0		0	0.01	ns	0	0		0	0.16
						(0, 0.03)						(0, 0.46)
		S. mokarran	0		0	0		0	0		0	0.01
												(0, 0.02)
	Labridae	*Cheilinus undulatus*[b]	0.14	ns	0.17	-		-	0.14	>*	0.04	0.26
			(0.05, 0.03)		(0.03, 0.33)				(0.05, 0.28)		(0, 0.09)	(0.14, 0.42)
VU	Ginglymostomatidae	*Nebrius ferrugineus*	0	ns	0	-		-	0	<***	0.16	0
			(0, 0.02)		(0, 0.02)				(0, 0.03)		(0.10, 0.22)	
	Stegostomatidae	*Stegostoma fasciatum*	0	ns	0	-		-	0		0	0
			(0, 0.01)									
	Carcharhinidae	*Negaprion acutidens*	0	ns	0	-		-	0		0	0
			(0, 0.01)									
	Dasyatidae	*Taeniura meyeni*	0.01	ns	0	-		-	0.02	Ns	0.06	0.02
			(0, 0.05)		(0, 0.03)				(0, 0.06)		(0.02, 0.12)	(0, 0.05)
		Urogymnus asperrimus	-		-	-		-	0	ns	0	-
									(0, 0.02)		(0, 0.01)	
	Serranidae	*Epinephelus lanceolatus*	0		0	0		0	0	ns	0	0
											(0, 0.02)	(0, 0.01)
		Plectropomus areolatus	0.19	ns	0	-		-	0		0	0
			(0, 1.37)									
		P. laevis	2.44	ns	0	-		-	1.65	ns	0	0.95
			(0, 7.43)						(0, 5.99)			(0, 3.36)
	Scaridae	*Bolbometopon muricatum*	0.5	ns	0	-		-	0	ns	0.15	43.4
			(0, 3.68)								(0, 1.12)	(8.52, 124.9)
NT	Carcharhinidae	*Carcharhinus amblyrhync*	1.76	ns	9.72	1.17	<***	21.21	0.51	<***	82.74	386.6
			(0, 5.89)		(0, 29.03)	(0, 3.40)		(11.5, 35.6)	(0, 2.73)		(52, 119)	(247, 560)
		C. galapagensis	0.14	ns	0.39	1.84	<**	21.61	-		-	2.21
			(0, 1.79)		(0, 2.58)	(0, 7.08)		(6.9, 48.9)				(0, 7.52)
		C. melanopterus	3.8	ns	4.4	0		0	2.86	ns	5.53	20.38
			(0, 8.96)		(0, 14.20)				(0, 7.86)		(0.46, 16)	(9.51, 35.24)
		Galeocerdo cuvier	0		0	0	ns	0.1	0		0	0.07
								(0, 0.55)				(0, 0.51)
		Triaenodon obesus	9.11	ns	17.27	2.82	<***	23.83	7.14	<***	57.39	53.07
			(1.7, 18)		(4.6, 34.9)	(0, 8.41)		(15.1, 33.2)	(1.1, 16)		(42, 74.1)	(29.8, 87.54)
	Myliobatidae	*Aetobatus narinari*	4.58	ns	0.99	5.78	ns	8.67	4.27	ns	2.37	17.61
			(0, 12.36)		(0, 5.25)	(1.4, 12)		(2.3, 16.97)	(0, 11.4)		(0.45, 4.98)	(7.11, 30.96)
	Mobulidae	*Manta alfredi*	0		0	1.12	ns	3.17	0		0	23.14
						(0, 3.15)		(0, 8.81)				(4.70, 62.6)
	Serranidae	*Hyporthodus quernus*	-		-	0	<***	7.21	-		-	-
								(2.2, 13.5)				
		Plectropomus leopardus	0.34	ns	0	-		-	0		0	-
			(0, 2.38)									
	Total	All taxa pooled	2.06	ns	2.69	1.21	<**	7.8	1.78	<**	9.19	32.89
			(0.3, 5.2)		(0.40, 6.57)	(0.1, 3.3)		(3.46, 14.3)	(0.3, 4.3)		(5.66, 13.7)	(17.88, 56)

Note that units for mean densities can be converted to individuals ha^{-1} by dividing by 100. Islands are grouped by region and population status (Inhabited vs. Uninhabited). Values are mean density km^{-2} with lower and upper 95% confidence intervals identified in parentheses Confidence intervals were omitted for species where the resampled mean abundance was equal to 0. Regions outside of the biogeographic range of a species are identified with a dash. Regional island groups with significantly higher resampled abundance values are identified with a < or > sign. Significance is given as: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; and ns = not significant

[a] 2011 IUCN Red List Categories: EN = Endangered; VU = Vulnerable; and NT = Near Threatened

[b] NOAA Species of Concern

Table 1.4. Summary results of belt transect surveys using a resampling approach (n = 10,000) to evaluate differences in mean densities (individuals ha^{-1}) included on the IUCN Red List of Threatened Species observed in the US Pacific Islands from 2000-2009.

			American Samoa			Hawaiian Archipelgo			Mariana Archipelago			PRIAs
Status[a]	Family	Species	Inhabited		Uninhabited	Inhabited		Uninhabited	Inhabited		Uninhabited	Uninhabite
VU	Serranidae	*Epinephelus polyphekadion*	0		0	-		-	0.21	ns	0	0.97
									(0, 0.89)			(0, 2.72)
	Chaetodontidae	*Chaetodon flavocoronatus*	-		-	-		-	0.91	ns	0	-
									(0, 4.76)			
LC	Serranidae	*Anyperodon leucogrammicus*	0		0	-		-	0		0	0
		Cephalopholis argus	61.45	<*	109.56	21.76	>***	0.64	0.89	<***	38.92	98.6
			(36.9, 88.5)		(73.8, 147.1)	(13.7, 32)		(0, 1.32)	(0, 2.68)		(27.51, 52.11)	(78.4, 119.5)
		C. leopardus	1.28	<***	46.47	-		-	1.13	ns	0.23	2.63
			(0, 4.76)		(13.1, 109.5)				(0, 4.17)		(0, 0.79)	(0, 6.46)
		C. miniata	0		0	-		-	0	ns	0.24	126.88
											(0, 0.93)	(91.2, 165.9)
		C. sexmaculata	0		0	-		-	0	ns	0.71	0.24
											(0, 1.72)	(0, 1.02)
		C. sonnerati	0		0	-		-	0	ns	0.16	0
											(0, 0.79)	
		C. spiloparaea	2.57	ns	1.22	-		-	0		0	1.31
			(0, 11.90)		(0, 4.76)							(0, 3.74)
		C. urodeta	212.42	<*	323.39	-		-	138.21	<***	339.92	190.06
			(150.7, 280)		(222, 425)				(98.2, 181)		(285, 398)	(129, 257)
		Epinephelus fasciatus	2.89	ns	0	-		-	2.57	<***	22.11	75.28
			(0, 12.69)						(0, 7.74)		(10, 36.5)	(25.9, 142.6)
		E. hexagonatus	0.66	ns	1.58	-		-	1.35	<**	13.27	1.94
			(0, 3.17)		(0, 7.14)				(0, 4.17)		(5.03, 23.54)	(0, 4.59)
		E. howlandi	0.65	ns	0.46	-		-	0	ns	0.27	1.13
			(0, 3.17)		(0, 2.38)						(0, 1.06)	(0, 2.38)
		E. macrospilos	0		0	-		-	-		-	0.61
												(0, 1.70)
		E. maculatus	0.08	ns	0	-		-	0	ns	0.31	0
			(0, 0.79)								(0, 1.19)	
		E. merra	0.82	ns	0.99	-		-	0.22	ns	0.29	3.07
			(0, 4.76)		(0, 3.57)				(0, 1.19)		(0, 1.19)	(0.34, 6.80)
		E. spilotoceps	0	ns	1.22	-		-	-		-	1.89
					(0, 4.76)							(0, 4.42)
		Variola albimarginata	0		0	-		-	0		0	-
		V. louti	5.11	>*	0	-		-	2.65	<**	11.51	6.74
			(0.79, 11.90)						(0, 6.55)		(5.95, 18.51)	(3.06, 11.05)
DD	Serranidae	*Aethaloperca rogaa*	-		-	-		-	0.1	ns	0.16	3.69
									(0, 0.60)		(0, 0.53)	(0.34, 8.16)
		Epinephelus melanostigma	0.24	<*	3.39	-		-	0	ns	0.91	3.17
			(0, 1.59)		(0, 9.52)						(0, 2.25)	(0.68, 6.13)
		E. retouti	0		0	-		-	0		0	1.32
												(0, 3.74)
		E. tauvina	0	ns	0.35	-		-	0	ns	0.21	1.86
					(0, 1.79)						(0, 0.79)	(0, 4.59)
		Gracila albomarginata	1.15	<**	13.17	-		-	0	<**	32.51	9.88
			(0, 3.97)		(4.76, 23.80)						(1.06, 116.26)	(4.42, 15.98)
	Total	All grouper species poole	17.02	<*	29.52	21.76	>***	0.64	8.24	<***	25.65	27.96
			(11.1, 25)		(18.5, 43.8)	(13, 31.5)		(0, 1.32)	(5.5, 11.3)		(18.5, 34.4)	(17.6, 40.4)

Note that the units for describing densities are different from Table 3 but can be converted to individuals km^{-2} by multiplying by 100.

Islands are grouped by region and population status (Inhabited vs. Uninhabited). Values are mean density ha^{-1} with lower and upper 95% confidence intervals identified in parentheses Confidence intervals were omitted for species where the resampled mean abundance was equal to 0. Regions outside of the biogeographic range of a species are identified with a dash. Regional island groups with significantly higher resampled abundance values are identified with a < or > sign. Significance is given as: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; and ns = not significant

[a] 2011 IUCN Red List Categories: VU = Vulnerable; LC = Least Concern; and DD = Data Deficient

Table 1.5. Summary results of towed-diver surveys conducted around the islands of American Samoa identifying the mean length (cm) and maximum length in parentheses of large-bodied fishes (> 50 cm TL) included on the IUCN Red List of Threatened Species. Uninhabited islands within the archipelago are shaded.

Family	Species	American Samoa				
		Ofu & Olosega	Tau	Tutuila	Rose	Swains
Ginglymostomatidae	*Nebrius ferrugineus*	175 (175)				230 (230)
Stegostomatidae	*Stegostoma fasciatum*			225 (225)		
Carcharhinidae	*Carcharhinus amblyrhynchos*	100 (100)	125 (175)	140 (225)	115 (175)	140 (175)
	C. galapagensis			225 (225)	175 (175)	
	C. melanopterus	125 (175)	125 (125)	175 (175)	130 (175)	90 (90)
	Galeocerdo cuvier					
	Negaprion acutidens		225 (225)			
	Triaenodon obesus	120 (175)	115 (125)	130 (175)	130 (175)	115 (175)
Sphyrnidae	*Sphyrna lewini*					
	S. mokarran					
Dasyatidae	*Taeniura meyeni*	90 (90)	105 (125)	125 (125)	150 (175)	125 (125)
	Urogymnus asperrimus					
Myliobatidae	*Aetobatus narinari*	105 (125)	95 (125)	95 (125)	90 (125)	125 (125)
Mobulidae	*Manta alfredi*					
Serranidae	*Epinephelus lanceolatus*					
	Hyporthodus quernus					
	Plectropomus areolatus	60 (60)				
	P. laevis	75 (90)	70 (80)	70 (125)		
	P. leopardus			75 (90)		
Labridae	*Cheilinus undulatus*	85 (175)	90 (175)	95 (175)	100 (150)	100 (175)
Scaridae	*Bolbometopon muricatum*		65 (65)	65 (65)		

Table 1.6. Summary results of towed-diver surveys conducted around the inhabited islands of the Hawaiian Archipelago identifying the mean length (cm) and maximum length in parentheses of large-bodied fishes (> 50 cm TL) included on the IUCN Red List of Threatened Species.

Family	Species	Hawaiian Archipelago						
		Hawaii	Kauai	Lanai	Maui	Molokai	Niihau-Lehua	Oahu
Ginglymostomatidae	*Nebrius ferrugineus*							
Stegostomatidae	*Stegostoma fasciatum*							
Carcharhinidae	*Carcharhinus amblyrhynchos*		175 (175)				105 (180)	
	C. galapagensis						105 (125)	
	C. melanopterus							
	Galeocerdo cuvier							
	Negaprion acutidens							
	Triaenodon obesus	125 (125)	145 (175)	175 (175)	125 (125)		145 (175)	150 (150)
Sphyrnidae	*Sphyrna lewini*	256 (225)				230 (230)		
	S. mokarran							
Dasyatidae	*Taeniura meyeni*							
	Urogymnus asperrimus							
Myliobatidae	*Aetobatus narinari*	115 (175)	100 (110)	110 (125)	115 (175)	90 (90)	125 (175)	110 (150)
Mobulidae	*Manta alfredi*		125 (125)		225 (225)		205 (270)	180 (225)
Serranidae	*Epinephelus lanceolatus*							
	Hyporthodus quernus							
	Plectropomus areolatus							
	P. laevis							
	P. leopardus							
Labridae	*Cheilinus undulatus*							
Scaridae	*Bolbometopon muricatum*							

Table 1.7. Summary results of towed-diver surveys conducted around the uninhabited islands of the Hawaiian Archipelago identifying the mean length (cm) and maximum length in parentheses of large-bodied fishes (> 50 cm TL) included on the IUCN Red List of Threatened Species. Uninhabited islands within the archipelago are shaded.

Family	Species	Hawaiian Archipelago							
		French Frigate	Kure	Laysan	Lisianski	Maro	Midway	Necker	Pearl & Hermes
Ginglymostomatidae	*Nebrius ferrugineus*								
Stegostomatidae	*Stegostoma fasciatum*								
Carcharhinidae	*Carcharhinus amblyrhynchos*	125 (225)	190 (225)			165 (175)	160 (175)	105 (175)	175 (225)
	C. galapagensis	110 (225)	145 (175)		140 (175)	145 (225)	155 (225)	65 (65)	160 (225)
	C. melanopterus								
	Galeocerdo cuvier		275 (275)						
	Negaprion acutidens								
	Triaenodon obesus	135 (200)			110 (175)	135 (175)	125 (125)	120 (125)	125 (200)
Sphyrnidae	*Sphyrna lewini*								
	S. mokarran								
Dasyatidae	*Taeniura meyeni*								
	Urogymnus asperrimus								
Myliobatidae	*Aetobatus narinari*	130 (175)	155 (175)	140 (175)	90 (125)	105 (175)	150 (225)	70 (90)	140 (225)
Mobulidae	*Manta alfredi*		125 (125)			270 (350)	300 (300)		310 (400)
Serranidae	*Epinephelus lanceolatus*								
	Hyporthodus quernus		80 (120)				80 (110)		
	Plectropomus areolatus								
	P. laevis								
	P. leopardus								
Labridae	*Cheilinus undulatus*						75 (90)		
Scaridae	*Bolbometopon muricatum*								

Table 1.8. Summary results of towed-diver surveys conducted around the inhabited islands of the Mariana Archipelago identifying the mean length (cm) and maximum length in parentheses of large-bodied fishes (> 50 cm TL) included on the IUCN Red List of Threatened Species.

Family	Species	Mariana Archipelago				
		Guam	Rota	Saipan	Tinian	Aguijan
Ginglymostomatidae	*Nebrius ferrugineus*	125 (125)			175 (175)	
Stegostomatidae	*Stegostoma fasciatum*					
Carcharhinidae	*Carcharhinus amblyrhynchos*	90 (90)		65 (65)		
	C. galapagensis					
	C. melanopterus	120 (125)	120 (125)	135 (150)	75 (90)	125 (125)
	Galeocerdo cuvier					
	Negaprion acutidens					
	Triaenodon obesus	175 (175)	125 (175)	150 (150)	130 (175)	135 (175)
Sphyrnidae	*Sphyrna lewini*					
	S. mokarran					
Dasyatidae	*Taeniura meyeni*	125 (125)	125 (125)	130 (175)	125 (125)	90 (90)
	Urogymnus asperrimus	100 (125)		125 (125)		90 (90)
Myliobatidae	*Aetobatus narinari*	135 (175)	150 (150)	135 (180)	105 (130)	108 (125)
Mobulidae	*Manta alfredi*					
Serranidae	*Epinephelus lanceolatus*					
	Hyporthodus quernus					
	Plectropomus areolatus					
	P. laevis	65 (85)	75 (90)			
	P. leopardus					
Labridae	*Cheilinus undulatus*	85 (125)	90 (175)	95 (150)	95 (125)	
Scaridae	*Bolbometopon muricatum*					

Table 1.9. Summary results of towed-diver surveys conducted around the uninhabited islands of the Mariana Archipelago identifying the mean length (cm) and maximum length in parentheses of large-bodied fishes (> 50 cm TL) included on the IUCN Red List of Threatened Species. Uninhabited islands within the archipelago are shaded.

Family	Species	Mariana Archipelago							
		Agrihan	Alamagan	Asuncion	Farallon de Pajaros	Guguan	Maug	Pagan	Sarigan
Ginglymostomatidae	*Nebrius ferrugineus*	165 (175)	165 (225)	175 (225)	190 (225)	185 (225)	185 (225)	165 (225)	185 (225)
Stegostomatidae	*Stegostoma fasciatum*								
Carcharhinidae	*Carcharhinus amblyrhynchos*	105 (175)	110 (150)	125 (175)	125 (200)	110 (125)	110 (175)	105 (150)	90 (125)
	C. galapagensis								
	C. melanopterus	65 (65)		65 (65)		175 (175)		120 (120)	150 (150)
	Galeocerdo cuvier								
	Negaprion acutidens								
	Triaenodon obesus	145 (175)	130 (175)	130 (175)	135 (175)	125 (175)	130 (175)	125 (175)	130 (175)
Sphyrnidae	*Sphyrna lewini*								
	S. mokarran								
Dasyatidae	*Taeniura meyeni*	110 (150)	115 (125)	100 (120)	125 (125)		100 (100)	130 (180)	125 (125)
	Urogymnus asperrimus								
Myliobatidae	*Aetobatus narinari*	110 (125)			125 (125)		90 (90)	105 (125)	105 (125)
Mobulidae	*Manta alfredi*								
Serranidae	*Epinephelus lanceolatus*				175 (175)				
	Hyporthodus quernus								
	Plectropomus areolatus								
	P. laevis								
	P. leopardus								
Labridae	*Cheilinus undulatus*	65 (65)	95 (125)			90 (90)			100 (150)
Scaridae	*Bolbometopon muricatum*							75 (90)	

Table 1.10. Summary results of towed-diver surveys conducted around the Pacific Remote Island Areas (PRIAs) identifying the mean length (cm) and maximum length in parentheses of large-bodied fishes (> 50 cm TL) included on the IUCN Red List of Threatened Species. Uninhabited islands within the archipelago are shaded.

Family	Species	Pacific Remote Island Areas (PRIAs)						
		Baker	Howland	Jarvis	Johnston	Kingman	Palmyra	Wake
Ginglymostomatidae	*Nebrius ferrugineus*							
Stegostomatidae	*Stegostoma fasciatum*							
Carcharhinidae	*Carcharhinus amblyrhynchos*	120 (175)	120 (225)	130 (225)	130 (230)	115 (225)	115 (200)	115 (225)
	C. galapagensis		135 (175)	125 (125)	210 (225)			
	C. melanopterus	105 (125)	110 (125)	125 (190)		125 (125)	115 (200)	
	Galeocerdo cuvier						300 (300)	
	Negaprion acutidens							
	Triaenodon obesus	135 (175)	145 (175)	120 (175)		115 (175)	120 (175)	
Sphyrnidae	*Sphyrna lewini*	200 (250)	165 (175)	250 (300)		195 (225)	205 (250)	
	S. mokarran			285 (300)				
Dasyatidae	*Taeniura meyeni*	70 (70)	80 (80)	105 (125)				
	Urogymnus asperrimus							
Myliobatidae	*Aetobatus narinari*	80 (90)	105 (125)	225 (225)	95 (125)	155 (175)	110 (175)	95 (150)
Mobulidae	*Manta alfredi*	230 (350)	330 (400)	235 (400)	210 (225)	280 (375)	245 (300)	
Serranidae	*Epinephelus lanceolatus*					185 (200)		
	Hyporthodus quernus							
	Plectropomus areolatus							
	P. laevis		65 (65)	65 (65)		65 (65)		
	P. leopardus							
Labridae	*Cheilinus undulatus*		150 (175)	95 (125)			95 (175)	110 (175)
Scaridae	*Bolbometopon muricatum*			90 (90)			125 (125)	90 (125)

Table 1.11. Summary results of belt-transect surveys conducted around the islands of American Samoa identifying the mean length (cm) and maximum length in parentheses of small-bodied fishes included on the IUCN Red List of Threatened Species. Uninhabited islands within the archipelago are shaded.

Family	Species	American Samoa				
		Ofu & Olosega	Tau	Tutuila	Rose	Swains
Serranidae	*Aethaloperca rogaa*					
	Anyperodon leucogrammicus					
	Cephalopholis argus	21 (48)	25 (48)	26 (53)	24 (53)	27 (43)
	C. leopardus	10 (13)		13 (18)	13 (28)	12 (23)
	C. miniata					
	C. sexmaculata					
	C. sonnerati					
	C. spiloparaea	12 (23)		12 (20)	15 (18)	27 (28)
	C urodeta	14 (28)	13 (28)	14 (28)	15 (28)	17 (28)
	Epinephelus fasciatus	32 (33)	19 (33)	18 (22)		
	E. hexagonatus	19 (23)			19 (23)	19 (23)
	E. howlandi	42 (43)	47 (53)		47 (53)	
	E. macrospilos					
	E. maculatus			27 (28)		
	E. melanostigma			27 (33)	26 (33)	
	E. merra		25 (28)	12 (23)	32 (33)	32 (33)
	E. polyphekadion					
	E. retouti					
	E. spilotoceps					25 (28)
	E. tauvina				57 (58)	
	Gracila albomarginata	12 (13)	23 (33)	12 (13)	27 (38)	29 (48)
	Variola albimarginata					
	V. louti	36 (63)	35 (38)	22 (48)		
Chaetodontidae	*Chaetodon flavocoronatus*					

Table 1.12. Summary results of belt transect surveys conducted around the inhabited islands of the Hawaiian Archipelago identifying the mean length (cm) and maximum length in parentheses of small-bodied fishes included on the IUCN Red List of Threatened Species.

Family	Species	Hawaiian Archipelago						
		Hawaii	Kauai	Lanai	Maui	Molokai	Niihau-Lehua	Oahu
Serranidae	*Aethaloperca rogaa*							
	Anyperodon leucogrammicus							
	Cephalopholis argus	30 (53)	28 (50)	24 (48)	29 (50)	30 (43)	32 (44)	26 (38)
	C. leopardus							
	C. miniata							
	C. sexmaculata							
	C. sonnerati							
	C. spiloparaea							
	C. urodeta							
	Epinephelus fasciatus							
	E. hexagonatus							
	E. howlandi							
	E. macrospilos							
	E. maculatus							
	E. melanostigma							
	E. merra							
	E. polyphekadion							
	E. retouti							
	E. spilotoceps							
	E. tauvina							
	Gracila albomarginata							
	Variola albimarginata							
	V. louti							
Chaetodontidae	*Chaetodon flavocoronatus*							

Table. 1.13. Summary results of belt transect surveys conducted around the uninhabited islands of the Hawaiian Archipelago identifying the mean length (cm) and maximum length in parentheses of small-bodied fishes included on the IUCN Red List of Threatened Species. Uninhabited islands within the archipelago are shaded.

Family	Species	Hawaiian Archipelago							
		French Frigate	Kure	Laysan	Lisianski	Maro	Midway	Necker	Pearl & Hermes
Serranidae	*Aethaloperca rogaa*								
	Anyperodon leucogrammicus								
	Cephalopholis argus							30 (33)	
	C. leopardus								
	C. miniata								
	C. sexmaculata								
	C. sonnerati								
	C. spiloparaea								
	C. urodeta								
	Epinephelus fasciatus								
	E. hexagonatus								
	E. howlandi								
	E. macrospilos								
	E. maculatus								
	E. melanostigma								
	E. merra								
	E. polyphekadion								
	E. retouti								
	E. spilotoceps								
	E. tauvina								
	Gracila albomarginata								
	Variola albimarginata								
	V. louti								
Chaetodontidae	*Chaetodon flavocoronatus*								

Table 1.14. Summary results of belt transect surveys conducted around the inhabited islands of the Mariana Archipelago identifying the mean length (cm) and maximum length in parentheses of small-bodied fishes included on the IUCN Red List of Threatened Species.

Family	Species	Mariana Archipelago				
		Guam	Rota	Saipan	Tinian	Aguijan
Serranidae	*Aethaloperca rogaa*	37 (38)				
	Anyperodon leucogrammicus					
	Cephalopholis argus	42 (43)	22 (25)	37 (39)	27 (28)	
	C. leopardus		12 (18)	12 (13)		
	C. miniata					
	C. sexmaculata					22 (23)
	C. sonnerati					
	C. spiloparaea					
	C. urodeta	12 (28)	15 (28)	14 (28)	15 (28)	15 (28)
	Epinephelus fasciatus	17 (23)		20 (33)	27 (28)	
	E. hexagonatus	22 (25)	12 (13)		19 (23)	
	E. howlandi					
	E. macrospilos					
	E. maculatus					
	E. melanostigma					
	E. merra				32 (33)	
	E. polyphekadion			27 (30)		
	E. retouti					
	E. spilotoceps					
	E. tauvina					
	Gracila albomarginata					
	Variola albimarginata					
	V. louti		12 (33)	22 (23)	32 (38)	32 (33)
Chaetodontidae	*Chaetodon flavocoronatus*		17 (18)	7 (8)		

Table 1.15. Summary results of belt transect surveys conducted around the uninhabited islands of the Mariana Archipelago identifying the mean length (cm) and maximum length in parentheses of small-bodied fishes included on the IUCN Red List of Threatened Species. Uninhabited islands within the archipelago are shaded.

Family	Species	Mariana Archipelago							
		Agrihan	Alamagan	Asuncion	Farallon de Pajaros	Guguan	Maug	Pagan	Sarigan
Serranidae	*Aethaloperca rogaa*		22 (23)						
	Anyperodon leucogrammicus								
	Cephalopholis argus	30 (48)	33 (48)	30 (53)	28 (58)	27 (43)	24 (43)	28 (53)	27 (43)
	C. leopardus								27 (30)
	C. miniata			37 (40)			22 (43)		
	C. sexmaculata		32 (33)	42 (43)			40 (43)		
	C. sonnerati						17 (17)		
	C. spiloparaea								
	C. urodeta	14 (28)	15 (28)	16 (28)	15 (28)	16 (28)	13 (28)	15 (28)	14 (28)
	Epinephelus fasciatus	25 (35)	25 (33)	28 (38)	24 (38)	23 (28)	22 (38)	24 (33)	25 (33)
	E. hexagonatus	10 (23)	18 (25)	16 (23)	19 (23)	20 (23)	17 (23)	17 (23)	16 (23)
	E. howlandi							17 (20)	37 (40)
	E. macrospilos								
	E. maculatus				42 (45)		22 (22)		
	E. melanostigma	32 (33)		25 (28)	17 (18)		19 (24)	27 (27)	
	E. merra			22 (25)			17 (18)		
	E. polyphekadion								
	E. retouti								
	E. spilotoceps								
	E. tauvina				27 (30)				
	Gracila albomarginata	27 (33)	30 (38)	37 (38)		35 (38)	8 (13)	36 (43)	
	Variola albimarginata								
	V. louti	37 (48)	27 (33)	33 (40)	27 (38)	28 (53)	28 (48)	32 (43)	42 (43)
Chaetodontidae	*Chaetodon flavocoronatus*								

Table 1.16. Summary results of belt transect surveys conducted around the Pacific Remote Island Areas (PRIAs) identifying the mean length (cm) and maximum length in parentheses of small-bodied fishes included on the IUCN Red List of Threatened Species. Uninhabited islands within the archipelago are shaded.

Family	Species	Pacific Remote Island Areas (PRIAs)						
		Baker	Howland	Jarvis	Johnston	Kingman	Palmyra	Wake
Serranidae	*Aethaloperca rogaa*	17 (28)	20 (42)					
	Anyperodon leucogrammicus							
	Cephalopholis argus	28 (53)	30 (58)	32 (53)		24 (48)	22 (48)	24 (53)
	C. leopardus	14 (19)	12 (13)	12 (18)		17 (18)	12 (18)	
	C. miniata	23 (43)	25 (43)	26 (43)			17 (18)	
	C. sexmaculata			25 (30)				
	C. sonnerati							
	C. spiloparaea							18 (43)
	C. urodeta	14 (23)	13 (28)	15 (28)		11 (23)	14 (23)	17 (18)
	Epinephelus fasciatus	14 (28)	17 (43)	18 (33)		17 (18)	17 (23)	19 (32)
	E. hexagonatus	19 (27)	20 (42)	22 (32)			19 (22)	20 (32)
	E. howlandi	45 (23)	39 (23)	37 (25)		32 (33)	27 (43)	
	E. macrospilos		27 (28)	27 (28)			32 (40)	
	E. maculatus							
	E. melanostigma	25 (33)	29 (38)	26 (33)		32 (33)	30 (33)	
	E. merra	15 (18)	22 (28)	25 (33)		32 (33)	16 (33)	20 (33)
	E. polyphekadion						43 (68)	57 (90)
	E. retouti		42 (53)	36 (48)			17 (20)	
	E. spilotoceps	20 (28)	19 (28)				23 (30)	
	E. tauvina	37 (40)				32 (35)	32 (35)	31 (73)
	Gracila albomarginata	28 (48)	34 (53)	30 (43)			25 (38)	
	Variola albimarginata							
	V. louti	44 (53)	43 (58)	47 (63)		46 (58)	45 (63)	
Chaetodontidae	*Chaetodon flavocoronatus*							

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Chapter 2.

SHIFTS IN THE SIZE-STRUCTURE OF REEF FISH ASSEMBLAGES ACROSS A GRADIENT OF HUMAN POPULATION DENSITY

ABSTRACT

Fisheries exploitation represents the greatest threat to coral reef fish resources because fisheries typically target large-bodied species that often occupy higher trophic levels. Even modest levels of extraction can alter the ecological function of the system by reducing the stock size (biomass), species composition, and size-structure of the fish assemblage. Using novel size-based biomass spectra analyses, we conducted a large-scale natural experiment across 49 Pacific islands to examine the effects of fishing on the size-structure of coral reef fish assemblages and determine if multiple forms of fisheries exploitation are present in coral reef ecosystems. Our analyses reveal striking evidence for a variety of effects fisheries exploitation can have on coral reef fish assemblages. When examining biomass spectra across the entire fish assemblage we found clear evidence of "*fishing down the food web*", a process by which large-bodied predatory species are exploited more quickly than species from lower trophic levels. These results were not surprising considering that top-predators contribute 45% on average to total fish biomass at remote islands while at inhabited islands they contribute to a little over 7%. However, when the same analyses were conducted across individual trophic levels, two other forms of exploitation were realized in the data. Within the mid-level carnivores, planktivores, and herbivores, we saw clear evidence of two other forms of fisheries exploitation, namely "*fishing through the food web*", whereby exploitation is realized

across the entire fish assemblage regardless of trophic level, and "*size-based fishing*", a form of fishing whereby the largest individuals across all trophic levels are targeted. Our findings highlight that the effects of fisheries exploitation on coral reefs are realized throughout the entire fish assemblage, across multiple trophic groups and not solely restricted to large-bodied top-predators. Together these findings highlight the complexity of coral reef fisheries and reinforce the importance of taking a multi-trophic group approach to monitoring and managing coral reef ecosystems.

INTRODUCTION

Body size is a fundamental attribute of an organism and thus has important implications to the structure and dynamics of ecological communities (Peters 1986, Begon et al. 1996). Many life history characteristics including growth, age at maturity, reproductive output, and lifespan are directly related to body size (Peters 1986). For example, large-bodied species tend to exhibit slow growth, late maturation, and long lifespan (Adams 1980, Peters 1986, Stearns 1992). Additionally, body size has important implications for predator-prey dynamics, foraging behavior, home range, and interspecific competition (Peters 1986). Large-bodied species play a fundamental role in structuring terrestrial and aquatic communities because they forage over large areas, occupy higher trophic levels, and are better competitors for resources (Peters 1986). However, many of these life history and behavioral characteristics make larger-bodied species vulnerable to exploitation and extinction risk (Dulvy et al. 2003, Reynolds et al. 2005). Global exploitation of many large-bodied species has led to growing concerns over the direct and indirect effects of their removal on ecosystem structure and function (Terborgh and Estes 2010, Estes et al. 2011). It is therefore imperative that efforts are made to examine the community-wide effects of large-bodied species in order to effectively manage communities at an ecosystem level.

Early efforts to examine the importance of body size in structuring ecological communities lead to Elton’s pioneering work identifying relationships between body size and an organism’s position in a food chain (Elton 1927). Arranging groups of organisms based on their size and abundance provided a visual representation of the structure of the community and is known as a pyramid of numbers (Elton 1927). These numerical representations of community structure were further developed by organizing groups of organisms into pyramids of biomass, production, and trophic level (Brown et al. 2004). Today, ecological pyramids are widely used by ecologists to gain insights into the processes that structure communities (Trebilco et al. 2013).

Metabolic theory complements our understanding of these complex community processes by describing the flow or transfer of energy between trophic groups (Brown and Gillooly 2003, Brown et al. 2004). Fundamental to metabolic theory are the predictable scaling relationships of and organism's body mass to its biomass density, rate of energy use, and abundance (Kleiber 1932). These predictable patterns scale as power laws across body size, with the rates and fluxes of biomass and energy transfer among trophic groups constrained by the laws of thermodynamics. In short, available energy decreases with increasing trophic level due to: (i) losses through respiration and heat production within trophic levels; and (ii) inefficiencies in energy or biomass transfer from one trophic level to the next (Kleiber 1932, Lindeman 1942, Brown and Gillooly 2003, Brown et al. 2004). Therefore, scaling relationships within a trophic level are predicted to be continuous and more energy efficient compared to the scaling relationships observed across successive trophic levels that are less energy efficient (no more than ≈10% energy transfer) and yield steeper scaling slope. Graphical representations of these scaling relationships, referred to as size spectra, provide conceptual insights into the flow and transfer of energy between trophic groups and reinforce the importance of body size in structuring ecological communities (Brown and Gillooly 2003, Brown et al. 2004). In general, there are strong theoretical expectations that relate body size to each abundance and biomass density of animal assemblages. Size spectra are used to represent the log-log linear relationship between body size and density, while biomass spectra represent the log-log-linear relationship between biomass class and biomass density within each class. Metabolic theory predicts that size spectra will reveal negative slopes while biomass spectra show positive slopes (Kerr and Dickie 2001).

While metabolic theory may predict null expectations of slopes of size or biomass spectra based on community development, it is well known that human intervention, in particular human exploitation, can significantly alter the pattern of these size distributions (Rice and Gislason 1996, Jennings et al. 2002, Jennings and Blanchard 2004, Graham et al. 2005). For example, fisheries scientists often use size-based assessments of the fish assemblage to gauge the community's responses to exploitation (Jennings et al. 2002, Dulvy et al. 2004, Jennings and Blanchard 2004, Graham et al. 2005, Shin et al. 2005, Wilson et al. 2010). Fisheries are typically size-selective and tend to target large-bodied species that are generally more valuable (Jennings and Kaiser 1998). In doing so, the fish assemblage shifts to one that is characterized by smaller-bodied species that occupy lower-trophic levels (Pauly et al. 1998). Thus, size-based assessments of fish assemblages serve as an important metric for assessing the direct and indirect effects of fishing (Rice and Gislason 1996, Duplisea et al. 1997, Shin and Cury 2004, Graham et al. 2005).

In most cases, size-based assessments are conducted on entire fish assemblages, ignoring possible differences in size-frequency relationships between different functional groups (e.g. predators *versus* herbivores) caused by targeted fishing (Trebilco et al. 2013). The rationale here is that higher trophic levels are typically composed of larger-bodied individuals, a pattern that is common in many pelagic fisheries. Such positive scaling of body size and trophic level is expected in single-channel trophic systems (e.g., single primary food source and step-wise predation through subsequent trophic levels). The positive scaling is further reinforced among fishes, where predation is typically realized through gape-limited predation, namely only prey that fit whole (or mostly whole) in the predator's mouth are consumed. However, such a clear linkage between body size and trophic level breaks down in many coastal fish assemblages, likely linked with the more diverse trophic resources that are available (e.g., plankton, benthic primary producers, benthic infauna). With more trophic pathways, there is capacity for the development of broad size distributions among fishes in multiple trophic levels. As such, size-based assessments of fish assemblages without regard for trophic groupings may be insufficient to fully interpret the specifics of fishery exploitation, especially when attempting to separate patterns of fishing as a function of size *versus* as a function of trophic level.

On coral reefs, systems with little-to-no fisheries exploitation are characterized by an abundance of large-bodied predatory species like sharks, jacks, and groupers that contribute to a significant portion of total fish biomass (Friedlander and DeMartini 2002, Sandin et al. 2008). As exploitation increases, the resultant size-structure of the assemblage becomes more negative and systems experiencing moderate levels of exploitation exhibit a reduction in the abundance and biomass of large-bodied species. As fisheries exploitation increases further, large-bodied species are depleted resulting in smaller-bodied species from lower trophic levels entering the fishery and results in the size-structure of the assemblage becoming further reduced. This process is referred to as "*fishing down the food web*" (Figure 2.1) and is widely accepted as being one of the dominant forms of fisheries exploitation (Pauly et al. 1998, Pauly and Palomares 2005, Polovina and Woodworth-Jefcoats 2013, Fenner 2014). However, alternative forms of fisheries exploitation may also be present (Essington et al. 2006). A form of fishing known as "*fishing through the food web*" (Figure 2.1) is characterized by a fishery targeting multiple trophic levels and size-classes simultaneously rather than solely targeting the largest-bodied individuals across the entire assemblage. As a result, the size-structure of unexploited and exploited stocks can yield different patterns. In the case of fishing down the food web, exploitation reduces the biomass of only the largest size classes and the slopes and intercepts are therefore similar between exploited and unexploited stocks. However, the reduction in larger size classes decreases the location of the inflection point (the location of maximum biomass for all size classes) in the exploited stock (Figure 2.1). In the case of fishing through the food web, the slopes and inflection points remain the same between exploited and unexploited stocks, but the intercept is lowered in the exploited stock (Figure 2.1). An alternative form of fisheries exploitation, "*size-based fishing*", may also be present (Figure 2.1), whereby the largest size classes within each species are exploited simultaneously. Size-based fishing shares characteristics with both the fishing down and fishing through the food web scenarios, in that all size classes are exploited though the larger sizes are exploited more intensively than the smaller sizes. In this exploitation scenario, the slope and the inflection point are reduced but the inflection point can either be reduced or remain the same for the exploited stock relative to the unexploited stock (Figure 2.1).

Size-based assessments have gained popularity over last decade and much of their attention has focused on the top-down (direct) effects of exploitation to the fish community. However, an important question remains – what are the indirect effects of fisheries exploitation and are the effects of fishing realized across all trophic levels of the fish assemblage? To address this question we explore the direct and non-lethal effects of varying levels of exploitation on the size-structure of coral reef fish assemblages at a functional group resolution across the tropical Pacific. Using size-based approaches, we conduct a large-scale natural experiment across 49 islands to determine if there is evidence of the three forms of fisheries exploitation, fishing down the food web, fishing through the food web, and sized-based fishing realized in coral reef fish assemblages. We also explore the knock-on (indirect) effects of removing large-bodied predatory species by examining changes in the size-structure of fishes from trophic groups that are not directly exploited by fisheries.

MATERIALS AND METHODS

Study Sites

To examine changes in the size-structure of coral reef fish assemblages we included quantitative survey data (belt-transect surveys) collected from 2002-2012 as part of the U.S. National Oceanic and Atmospheric Administration (NOAA) Pacific Reef Assessment and Monitoring Program (RAMP), The National Geographic Pristine Seas Program, and the Scripps Institution of Oceanography Coral Reef Ecology Program. Together these efforts include 49 islands, atolls and reefs (hereafter referred to as islands) spanning across the western and central tropical Pacific (Figure 2.2, Table 2.1). These islands and reefs are geographically located within 4 distinct geopolitical regions: American Samoa; Hawaiian Archipelago; Mariana Archipelago; and the Remote Pacific Islands. The islands span over 7000 km in longitude (measured at equator) across the western and central Pacific from 144.8° E to 49.8° W longitude and from 28.4° N to 14.6° S Latitude. Within each region, islands were classified as either “inhabited” (n=19) or “remote” (n=30) based on the supposition that human population density serves as a proxy for fisheries exploitation because overall fish biomass is significantly reduced near human population centers (DeMartini et al. 2008, Sandin et al. 2008, Williams et al. 2011). Therefore, islands were classified as remote if they supported no permanent human population, were geographically located at least 100 km away from population centers, or had management plans in place that restrict nearshore fisheries (e.g. Marine National Monument or National Wildlife Reserve). Conversely, all islands were classified as inhabited if they supported permanent human populations and there was a reasonable expectation that they were exposed to direct human impacts (e.g. fisheries exploitation). Within each region, islands served as replicates and all regions included at least two replicates of either population classification (inhabited vs. remote).

American Samoa is comprised of five islands, all of which are considered unincorporated territories of the United States. Tutuila is the largest and most densely populated island followed by the smaller and less densely populated Manu’a Islands, Ta’u and Ofu-Olosega. Recreational, subsistence, and to a lesser extent commercial fisheries are present in surrounding waters of these populated islands resulting in them being classified as inhabited for this assessment. Rose Atoll is uninhabited and remote, located over 100 km away from the nearest populated island Ta’u. Additionally, Rose was designated a U.S. Fish and Wildlife National Wildlife Reserve (NWR) in 1973 and further protected after being designated a Marine National Monument under Executive Order in 2009 (Bush 2009). Swains is also remote and located 360 km away from

Tutuila. A handful (<10) of resident caretakers reside on Swains but their impact on nearshore fisheries resources is considered negligible. Therefore, due the remoteness and minimal resident population, Swains was considered remote for this assessment.

The Hawaiian Archipelago can be divided into distinct sub-regions, the main Hawaiian islands (MHI) and the northwestern Hawaiian islands (NWHI). The MHI are densely populated and urbanized, extending roughly 500 km from Hawaii at the southern-most end of the archipelago northwest to Lehua located about halfway up the archipelago. The fisheries resources surrounding the MHI, especially near population centers, are heavily fished compared to those observed in the NWHI (Friedlander and DeMartini 2002). As such the MHI (n=8) were classified as inhabited for this assessment (Table 1). In contrast, the NWHI are uninhabited with the exception of a handful of islands inhabited by a small number of field researchers or contractors for few months a year, and Midway Atoll, the only NWHI where a staff of contractors and management staff reside full time to maintain an emergency runway for transpacific commercial and military aircraft. In addition to having low or no human inhabitation, the NWHI are isolated from the MHI with all islands being >500 km away from the closest inhabited MHI. This isolation has resulted in the nearshore fish assemblages being *de facto* protected from direct human impacts. However, legal action to protect the nearshore resources of the NWHI were realized with the establishment of the NWHI Coral Reef Ecosystem Reserve under Executive Order in 2000, and further protected by being designated a Marine National Monument under Presidential Proclamation in 2006. Based on the isolation from the MHI and the protection measures in place we classified the eight NWHI included in this assessment as remote.

The islands within the Mariana Archipelago can also be divided into two distinct groups based on human population density and geographic location. At the southern end of the archipelago are the most densely populated and urbanized islands, with Guam being the largest and most densely populated island followed by Saipan and Tinian. We classified five islands in the Mariana Archipelago as inhabited and included Aguijan even though it is uninhabited because of its close proximity to the inhabited islands Tinian and Saipan (<9 km and 30 km, respectively). The remaining eight islands included in this assessment were classified as remote based on having low or no human inhabitation and/or being located >150 km away from the densely populated southern islands.

The last geographic region included in this assessment was the Pacific Remote Island Areas and included 15 islands from two distinct political territorial jurisdictions, unaffiliated U.S. territorial islands and islands under the jurisdiction of the Republic of Kiribati. The U.S. territorial islands span >4300 km across the central and western Pacific and are all located >500 km (in many cases >1000 km) away from densely populated islands. With the exception of Wake Atoll, all of the U.S. territorial islands are uninhabited and have been protected as National Wildlife Reserves for at least ten years and were further protected in 2009 after being designated Marine National Monuments under Presidential Executive Order (Bush 2009). Wake Atoll serves as a remote airfield for the U.S. Department of Defense (DOD) and is inhabited year-round by a resident population of about 100 contractors and U.S. military personnel. The island and surrounding waters are co-managed by the DOD and the U.S. Fish and Wildlife Service (USFWS) and fishing is restricted to offshore pelagic species on an infrequent basis. Palmyra Atoll is the only other U.S. territorial island in the Pacific Remote Island Areas that is inhabited by a staff of caretakers and scientists and operates as a research station. The Nature Conservancy oversees the operation of the station while the USFWS manages all scientific activities taking place in surrounding waters. As such, all seven of the U.S. territorial islands in the Line Islands were classified as remote for this assessment. Additionally, we included data from eight islands under the jurisdiction of the Republic of Kiribati, all of which are biogeographically located in the Line Islands Archipelago. The five southern-most islands in the archipelago (Malden, Starbuck, Millennium, Flint, and Vostok) are uninhabited and remote, located >650 km from the closest populated island Kiritimati. Although the Republic of Kiribati does not formally protect the nearshore waters surrounding the islands, their remoteness affords protection from direct human disturbances including nearshore fisheries. The remaining three islands under the jurisdiction of the Republic of Kiribati (Teraina, Tabuaeran, and Kiritimati) are all inhabited and the nearshore fisheries resources experience direct effects of exploitation (DeMartini et al. 2008, Sandin et al. 2008). As a result, these three islands were classified as inhabited while the seven U.S. territorial islands and the five southern-most Kiribati islands were classified as remote.

S*urvey Methods*

Quantitative underwater surveys of the reef-associated fish assemblages were conducted at all islands included in this assessment. Belt transect surveys were employed, with the methodological details described elsewhere (Friedlander and DeMartini 2002, DeMartini et al. 2008, Sandin et al. 2008, Friedlander et al. 2010). In summary, belt transect surveys consisted of a pair of SCUBA divers laying out three 25 m transects at each station, and all fishes encountered in a predefined area were identified to species and total length (TL estimated to the nearest 5 cm size class). The dive team made two passes for each transect. On the outbound swim, divers surveyed an 8-m swath (200 m^2) to quantify fishes ≥20 cm TL and surveyed a 4-m swath (100 m^2) on the return swim to enumerate fishes <20 cm TL. All surveys in this assessment were restricted to the upper forereef slope and targeted depths between 8-15 m. The unit of replication was the station, which was composed of 2-5 transects. A total of 1307 stations were included in this assessment, 787 stations from remote islands and 520 from inhabited islands (Table 2.1).

Species were assigned to one of five distinct trophic groups (Top-predators [Sharks], Top-predators [Bony Fishes], Mid-level Carnivores, Planktivores, and Herbivores) based on web-based (i.e. www.fishbase.org) and published (Myers 1999, Randall 2005, 2007) sources identifying the feeding ecology and trophic role of individual species. Top-predators only included large-bodied primarily piscivorous species that are known to play an important role in structuring fish assemblages (e.g. Sharks, carangids, large-bodied groupers, large-bodied snappers, and barracudas). All small-to-medium bodied omnivorous carnivores were categorized as mid-level carnivores. Planktivores included all species that feed primarily on allochthonous and autochthonous sources of zooplankton. Lastly, herbivores included all species that feed primarily on early stage algae (e.g. low-lying turf algae), late stage algae (e.g. upright fleshy seaweeds), and calcified algae (e.g. encrusting algae that contain $CaCO_3$). Species that forage among benthic algae though putatively derive the bulk of their nutrition from detritus (e.g. *Ctenochaetus spp*.) were also categorized as herbivores. For species where information pertaining to feeding ecology and trophic role was lacking, we relied on expert opinion and the trophic role of congeners.

Identification of Fisheries Targets

Fisheries on coral reefs are difficult to characterize because they often incorporate a range of exploitation including recreational, artisanal fisheries, small-scale commercial, and in some cases large-scale commercial operations. Within each type of fishery, the gears and species targeted are oftentimes variable making it difficult for monitoring agencies to track landings. Lastly, the spatial scales at which coral reefs exist combined with the number of boat launches or market-access points make onsite assessment and monitoring challenging. The number of personnel and time required to perform accurate assessments of shallow-water fisheries catches is unfeasible for many island governments.

Given these constraints our goal here was not to provide a comprehensive evaluation of fisheries catches for each region included in this study, rather to provide a general characterization of the shallow-water coral reef fisheries targets for each region using the best available data. To accomplish this we incorporated data made available from published manuscripts, government reports, and online resources. Our efforts yielded published data from American Samoa (Zeller et al. 2006a, Zeller et al. 2006b, Craig et al. 2008, Sabater and Carroll 2009, Sabater and Tulafono 2011, Carroll et al. 2012), the Hawaiian Archipelago (WPRFMC 2011, Williams and Ma 2013), and Mariana Archipelago (Hensley and Sherwood 1993, Myers 1993, Houk et al. 2012, MacDuff and Roberto 2012, Tibbats and Flores 2012). To the best of our knowledge there are only limited published sources of catch data available for the Kiribati Line Islands and no fisheries are present in the US Pacific Remote Island Areas (Sandin et al. 2008, Walsh 2009).

In addition to published sources we included data provided through the NOAA Pacific Islands Fisheries Science Center, Western Pacific Fisheries Information Network (WPacFIN) that provides the best available fisheries data from the western Pacific (www.pifsc.noaa.gov/wpacfin/). Established in 1981, WPacFIN works directly with state and territorial agencies from American Samoa (Department of Marine and Wildlife Resources), Hawaiian Archipelago (Division of Aquatic Resources), and Mariana Archipelago (Division of Aquatic and Wildlife Resources and Division of Fish and Wildlife) to obtain fishery dependent data collected through Creel (angler) surveys.

Lastly, we used the results of the belt transect surveys to identify species present within each region that are considered potential fisheries targets. These species were identified based off of expert opinion (SIO Coral Reef Ecology Lab), identification of congeners as fisheries targets, and observations of species within fisheries in other regions throughout the Pacific. We compiled data from each of these published, online, and expert sources and created a list of the most commonly targeted coral reef fishes by family and trophic group for each region (Table 2.2). Due to the fact that catch data are more than likely limited or under-represented we incorporated the results of the belt transect surveys to identify the number of potential fisheries target species (species observed) for each family across each region.

Data Analyses

Data from belt transect surveys served as the input to estimate size-specific abundances for each species. Numbers of individuals were converted to weight (in grams) using length-weight parameters specific for each species based on allometric scaling:

$$W=aL^b, \qquad (2.1)$$

where W is an individual fish's weight in grams, a is a constant, L is the standard length in mm, and b is the species-specific allometric scaling parameter. Length-weight parameters (a and b) were obtained from online (www.fishbase.org), published (Kulbicki et al. 2005) and, un-published sources (NOAA, Coral Reef Ecosystem Division and The Scripps Institution of Oceanography, Coral Reef Ecology Lab). For species where length-weight information was unavailable, the parameters from congeneric species (same Genus) were used. Using these parameters, the biomass of each surveyed fish was estimated based on size and species identity. For each station, biomass distributions were estimated by summing biomass estimates for all surveyed individuals.

We plotted ln-transformed biomass density against ln-scaled biomass class in order to produce a biomass size spectrum for each trophic group; the slope and intercept were then calculated for this relationship. This was accomplished by binning fish biomass values into one of 12 biomass size classes that were defined using an exponential function (e^x). For example, biomass size class one included the summed biomass of all fishes with an individual biomass value between 1 - 2.72 g (e^0 and e^1). Island-specific mean biomass values for each biomass class were estimated by summing biomass estimates across all individuals within each size class.

As predicted by metabolic theory, the relationship between biomass density and biomass class is a positive power function (positive linear when both axis are log-transformed) across a range of values. Importantly, in practice there exists a biomass class with a maximum summed biomass, beyond which subsequent biomass classes have decreasing summed biomass (i.e., representing rare but large-bodied individuals). As such, the resultant empirical relationship reveals a peaked shape, with log-log linearity to a biomass class with maximum summed biomass, and subsequent decreasing summed biomass (Figure 2.1).

The shape of the biomass spectrum has been used to describe important features of animal assemblages (Boudreau and Dickie 1992, Kerr and Dickie 2001). We identify three statistical features that allow for characterization of fish assemblages; i) Total biomass is defined as the summed biomass across all biomass classes; ii) The inflection point is defined as the biomass class with the maximum summed biomass; and iii) Slope is defined as the slope of the linear regression model fit to the log-log transformed biomass spectrum. Importantly, we estimate the slope within the range from the smallest biomass class with non-zero total biomass to the biomass class with maximum summed biomass. The slope is only estimated when there are at least three non-zero biomass classes in sequence (i.e., no zero-biomass biomass classes within the range of model estimation).

By using statistical features to characterize fish assemblages (i.e., Biomass, Inflection Point, and Slope) we look for evidence of three distinct forms of fishing on coral reefs based on the supposition that each form of fishing exhibits a unique combination of statistical features. In the case of fishing down the food web, fisheries target large-bodied species that tend to occupy higher trophic levels, resulting in a reduction of total fish biomass, a shift of the inflection point to smaller size classes, but no change in the slope of the log-biomass class distributions (Figure 2.1). In the case of fishing through the food web, fisheries target all fish size classes regardless of trophic level resulting in a reduction of total fish biomass but the inflection point and slope of the log-biomass class distribution (Figure 2.1). Lastly, in the case of size-based fishing, fisheries target the largest individuals across all trophic groups resulting in a reduction of total fish biomass and a reduction in the slope of the log-biomass class distribution. However, the inflection point can either remain the same or shift to lower size classes, depending on the quantitative disparity in fishing pressure on larger *versus* smaller individuals (Figure 2.1).

A statistical bootstrapping approach was used to obtain probability density estimates for the model outputs across each trophic group and all groups combined(Efron and Tibshirani 1986, Chernick 2008). This bootstrapping approach was used to evaluate differences in the mean biomass, inflection point, and slope (model output parameters) between inhabited and remote islands within each geopolitical region. Island-specific biomass survey data served as the input for the bootstrapping analysis. Bootstrap replicates were created by drawing a random sample of stations, with replacement for each island. A bootstrap sample size of seven surveys was set as the minimum sampling effort and all islands with less than the minimum were excluded from the analysis. The resampling approach was completed 10,000 times to generate probability distributions for each model output parameter across trophic groups and geopolitical region. To evaluate differences between inhabited and remote islands for each model output parameter, we compared the number of times the difference between each bootstrap replicate from remote *versus* inhabited island was either positive or negative. Positive differences for each bootstrap replicate denoted that remote islands yielded a greater mean value for the model parameter output while negative differences denoted cases where inhabited islands yielded greater output parameter estimates. Levels of significance were based off of the number of times the bootstrap replicate was either positive or negative and a corresponding level of significance was assigned (<0.05, <0.01, or <0.001, based on a two-tailed approach). All analyses were performed using R version 3.1.2 (R Development Core Team, www.r-project.org).

RESULTS

Total mean (± 1 SE) fish biomass at remote islands was observed to be greater than 4 times that of inhabited islands (203.42 ± 24.13 g m^{-2} versus 48.91 ± 11.22 g m^{-2}). The greatest total mean fish biomass, 525.11 ± 65.02 g m^{-2} was observed at Starbuck Island in the Pacific Remote Island Areas; the lowest mean biomass was observed at Guam in the Marianas Archipelago and was almost 30 times lower, equaling 18.01 ± 2.5 g m^{-2} (Figure 2.3, Table 2.1). Of note were the stark differences in the contributions of different trophic levels to overall mean fish biomass between inhabited and remote islands. This was particularly evident in the top-predators (sharks and bony fishes), which on average contributed 45% to the total mean fish biomass at remote islands, but only 8% at inhabited islands. In fact, sharks contributed to 19% of the total mean fish biomass at remote islands, but <1% at inhabited islands, while top-predator bony fishes contributed to 26% of the total mean fish biomass at remote islands and only 7% at inhabited islands.

The number of reported fishery target species differed between regions and equaled 81 species in American Samoa, 89 species in the Hawaiian Archipelago, and 183 species in the Mariana Archipelago. However, based on our expert opinion of targeted species seen in our belt transects, these numbers are likely underestimated and more realistically equal 156 species in American Samoa and 106 species in the Hawaiian Archipelago (Table 2.2). Only in the Mariana Archipelago were our estimates of the total number of fishery target species lower than that reported. There were no reported fishery targets for the Pacific Remote Island Areas, but using the same methods we estimate this to be 165 species in total. Of the five trophic groups included in this assessment, the mid-level carnivores contributed most highly to the diversity of fisheries targets in all regions, making up 26 of the total 34 families identified overall. Surgeonfishes and parrotfishes from the herbivore trophic group were the most specious group of fisheries targets overall, with between 18 and 29 species of surgeonfish and 7 and 18 species of parrotfishes identified across the study region (Table 2.2).

The results of the biomass spectrum analysis revealed striking evidence for the effects of fisheries exploitation on coral reef fish assemblages. When all trophic groups were combined, we observed significant differences in the total mean fish biomass and the inflection points of the biomass spectra between inhabited and remote islands for 3 of the 4 geopolitical regions (Hawaiian Archipelago, Mariana Archipelago, and PRIAs) (Figures 2.4 and 2.9, Table 2.3). In all three cases we observed strong evidence for fishing down the food web as the dominant form of fisheries exploitation, defined by a reduction in total fish biomass, reduction in the inflection point (i.e. a greater proportion of total fish biomass is found in smaller size classes), and no change in the slope of the biomass spectra between inhabited and remote islands (Figures 2.4 and 2.9, Table 2.3).

For the fourth geopolitical region (American Samoa), there was no clear evidence of the effects of any of the three forms of fisheries exploitation identified.

When the biomass spectrum analyses were re-calculated for each trophic group individually, fishing down the food web no longer remained the only form of fisheries exploitation evident in the data. The top-predators did show strong evidence for fishing down the food web as the dominant form of fisheries exploitation across all regions with the exception of American Samoa (Figures 2.5 and 2.9, Table 2.4); here no clear evidence of any form of fisheries exploitation was evident in the top-predator data. For the mid-level carnivores, we observed evidence of size-based fishing in the Hawaiian Archipelago, realized by a significant decrease in the mean fish biomass, a reduction in the slope of the biomass spectra, and no change in the inflection point at inhabited islands as compared to remote islands (Figures 2.6 and 2.9, Table 2.5). In the Mariana Archipelago, we observed evidence of fishing through the food web for mid-level carnivores realized by a significant decrease in the mean fish biomass, but no difference in the inflection point or slope at inhabited islands as compared to remote islands (Figures 2.6 and 2.9, Table 2.5). No evidence of fisheries exploitation was observed for mid-level carnivores in either American Samoa or the Pacific Remote Island Areas. For the planktivores, we observed evidence for all three forms of fisheries exploitation depending on the region in question. We observed evidence for sized-based fishing in the Hawaiian Archipelago, fishing down the food web in the Mariana Archipelago, and fishing through the food web in the Pacific Remote Island Areas (Figures 2.7 and 2.9, Table 2.6). In American Samoa, as for the top-predators and mid-level carnivores, there was no evidence of any of the three forms of fisheries exploitation evident in the data. Finally for the herbivores, evidence of fishing through the food web was observed in the Hawaiian and Mariana Archipelagos (Figures 2.8 and 2.9, Table 2.7). No evidence for any of the three forms of fisheries exploitation on the herbivore trophic group was evident in American Samoa and the PRIAs. Interestingly, at the two archipelagoes with the greatest human population densities (Hawaiian and Mariana Archipelagos), we observed one of the three forms of fisheries exploitation identified across all trophic groups.

DISCUSSION

Using novel size-based biomass spectrum analyses, we conducted a large-scale natural experiment across 49 Pacific islands to examine the effects of fishing on the size-structure of coral reef fish assemblages. Our analyses revealed striking evidence for the effects of fisheries exploitation on coral reefs. When taking a traditional approach whereby analyses were conducted across the entire fish assemblage (regardless of trophic level), we found clear evidence of "*fishing down the food web*" (Pauly et al. 1998), a broadly recognized form of fisheries exploitation (Figure 2.9). However, when the same analyses were conducted across individual trophic levels, evidence for fishing down the food web did not always hold true. At lower trophic levels, other forms of fisheries exploitation were realized in the data, highlighting the intricate ways in which fishing can alter the assemblage structure of a diverse, complex, multi-trophic fishery.

The process of fishing down the food web has become the classic model to describe the effects of fisheries exploitation on marine communities (Pauly et al. 1998, Myers and Worm 2003). This model is founded on the strong linkage between an organism's body size and its trophic position, whereby larger bodied species are generally top-predators. Because most fisheries tend to target large-bodied species, even moderate levels of exploitation can reduce the size-structure and mean trophic level of the fish assemblage. The process of fishing down the food web is widespread and has been documented in many pelagic and demersal commercial fisheries (Pauly and Palomares 2005, Polovina and Woodworth-Jefcoats 2013, Fenner 2014). Across Pacific coral reefs, we also saw clear evidence of fishing down the food web, with a dramatic reduction in large-bodied predatory species where fishing occurs (Figure 2.9). Interestingly, in our study system, top-predators contribute 45% on average to total fish biomass at remote islands compared to inhabited islands where they contribute to a little over 7% (Figure 2.3). Therefore, when pooling all trophic levels and considering that large-bodied top-predators are generally the first species to be targeted by fishers, it is not surprising that fishing down the food web is realized as the dominant form of exploitation on coral reefs. However, on coral reefs medium-to-large-bodied species can be observed across all major trophic groups and while top-predators contribute a large proportion toward total fish biomass they contribute relatively little to the overall diversity of species targeted by coral reef fisheries (Table 2.2). Therefore, unlike in most classic examples of fishing down the food web, in complex systems such as coral reefs, the linkage between body size and trophic position begins to break down when exploring biomass spectra patterns across individual trophic groups.

Size-based assessments serve as useful tools for examining the effects of fisheries exploitation on fish assemblages (Jennings et al. 2002, Dulvy et al. 2004, Graham et al. 2005, Shin et al. 2005, Trebilco et al. 2013). Although traditional approaches provide valuable insight into the direct effects of fisheries exploitation on the entire fish assemblage, they may lack sensitivity and overlook potential differences in biomass-size-spectra relationships realized across different trophic levels. By performing size-based biomass spectra analyses across individual trophic groups, we examined the broad effects of exploitation on coral reef fishes. Importantly, when adopting this novel approach, while fishing down the food web was still the dominant form of fisheries exploitation evident within the top-predator trophic level, we found evidence of two additional forms of fishing at lower trophic levels; "*fishing through the food web*" (Essington et al. 2006) and "*size-based fishing*" (Figure 2.9). These two forms of fisheries exploitation were variable between regions and trophic groups and their effect on the biomass spectra patterns appeared to be strongly influenced by variations in human population density and the putative array of fishing gears used within each region (Figure 2.9).

In general the diversity of fishing methods were positively related to population densities within each region, with the inhabited islands of the Hawaiian Archipelago having both the widest array of fishing methods and the highest local human population densities (Friedlander and DeMartini 2002, Friedlander et al. 2007). It was only here that evidence for size-based fishing was realized, suggesting the wide array of fishing methods indiscriminately targets larger bodied individuals, regardless of trophic level. Sized-based fishing, therefore, may represent a mature state of fisheries exploitation on coral reefs where multiple gear types are employed by a range of user groups including artisanal, recreational, and commercial fishers to indiscriminately harvest species across multiple trophic levels. In contrast, at inhabited islands with lower population densities, fisheries were less developed and the array of fishing methods employed was generally limited to those that target individual species or trophic groups. For example, most top-predatory species can be fished readily using hook-and-line or spear, while species from lower trophic groups often require alternative harvesting methods (i.e. nets and traps) that involve additional effort and resources (Figure 2.9).

In our study system, the inhabited islands of the Pacific Remote Island Areas were the least densely populated at the regional level. Here, although we saw clear evidence of fishing down the food web and removal of top-predatory species, with the exception of the large-bodied planktivores, we saw little evidence for the effects of fisheries exploitation on lower trophic levels. These results could be linked to the relatively low levels of exploitation of lower trophic levels in this region or to a potential ecological feedback resulting from top-predator removal (e.g., mesopredator release or compensatory prey release).

Interestingly, in American Samoa we saw no evidence of any form of fisheries exploitation in the data (2.9). These results were surprising considering that fisheries exploitation is known to occur at inhabited islands of the region and has been well documented in fisheries catch data and published reports (Craig et al. 1997, Zeller et al. 2006a, Zeller et al. 2006b, Craig et al. 2008, Sabater and Carroll 2009, Sabater and Tulafono 2011, Carroll et al. 2012). Additionally, the remote islands of the region (Rose and Swains) are among the most isolated sites included in our study (the closest inhabited islands are 140 km and 300 km away respectively). It is therefore unlikely that fisheries exploitation can be attributed to the low total mean fish biomass values and lack of top-predators (sharks) observed at Rose and Swains compared to other remote sites included in our study. A possible explanation for these observations may be due to the low replication in American Samoa (3 inhabited islands *versus* 2 remote islands) compared to the other regions included in this study.

In sum, our observations from this large-scale natural experiment provide important insights into the effects of fisheries exploitation on coral reefs. Importantly, we found strong evidence for the presence of multiple forms of fisheries exploitation realized across multiple trophic groups. Together these findings highlight the complexity of coral reef fisheries and reinforce the importance of taking a multi-trophic group approach to monitoring and managing coral reef ecosystems.

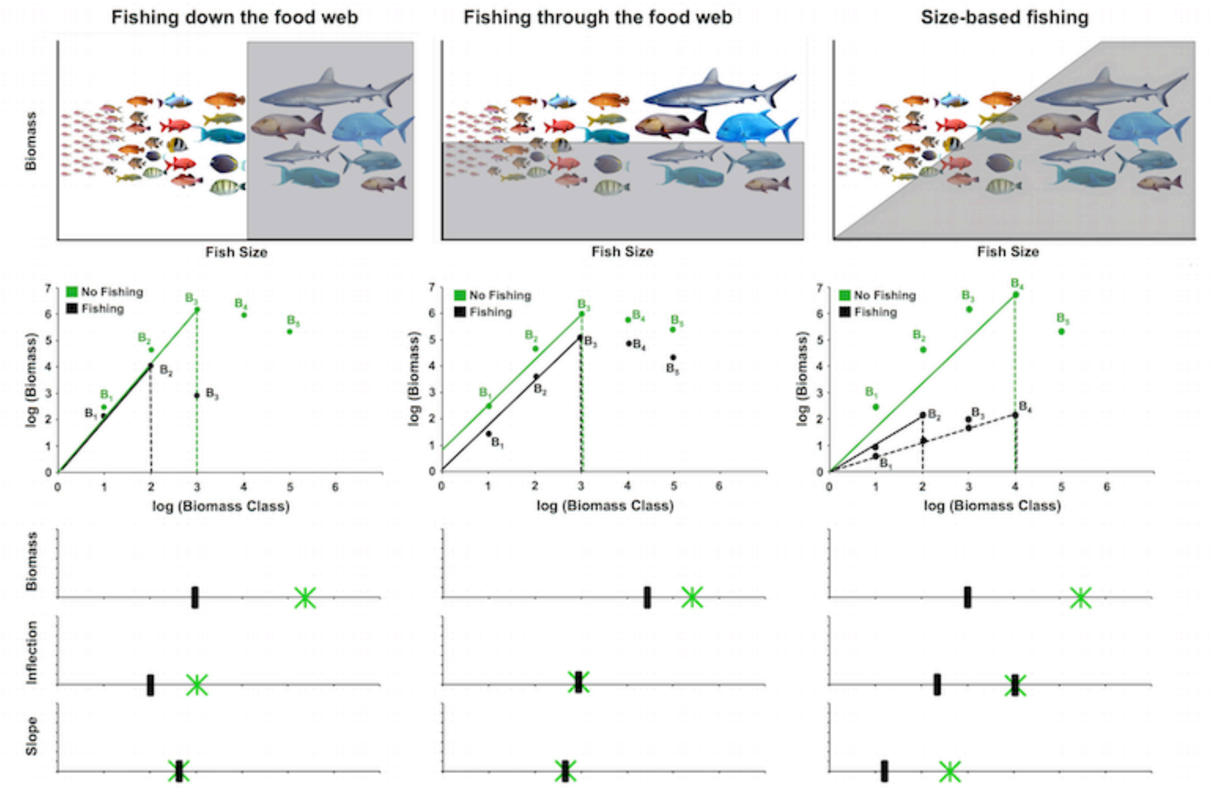

Figure 2.1. Conceptual figure depicting biomass size-spectra and the effects of three scenarios of fisheries exploitation on coral reef fish assemblages: 1) Fishing down the food web; 2) Fishing through the food web; and 3) Sized-based fishing (top panel). Shaded areas indicate the distribution of fishing effort across species from different size classes. Lower two panels compare the hypothesized effects of the three types of fisheries exploitation on the mean biomass, slope of the biomass size-spectrum, and the inflection point of the biomass distributions between sites where fisheries exploitation is present (Black lines and points represent inhabited islands) and where fisheries exploitation is absent (Green lines and points represent remote islands). Note that with size-base fishing, the effects of fisheries exploitation can lead to a reduction in the inflection point or no change in the inflection point.

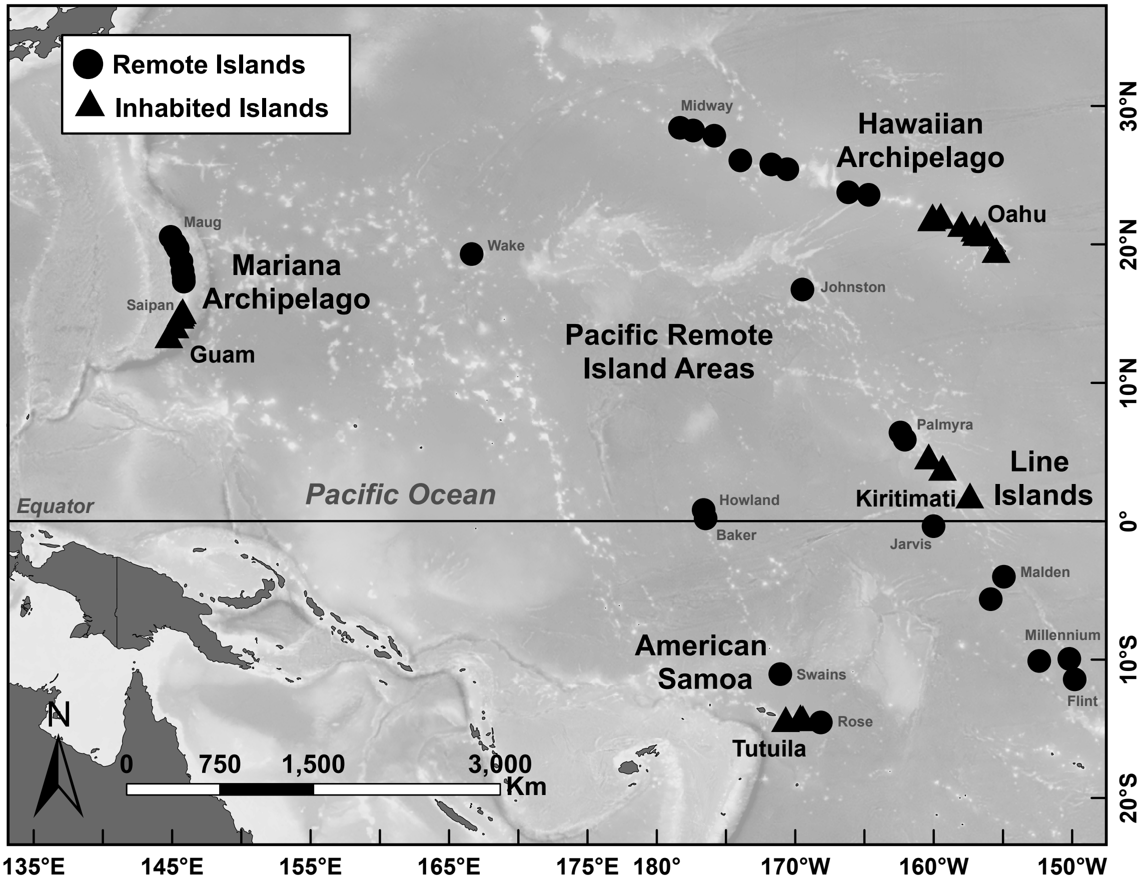

Figure 2.2. Central and western Pacific identifying 49 remote (filled circles) and inhabited (filled triangles) islands located within 4 geopolitical regions: Mariana Archipelago, Hawaiian Archipelago, Pacific Remote Island Areas, and islands of American Samoa.

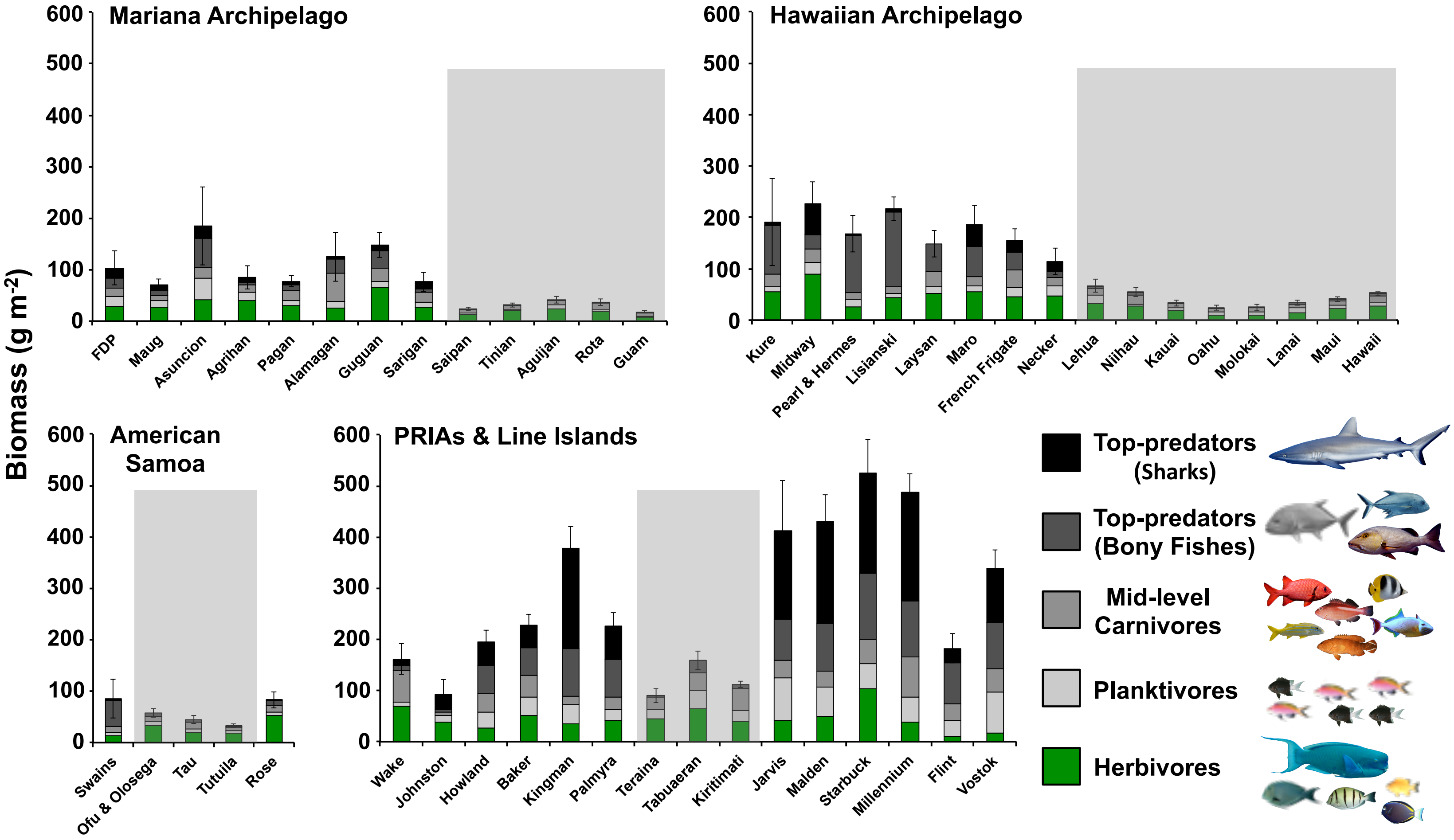

Figure 2.3. Mean fish biomass by region and trophic grouping. Vertical error bars represent ± 1 SE of total mean fish biomass for each island. Within each region, islands are ordered by latitude and longitude with islands furthest west and north to the left. Shaded portions of figure indicate inhabited islands within each region.

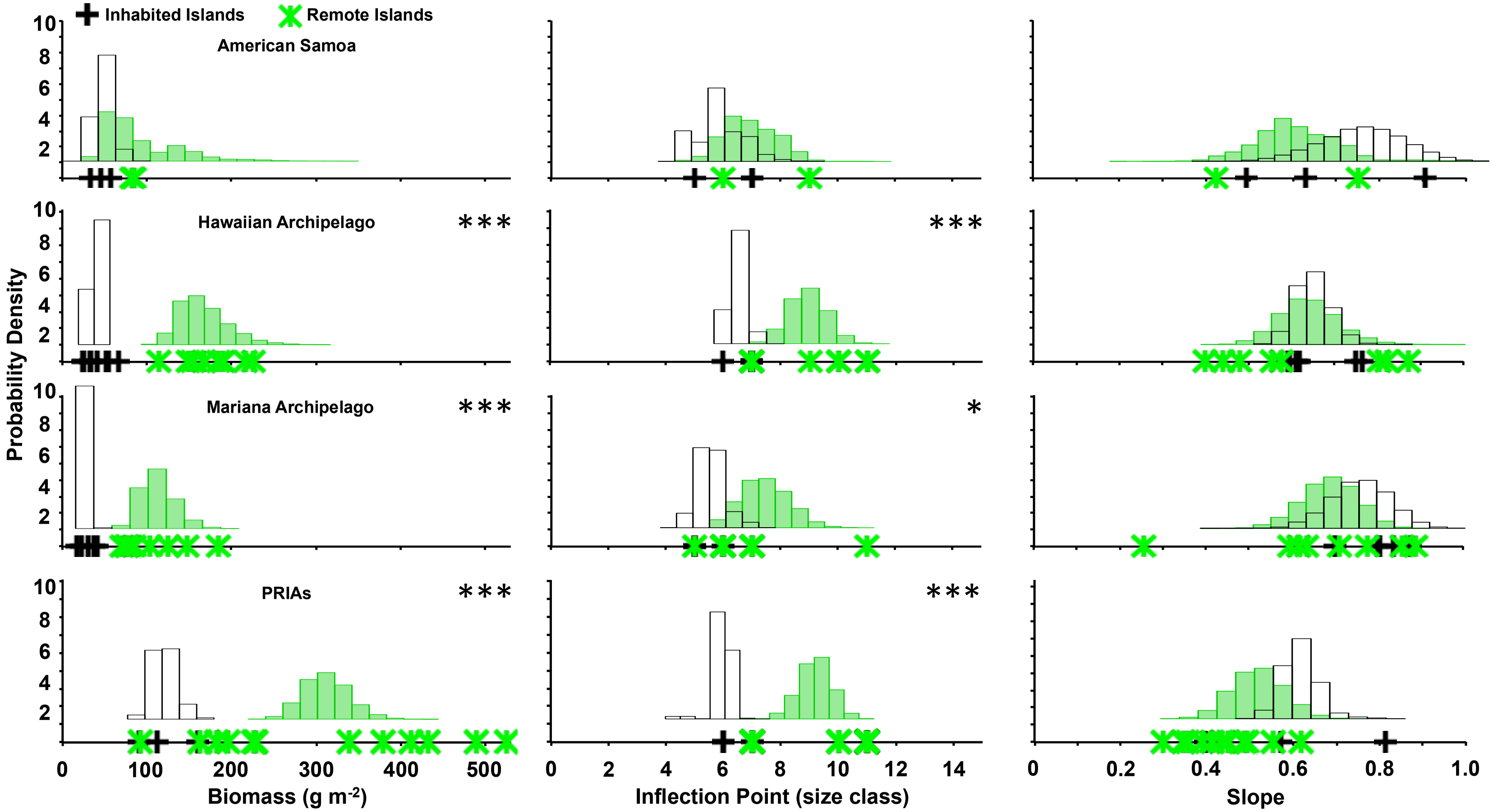

Figure 2.4. Model outputs of biomass spectra for **all species combined** with island-specific values of total mean fish biomass, inflection point, and slope provided along the x-axis of each plot. The estimated values of response metrics based on all data from each island are presented as black crosses for inhabited islands and as green x's for remote islands. Histograms indicate the probability density outputs for bootstrapped model comparisons for inhabited (black outline) and remote (solid green) islands. Scale for probability density values (y-axis) are multiples of 1000. Significant differences for bootstrapped model comparisons are given as: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

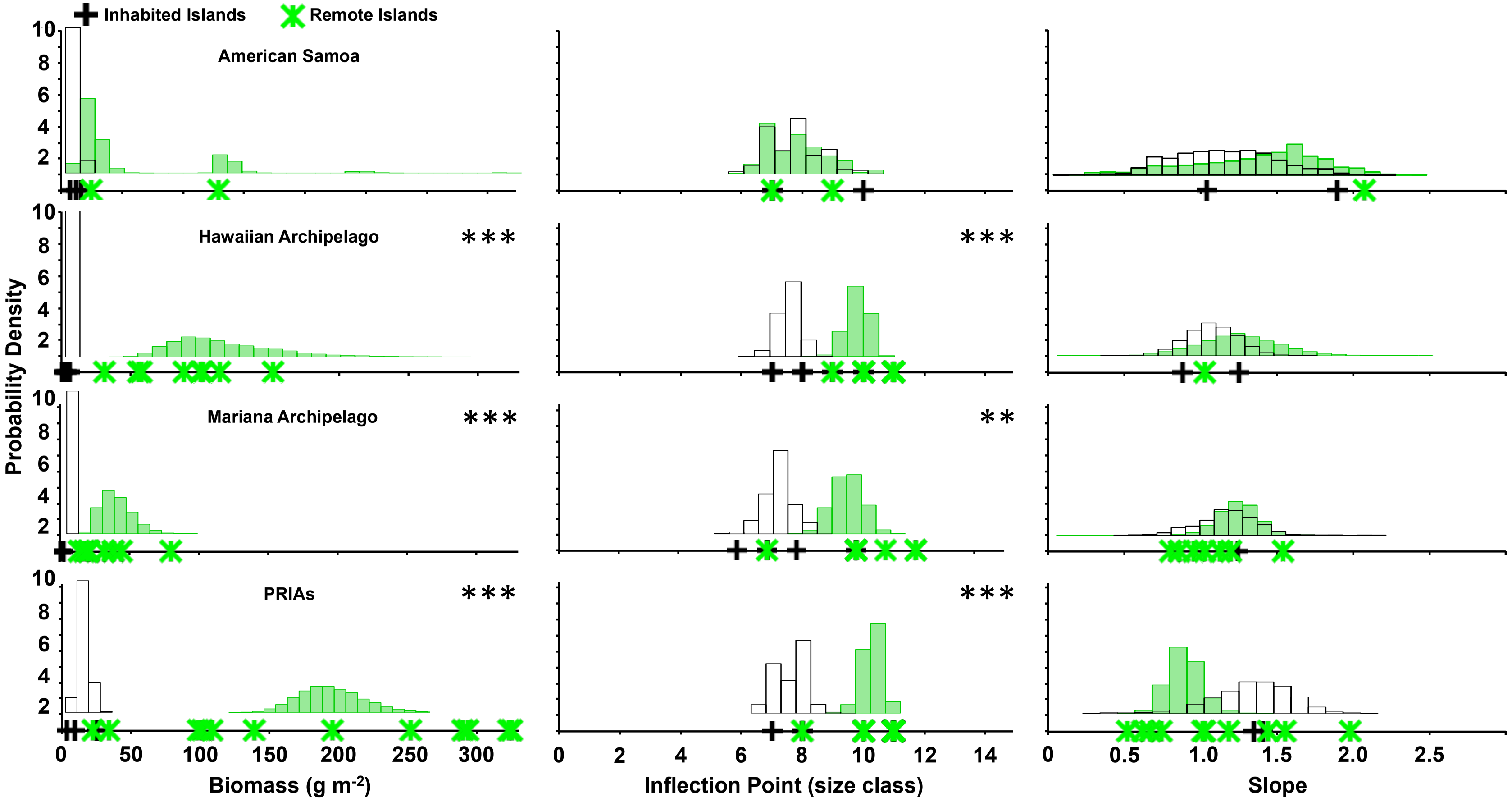

Figure 2.5. Model outputs of biomass spectra for **top-predators (sharks & bony fishes)** with island-specific values of total mean fish biomass, inflection point, and slope provided along the x-axis of each plot. The estimated values of response metrics based on all data from each island are presented as black crosses for inhabited islands and as green x's for remote islands. Histograms indicate the probability density outputs for bootstrapped model comparisons for inhabited (black outline) and remote (solid green) islands. Scale for probability density values (y-axis) are multiples of 1000. Significant differences for bootstrapped model comparisons are given as: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

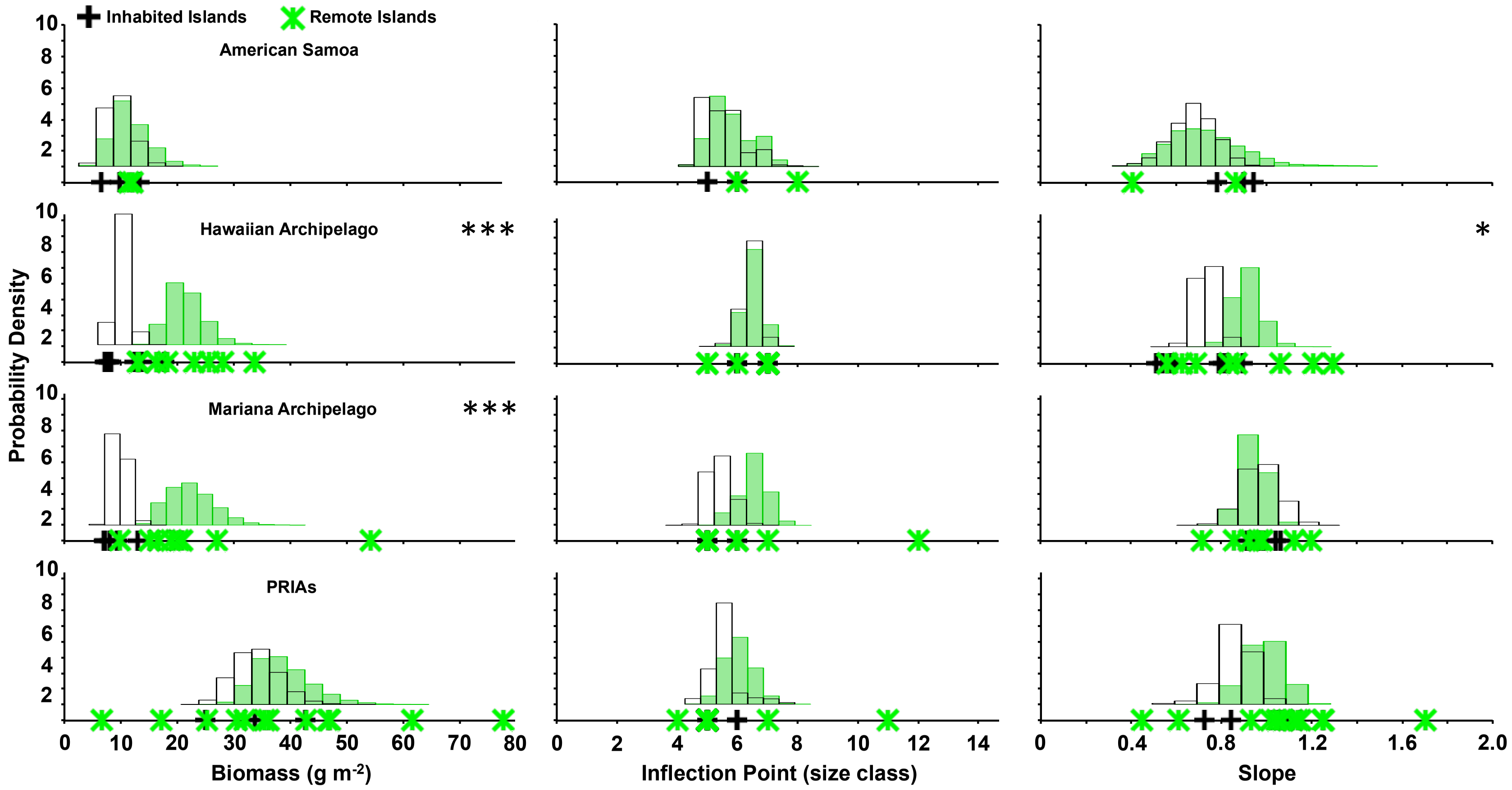

Figure 2.6. Model outputs of biomass spectra for **mid-level carnivores** with island-specific values of total mean fish biomass, inflection point, and slope provided along the x-axis of each plot. The estimated values of response metrics based on all data from each island are presented as black crosses for inhabited islands and as green x's for remote islands. Histograms indicate the probability density outputs for bootstrapped model comparisons for inhabited (black outline) and remote (solid green) islands. Scale for probability density values (y-axis) are multiples of 1000. Significant differences for bootstrapped model comparisons are given as: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

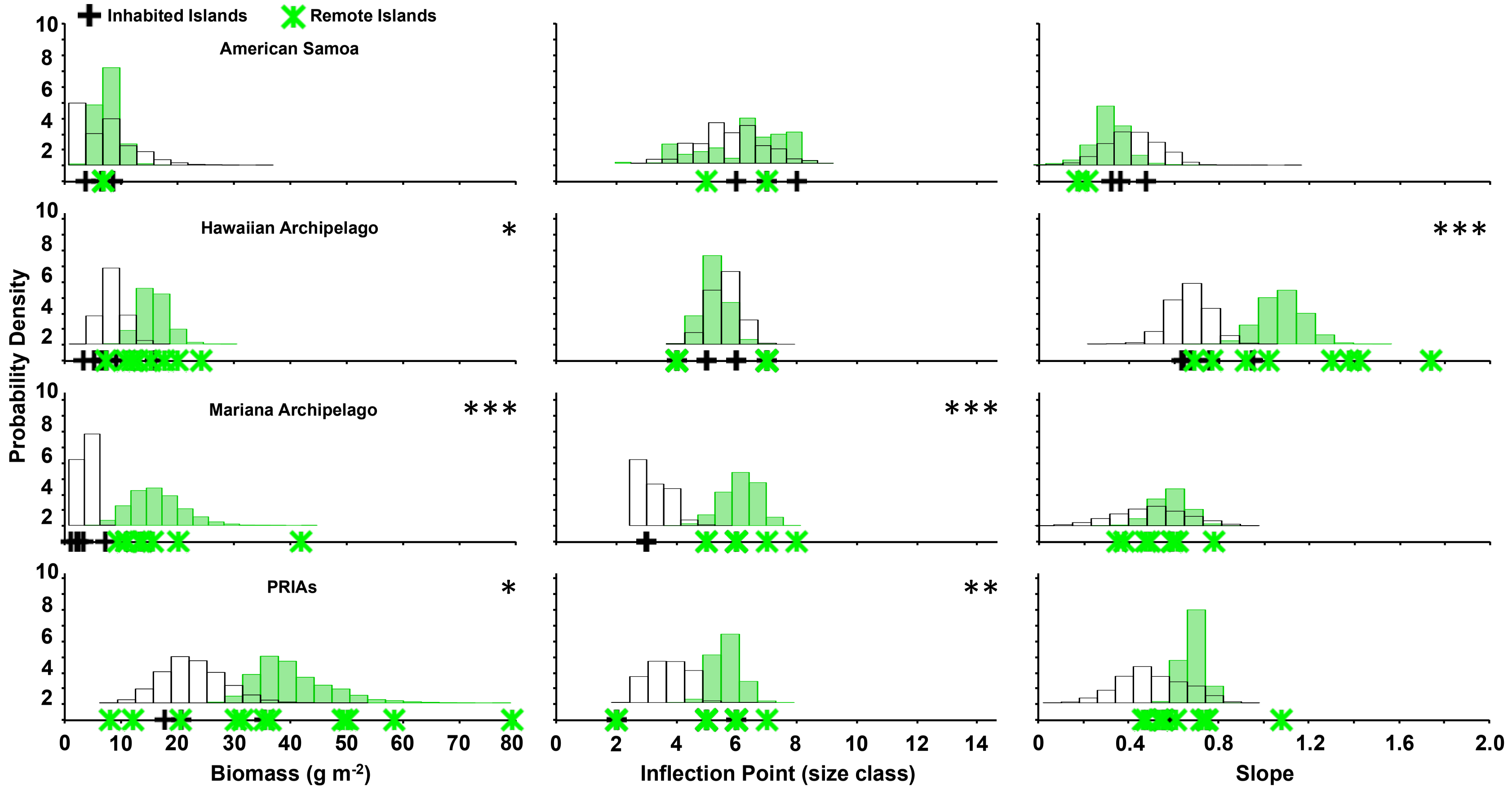

Figure 2.7. Model outputs of biomass spectra for **planktivores** with island-specific values of total mean fish biomass, inflection point, and slope provided along the x-axis of each plot. The estimated values of response metrics based on all data from each island are presented as black crosses for inhabited islands and as green x's for remote islands. Histograms indicate the probability density outputs for bootstrapped model comparisons for inhabited (black outline) and remote (solid green) islands. Scale for probability density values (y-axis) are multiples of 1000. Significant differences for bootstrapped model comparisons are given as: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

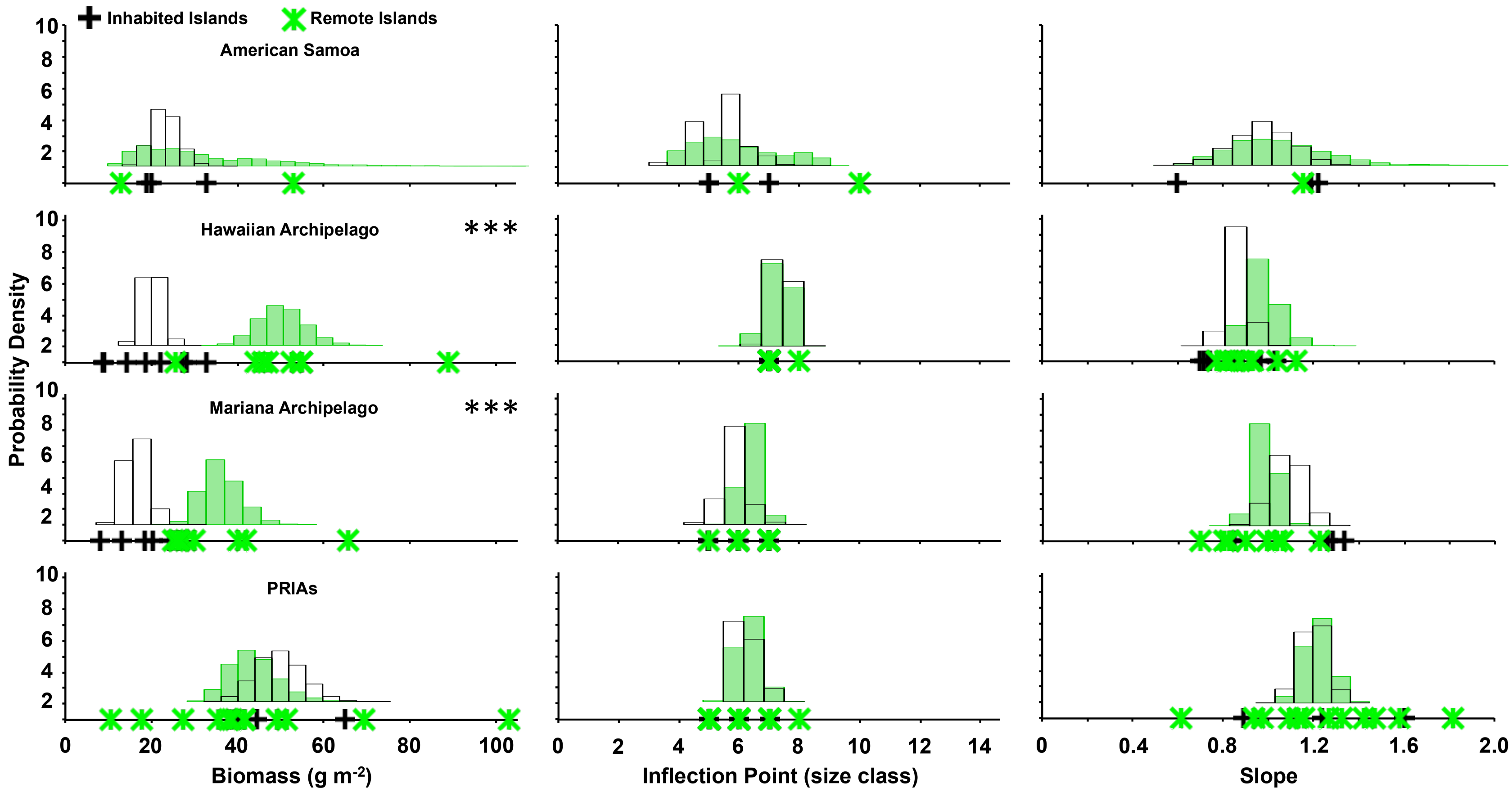

Figure 2.8. Model outputs of biomass spectra for **herbivores** with island-specific values of total mean fish biomass, inflection point, and slope provided along the x-axis of each plot. The estimated values of response metrics based on all data from each island are presented as black crosses for inhabited islands and as green x's for remote islands. Histograms indicate the probability density outputs for bootstrapped model comparisons for inhabited (black outline) and remote (solid green) islands. Scale for probability density values (y-axis) are multiples of 1000. Significant differences for bootstrapped model comparisons are given as: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

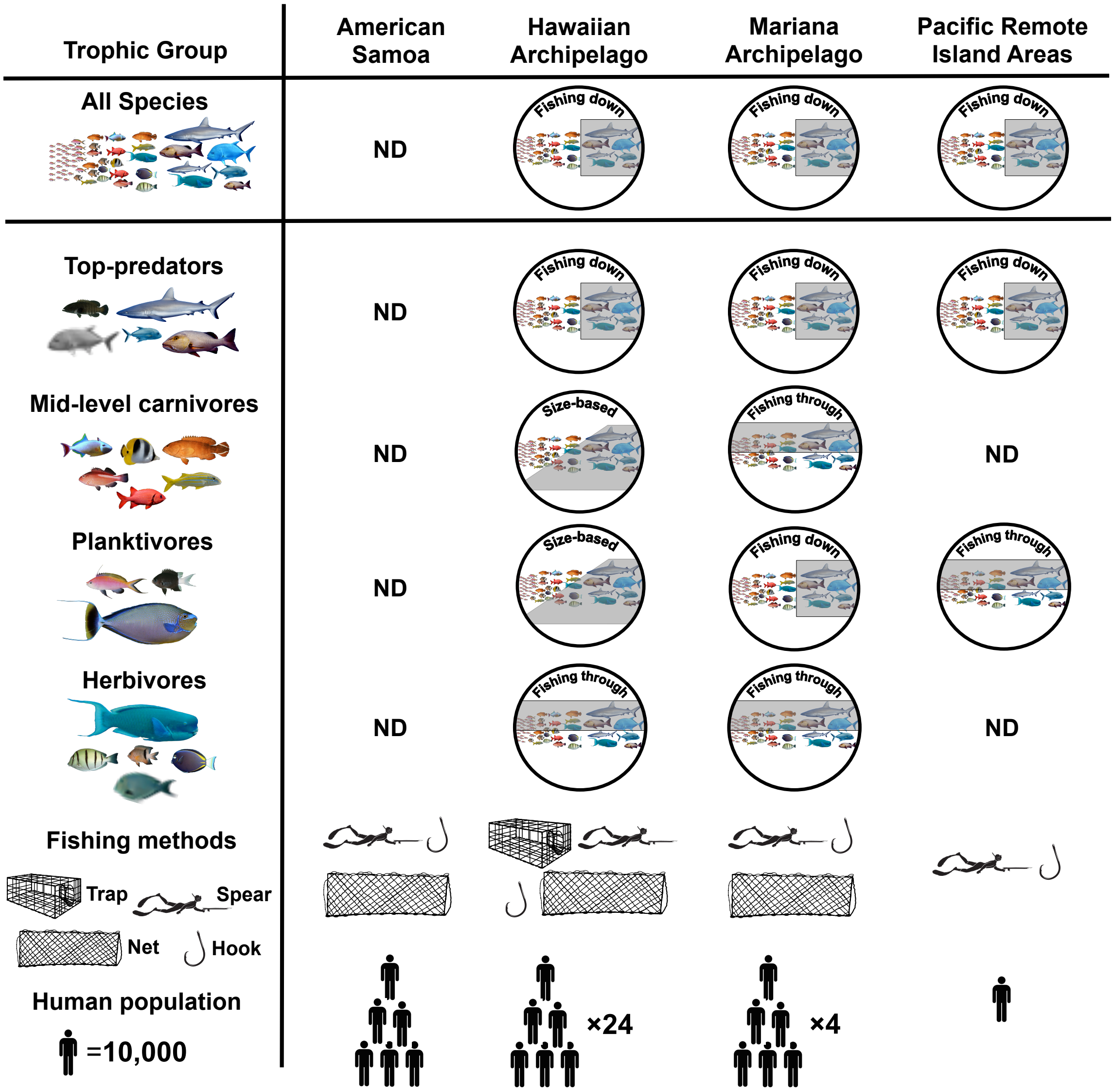

Figure 2.9. Summary output of biomass spectrum analyses identifying the form of fishing observed within each geopolitical region for each major trophic group. Forms of fishing are fishing down the food web, fishing through the food web, and size based fishing. ND indicates no observed differences in comparisons of biomass spectra model outputs between inhabited and remote islands. Common fishing methods are identified for each geopolitical region along with the human population density. See methods for complete description of data sources.

Table 2.1. Summary data for study sites including geographic position, survey effort (N), and island-specific total mean fish biomass with ± 1 SE of total mean fish biomass in parentheses. Shaded portions of table indicate inhabited islands.

Region	**Island**	**Latitude**	**Longitude**	**N**	**Mean Biomass (g m^{-2})**
American Samoa	Swains	-11.06	-171.08	28	85.17 (37.82)
	Rose	-14.55	-168.16	36	82.98 (15.82)
	Ofu & Olosega	-14.17	-169.64	34	57.83 (8.46)
	Tau	-14.23	-169.47	33	44.76 (7.54)
	Tutuila	-14.29	-170.70	72	33.40 (3.53)
Hawaiian Archipelago	Kure	28.42	-178.33	29	190.59 (84.27)
	Midway	28.23	-177.37	21	226.48 (43.15)
	Pearl & Hermes	27.86	-175.85	32	168.13 (35.43)
	Lisianski	26.06	-173.97	44	216.99 (23.06)
	Laysan	25.77	-171.73	23	148.83 (25.90)
	Maro	25.43	-170.57	48	185.16 (38.76)
	French Frigate Shoals	23.76	-166.17	31	154.71 (23.36)
	Necker	23.58	-164.70	9	114.17 (25.72)
	Lehua	22.02	-160.10	8	66.57 (12.40)
	Niihau	21.90	-160.15	18	54.48 (8.64)
	Kauai	22.07	-159.50	28	33.39 (6.19)
	Oahu	21.48	-157.99	19	24.05 (5.03)
	Molokai	21.14	-157.03	13	24.79 (6.58)
	Lanai	20.84	-156.93	18	33.43 (5.14)
	Maui	20.81	-156.35	35	41.07 (4.80)
	Hawaii	19.60	-155.50	60	51.30 (3.78)
Mariana Archipelago	Farallon de Pajaros	20.54	144.89	13	103.18 (33.34)
	Maug	20.02	145.22	34	70.95 (11.50)
	Asuncion	19.69	145.40	15	184.29 (75.83)
	Agrihan	18.77	145.67	18	84.54 (22.60)
	Pagan	18.10	145.76	33	77.01 (10.40)
	Alamagan	17.60	145.83	11	124.79 (47.38)
	Guguan	17.31	145.84	11	147.86 (24.19)
	Sarigan	16.70	145.78	12	76.45 (18.64)
	Saipan	15.18	145.75	30	23.30 (3.33)
	Tinian	15.02	145.63	19	31.18 (3.91)
	Aguijan	14.85	145.56	8	41.49 (7.19)
	Rota	14.16	145.21	23	36.90 (6.42)
	Guam	13.44	144.76	39	18.01 (2.50)
Pacific Remote Island Areas (Line Islands)	Wake	19.30	166.63	36	161.58 (29.79)
	Johnston	16.74	-169.48	7	91.59 (29.61)
	Howland	0.81	-176.62	26	195.37 (22.57)
	Baker	0.19	-176.48	29	228.18 (20.96)
	Kingman	6.41	-162.40	53	378.82 (42.49)
	Palmyra	5.88	-162.08	65	225.86 (27.22)
	Teraina	4.68	-160.38	10	90.45 (13.97)
	Tabuaeran	3.86	-159.36	25	159.51 (18.28)
	Kiritimati	1.87	-157.40	28	112.29 (6.25)
	Jarvis	-0.37	-160.02	29	412.02 (98.07)
	Malden	-4.02	-154.93	25	431.38 (51.48)
	Starbuck	-5.64	-155.88	20	525.11 (65.02)
	Millennium	-9.95	-150.21	25	488.40 (35.63)
	Flint	-11.43	-149.82	14	182.63 (28.51)
	Vostok	-10.10	-152.38	10	339.23 (35.97)

Table 2.2. List of key targeted coral reef taxa based on the best available data from visual censuses and expert opinion for the 4 geopolitical regions included in this assessment. Values in parenthesis indicate the number of species confirmed as fisheries targets based on regional catch statistics and published data (See methods for complete description of data sources).

Trophic Group	Common Name	Family	American Samoa	Hawaiian Archipelago	Mariana Archipelago	PRIAs (Line Islands)
Top-predators (Sharks)	Reef Sharks	Carcharhinidae	2 (4)	3 (4)	3 (6)	4
	Nurse Shark	Ginglymostomatidae			1 (1)	
		Total	2 (4)	3 (4)	4 (7)	4
Top-predators (Bony Fishes)	Jacks	Carangidae	6 (6)	5 (8)	8 (8)	7
	Emperors	Lethrinidae	1		1 (1)	1
	Snappers	Lutjanidae	2 (1)	1 (1)	2 (2)	2
	Groupers	Serranidae	5 (3)	2 (1)	4 (6)	4
	Barracudas	Sphyraenidae	2 (1)	1 (1)	1 (2)	2
		Total	16 (11)	9 (11)	16 (19)	16
Mid-level Carnivores	Trumpetfish	Aulostomidae	1 (1)	1 (1)	1 (1)	1
	Triggerfishes	Balistidae	8	5 (3)	7 (9)	8
	Flounder	Bothidae		(1)	(1)	1
	Jacks	Carangidae	2 (3)	3 (5)	1 (5)	2
	Morwong	Cheilodactylidae		1		
	Hawkfishes	Cirrhitidae	2	1 (1)	2 (1)	2
	Conger Eels	Congridae		1 (1)	(1)	
	Stingrays	Dasyatidae			1 (1)	1
	Porcupinefishes	Diodontidae	1	2 (1)	1 (1)	1
	Spadefishes	Ephippidae			1 (1)	
	Cornetfish	Fistulariidae	1	1	1 (1)	1
	Sweetlips	Haemulidae	3		1 (3)	
	Squirrelfishes & Soldierfishes	Holocentridae	7 (1)	7 (3)	8 (10)	7
	Wrasses	Labridae	7 (2)	4 (4)	6 (7)	7
	Emperors	Lethrinidae	3 (3)	1 (1)	6 (6)	4
	Snappers	Lutjanidae	6 (5)	3 (3)	5 (5)	6
	Tilefishes	Malacanthidae	1		1 (1)	1
	Filefishes	Monacanthidae	1	1	(1)	1
	Goatfishes	Mullidae	7 (5)	8 (9)	7 (8)	8
	Moray Eels	Muraenidae	3 (1)	3 (1)	2 (3)	3
	Eagle ray	Myliobatidae	(1)	1	1 (1)	1
	Knifejaws	Oplegnathidae		2	1	1
	Parrotfishes	Scaridae			(1)	1
	Scorpionfishes	Scorpaenidae		2 (1)	(1)	
	Groupers	Serranidae	8 (6)		10 (12)	11
	Barracudas	Sphyraenidae		(1)	(1)	
		Total	61 (28)	47 (36)	64 (83)	68
Planktivores	Surgeonfishes	Acanthuridae	7 (1)	4 (3)	8 (8)	8
	Triggerfishes	Balistidae	4	4 (1)	3 (5)	3
	Fusiliers	Caesionidae	5 (2)		4 (4)	3
	Jacks	Carangidae	1 (2)	2 (2)	(2)	2
	Squirrelfishes & Soldierfishes	Holocentridae	5 (4)	4 (4)	5 (8)	5
	Snappers	Lutjanidae	2 (1)		2 (2)	1
	Manta Ray	Mobulidae				1
	Bigeyes	Priacanthidae	1	2 (2)	1 (1)	1
		Total	25 (10)	16 (12)	23 (30)	24
Herbivores	Surgeonfishes	Acanthuridae	28 (14)	18 (16)	24 (23)	29
	Triggerfishes	Balistidae	1 (1)	1 (1)	1 (1)	1
	Milkfish	Chanidae	1 (1)	1 (1)	(1)	1
	Chubs	Kyphosidae	3 (2)	4 (3)	3 (2)	4
	Parrotfishes	Scaridae	18 (11)	7 (6)	17 (18)	18
	Rabbitfishes	Siganidae	1		1 (1)	
		Total	52 (29)	31 (27)	46 (46)	53
		Grand Total	156 (81)	106 (89)	152 (183)	165

Table 2.3. Model outputs of biomass spectra for **all species combined** divided into the four geopolitical regions. Class describes the range of biomass size class values included in the model numbered 1-12 (see methods for full description of biomass size class classification). Shaded portions of table indicate inhabited islands. Statistical fits of the linear model are: *F*, test statistic; *p*, significance value; r^2, overall variation explained (%); df, degrees of freedom.

Region	**Island**	**Biomass Class**		**Intercept**	**Slope**	**F**	***p***	**r^2**	**df**
		Minimum	**Maximum**						
American Samoa	Swains	1	9	-0.57	0.42	52.26	<0.001	0.88	7
	Rose	1	6	-1.19	0.75	25.09	0.007	0.86	4
	Ofu & Olosega	1	5	-1.82	0.91	22.42	0.018	0.88	3
	Tau	1	7	-1.50	0.63	25.99	0.004	0.84	5
	Tutuila	1	7	-0.99	0.49	10.13	0.024	0.67	5
Hawaiian Archipelago	Kure	1	9	-0.86	0.58	26.68	0.001	0.79	7
	Midway	1	11	0.02	0.40	15.06	0.004	0.63	9
	Pearl & Hermes	1	10	-0.71	0.48	18.71	0.003	0.70	8
	Lisianski	1	10	-1.03	0.56	25.76	0.001	0.76	8
	Laysan	1	7	-2.09	0.87	19.04	0.007	0.79	5
	Maro	1	11	-0.58	0.44	14.91	0.004	0.62	9
	French Frigate	1	7	-1.62	0.80	45.44	0.001	0.90	5
	Necker	1	7	-2.04	0.82	92.64	<0.001	0.95	5
	Lehua	1	7	-1.27	0.62	21.40	0.006	0.81	5
	Niihau	1	7	-2.07	0.75	59.83	0.001	0.92	5
	Kauai	1	7	-1.90	0.62	39.95	0.001	0.89	5
	Oahu	1	7	-1.81	0.59	45.52	0.001	0.90	5
	Molokai	1	6	-2.27	0.76	27.60	0.006	0.87	4
	Lanai	1	7	-1.62	0.59	83.43	<0.001	0.94	5
	Maui	1	7	-1.52	0.60	31.87	0.002	0.86	5
	Hawaii	1	7	-1.23	0.61	63.78	<0.001	0.93	5
Mariana Archipelago	Farallon de Pajaros	1	6	-1.95	0.89	106.79	<0.001	0.96	4
	Maug	1	6	-1.29	0.71	76.63	0.001	0.95	4
	Asuncion	1	11	0.75	0.26	8.03	0.020	0.47	9
	Agrihan	1	6	-1.25	0.78	39.55	0.003	0.91	4
	Pagan	1	7	-0.90	0.62	31.50	0.002	0.86	5
	Alamagan	1	7	-0.77	0.60	27.90	0.003	0.85	5
	Guguan	1	5	-0.88	0.86	31.01	0.011	0.91	3
	Sarigan	1	7	-1.17	0.64	37.98	0.002	0.88	5
	Saipan	1	5	-1.79	0.80	26.45	0.014	0.90	3
	Tinian	1	5	-1.98	0.88	41.71	0.008	0.93	3
	Aguijan	1	5	-1.38	0.84	11.63	0.042	0.79	3
	Rota	1	6	-1.59	0.70	24.77	0.008	0.86	4
	Guam	1	5	-2.35	0.81	14.39	0.032	0.83	3
Pacific Remote Island Areas (Line Islands)	Wake	1	11	-0.40	0.39	20.36	0.001	0.69	9
	Johnston	1	11						
	Howland	1	7	0.31	0.49	10.63	0.022	0.68	5
	Baker	1	7	-0.13	0.62	28.32	0.003	0.85	5
	Kingman	1	11	-0.30	0.49	64.10	<0.001	0.88	9
	Palmyra	1	10	-0.18	0.45	41.83	<0.001	0.84	8
	Teraina	1	6	-0.04	0.57	14.01	0.020	0.78	4
	Tabuaeran	1	6	-0.85	0.81	26.53	0.007	0.87	4
	Kiritimati	1	7	0.73	0.40	10.06	0.025	0.67	5
	Jarvis	1	11	1.31	0.30	12.47	0.006	0.58	9
	Malden	1	11	0.99	0.35	12.95	0.006	0.59	9
	Starbuck	1	11	0.52	0.43	15.60	0.003	0.63	9
	Millennium	1	11	0.65	0.41	34.10	<0.001	0.79	9
	Flint	1	7	0.02	0.55	26.17	0.004	0.84	5
	Vostok	1	10	0.87	0.35	10.35	0.012	0.56	8

Table 2.4. Model outputs of biomass spectra for **top-predators (sharks & bony fishes)** divided into the four geopolitical regions. Class describes the range of biomass size class values included in the model numbered 1-12 (see methods for full description of biomass size class classification). Shaded portions of table indicate inhabited islands. Statistical fits of the linear model are: *F*, test statistic; *p*, significance value; r^2, overall variation explained (%); df, degrees of freedom.

Region	**Island**	**Biomass Class**		**Intercept**	**Slope**	**F**	***p***	**r^2**	**df**
		Minimum	**Maximum**						
American Samoa	Swains	2	9						
	Rose	1	7	-12.07	2.07	98.20	<0.001	0.95	5
	Ofu & Olosega	1	7	-11.00	1.89	51.06	0.001	0.91	5
	Tau	2	7						
	Tutuila	1	10	-8.74	1.04	17.22	0.003	0.68	8
Hawaiian Archipelago	Kure	4	9						
	Midway	2	11						
	Pearl & Hermes	1	10						
	Lisianski	1	10						
	Laysan	2	10						
	Maro	2	11						
	French Frigate	4	11	-7.41	1.03	111.41	<0.001	0.95	6
	Necker	2	11						
	Lehua	4	9	-6.55	0.88	22.04	0.009	0.85	4
	Niihau	2	8						
	Kauai	2	8	-10.02	1.25	168.90	<0.001	0.97	5
	Oahu	2	7						
	Molokai	2	8						
	Lanai	2	7						
	Maui	2	10						
	Hawaii	2	7						
Mariana Archipelago	Farallon de Pajaros	1	10	-7.82	1.20	33.21	<0.001	0.81	8
	Maug	1	12	-7.98	0.95	33.90	<0.001	0.77	10
	Asuncion	4	11	-4.91	0.80	24.25	0.003	0.80	6
	Agrihan	2	10	-6.21	0.86	89.88	<0.001	0.93	7
	Pagan	1	10	-7.26	1.02	34.88	<0.001	0.81	8
	Alamagan	2	7	-8.44	1.54	22.55	0.009	0.85	4
	Guguan	1	10	-7.13	1.13	30.33	0.001	0.79	8
	Sarigan	1	12						
	Saipan	2	7						
	Tinian	2	7						
	Aguijan	2	6						
	Rota	1	8	-9.06	1.24	19.96	0.004	0.77	6
	Guam	2	10						
Pacific Remote Island Areas (Line Islands)	Wake	4	11	-3.50	0.52	14.13	0.009	0.70	6
	Johnston	2	11						
	Howland	1	11	-6.15	1.02	33.25	<0.001	0.79	9
	Baker	1	8	-10.72	1.98	44.03	0.001	0.88	6
	Kingman	1	11	-9.09	1.44	72.19	<0.001	0.89	9
	Palmyra	1	10	-9.52	1.55	43.36	<0.001	0.84	8
	Teraina	2	8						
	Tabuaeran	4	8	-7.80	1.35	13.82	0.034	0.82	3
	Kiritimati	1	7	-7.79	1.41	30.86	0.003	0.86	5
	Jarvis	2	11	-6.90	1.18	37.28	<0.001	0.82	8
	Malden	2	11						
	Starbuck	4	11	-2.80	0.75	16.86	0.006	0.74	6
	Millennium	2	11	-5.00	1.01	25.01	0.001	0.76	8
	Flint	2	10	-2.67	0.67	12.13	0.010	0.63	7
	Vostok	4	10	-1.90	0.62	11.80	0.019	0.70	5

Table 2.5. Model outputs of biomass spectra for **mid-level carnivores** divided into the four geopolitical regions. Class describes the range of biomass size class values included in the model numbered 1-12 (see methods for full description of biomass size class classification). Shaded portions of table indicate inhabited islands. Statistical fits of the linear model are: *F*, test statistic; *p*, significance value; r^2, overall variation explained (%); df, degrees of freedom.

Region	**Island**	**Biomass Class**		**Intercept**	**Slope**	**F**	***p***	**r^2**	**df**
		Minimum	**Maximum**						
American Samoa	Swains	1	8	-1.95	0.41	7.47	0.034	0.55	6
	Rose	1	6	-3.43	0.87	12.55	0.024	0.76	4
	Ofu & Olosega	1	5	-3.36	0.90	10.88	0.046	0.78	3
	Tau	1	6	-2.95	0.78	17.89	0.013	0.82	4
	Tutuila	1	5	-3.71	0.94	13.30	0.036	0.82	3
Hawaiian Archipelago	Kure	1	7	-2.03	0.63	7.60	0.040	0.60	5
	Midway	1	7	-2.33	0.69	10.96	0.021	0.69	5
	Pearl & Hermes	1	5	-3.99	1.21	6.79	0.080	0.69	3
	Lisianski	1	5	-4.39	1.29	7.72	0.069	0.72	3
	Laysan	1	7	-3.34	0.87	9.84	0.026	0.66	5
	Maro	1	7	-3.41	0.83	11.17	0.021	0.69	5
	French Frigate	1	6	-3.37	1.06	29.87	0.005	0.88	4
	Necker	1	7	-2.12	0.56	13.58	0.014	0.73	5
	Lehua	1	6	-1.82	0.51	8.28	0.045	0.67	4
	Niihau	1	6	-3.32	0.89	26.79	0.007	0.87	4
	Kauai	1	7	-2.56	0.54	13.23	0.015	0.73	5
	Oahu	1	6	-2.63	0.59	6.77	0.060	0.63	4
	Molokai	1	6	-3.47	0.81	9.70	0.036	0.71	4
	Lanai	1	7	-2.94	0.57	7.23	0.043	0.59	5
	Maui	1	6	-3.51	0.79	7.93	0.048	0.66	4
	Hawaii	1	6	-3.12	0.82	9.50	0.037	0.70	4
Mariana Archipelago	Farallon de Pajaros	1	5	-3.67	1.12	11.80	0.041	0.80	3
	Maug	1	5	-3.42	0.97	7.75	0.069	0.72	3
	Asuncion	1	7	-2.55	0.71	19.69	0.007	0.80	5
	Agrihan	1	6	-3.02	0.85	8.47	0.044	0.68	4
	Pagan	1	6	-3.17	0.92	12.73	0.023	0.76	4
	Alamagan	1	12						
	Guguan	1	5	-3.37	1.20	13.38	0.035	0.82	3
	Sarigan	1	5	-3.08	0.98	9.54	0.054	0.76	3
	Saipan	1	5	-3.51	0.99	7.53	0.071	0.72	3
	Tinian	1	5	-3.84	1.06	10.79	0.046	0.78	3
	Aguijan	1	5	-3.23	0.91	7.82	0.068	0.72	3
	Rota	1	6	-3.62	0.96	13.25	0.022	0.77	4
	Guam	1	5	-3.98	1.04	10.32	0.049	0.77	3
Pacific Remote Island Areas (Line Islands)	Wake	1	11	-2.22	0.45	13.42	0.005	0.60	9
	Johnston	1	4	-5.71	1.70	8.29	0.102	0.81	2
	Howland	1	5	-2.68	1.02	15.54	0.029	0.84	3
	Baker	1	5	-2.87	1.12	44.66	0.007	0.94	3
	Kingman	1	7	-2.17	0.61	12.48	0.017	0.71	5
	Palmyra	1	5	-3.16	0.93	7.89	0.067	0.72	3
	Teraina	1	6	-2.39	0.84	12.61	0.024	0.76	4
	Tabuaeran	1	5	-2.81	1.06	19.23	0.022	0.87	3
	Kiritimati	1	6	-1.50	0.72	11.27	0.028	0.74	4
	Jarvis	1	5	-3.23	1.15	46.81	0.006	0.94	3
	Malden	1	5	-2.52	1.07	9.47	0.054	0.76	3
	Starbuck	1	5	-3.40	1.25	19.74	0.021	0.87	3
	Millennium	1	5	-2.93	1.25	34.79	0.010	0.92	3
	Flint	1	5	-2.91	1.14	28.96	0.013	0.91	3
	Vostok	1	5	-2.36	1.05	27.04	0.014	0.90	3

Table 2.6. Model outputs of biomass spectra for **planktivores** divided into the four geopolitical regions. Class describes the range of biomass size class values included in the model numbered 1-12 (see methods for full description of biomass size class classification). Shaded portions of table indicate inhabited islands. Statistical fits of the linear model are: *F*, test statistic; *p*, significance value; r^2, overall variation explained (%); df, degrees of freedom.

Region	Island	Biomass Class		Intercept	Slope	F	*p*	r^2	df
		Minimum	Maximum						
American Samoa	Swains	1	7	-1.53	0.22	0.63	0.463	0.11	5
	Rose	1	5	-1.45	0.17	0.19	0.690	0.06	3
	Ofu & Olosega	1	8	-1.92	0.32	6.15	0.048	0.51	6
	Tau	1	7	-2.89	0.47	11.19	0.020	0.69	5
	Tutuila	1	6	-2.32	0.36	3.55	0.132	0.47	4
Hawaiian Archipelago	Kure	1	4	-4.31	1.37	6.28	0.129	0.76	2
	Midway	1	4	-3.11	1.30	5.34	0.147	0.73	2
	Pearl & Hermes	1	4	-3.68	1.42	36.77	0.026	0.95	2
	Lisianski	1	7	-3.84	0.77	14.63	0.012	0.75	5
	Laysan	1	7	-4.52	0.92	12.94	0.016	0.72	5
	Maro	1	4	-5.90	1.74	8.51	0.100	0.81	2
	French Frigate	1	7	-2.64	0.69	86.80	<0.001	0.95	5
	Necker	1	7	-4.96	1.02	18.12	0.008	0.78	5
	Lehua	1	7	-2.85	0.63	7.21	0.044	0.59	5
	Niihau	1	5	-3.64	0.67	2.32	0.225	0.44	3
	Kauai	1	5	-3.22	0.64	2.85	0.190	0.49	3
	Oahu	1	6	-3.85	0.75	16.87	0.015	0.81	4
	Molokai	1	5	-4.23	0.94	7.81	0.068	0.72	3
	Lanai	1	6	-3.64	0.76	14.29	0.019	0.78	4
	Maui	1	4	-3.68	0.95	6.15	0.131	0.75	2
	Hawaii	1	6	-3.30	0.67	8.28	0.045	0.67	4
Mariana Archipelago	Farallon de Pajaros	1	6	-2.84	0.78	56.11	0.002	0.93	4
	Maug	1	6	-2.31	0.61	12.34	0.025	0.76	4
	Asuncion	1	6	-1.09	0.59	13.54	0.021	0.77	4
	Agrihan	1	5	-2.24	0.59	3.39	0.163	0.53	3
	Pagan	1	6	-2.04	0.49	5.35	0.082	0.57	4
	Alamagan	1	8	-1.83	0.35	2.94	0.137	0.33	6
	Guguan	1	5	-1.19	0.38	1.58	0.298	0.35	3
	Sarigan	1	7	-2.49	0.47	12.58	0.016	0.72	5
	Saipan	1	3						
	Tinian	1	3						
	Aguijan	1	3						
	Rota	1	3						
	Guam	1	3						
Pacific Remote Island Areas (Line Islands)	Wake	1	7	-2.98	0.46	1.85	0.232	0.27	5
	Johnston	1	5	-4.12	1.08	8.09	0.065	0.73	3
	Howland	1	2						
	Baker	1	6	-0.68	0.48	3.88	0.120	0.49	4
	Kingman	1	6	-2.17	0.75	8.83	0.041	0.69	4
	Palmyra	1	5	-1.65	0.56	2.99	0.182	0.50	3
	Teraina	1	2						
	Tabuaeran	1	6	-1.26	0.58	3.29	0.144	0.45	4
	Kiritimati	1	2						
	Jarvis	1	2						
	Malden	1	6	-0.78	0.61	3.61	0.130	0.47	4
	Starbuck	1	6	-1.74	0.73	3.06	0.155	0.43	4
	Millennium	1	5	-0.82	0.55	1.92	0.260	0.39	3
	Flint	1	5	-0.72	0.54	4.71	0.118	0.61	3
	Vostok	1	5	-1.06	0.75	3.43	0.161	0.53	3

Table 2.7. Model outputs of biomass spectra for **herbivores** divided into the four geopolitical regions. Class describes the range of biomass size class values included in the model numbered 1-12 (see methods for full description of biomass size class classification). Shaded portions of table indicate inhabited islands. Statistical fits of the linear model are: *F*, test statistic; *p*, significance value; r^2, overall variation explained (%); df, degrees of freedom.

Region	Island	Biomass Class		Intercept	Slope	F	*p*	r^2	df
		Minimum	Maximum						
American Samoa	Swains	1	10						
	Rose	1	6	-3.43	1.15	25.57	0.007	0.86	4
	Ofu & Olosega	1	5	-3.49	1.19	18.55	0.023	0.86	3
	Tau	1	5	-4.17	1.22	15.01	0.030	0.83	3
	Tutuila	1	7	-2.10	0.60	7.29	0.043	0.59	5
Hawaiian Archipelago	Kure	1	8	-2.61	0.77	42.66	0.001	0.88	6
	Midway	1	7	-3.84	1.12	75.63	<0.001	0.94	5
	Pearl & Hermes	1	7	-3.10	0.83	16.60	0.010	0.77	5
	Lisianski	1	7	-2.35	0.81	26.04	0.004	0.84	5
	Laysan	1	7	-2.93	0.92	24.76	0.004	0.83	5
	Maro	1	7	-2.54	0.87	23.06	0.005	0.82	5
	French Frigate	1	7	-3.22	0.93	39.64	0.001	0.89	5
	Necker	1	7	-3.90	1.04	276.66	<0.001	0.98	5
	Lehua	1	7	-4.35	1.03	50.22	0.001	0.91	5
	Niihau	1	7	-4.54	1.03	42.31	0.001	0.89	5
	Kauai	1	7	-4.81	0.97	115.74	<0.001	0.96	5
	Oahu	1	7	-4.50	0.85	21.88	0.005	0.81	5
	Molokai	1	7	-3.54	0.70	16.11	0.010	0.76	5
	Lanai	1	7	-3.33	0.73	33.81	0.002	0.87	5
	Maui	1	7	-2.90	0.72	29.03	0.003	0.85	5
	Hawaii	1	7	-2.72	0.74	37.58	0.002	0.88	5
Mariana Archipelago	Farallon de Pajaros	1	6	-4.64	1.22	83.17	0.001	0.95	4
	Maug	1	6	-3.38	0.99	26.38	0.007	0.87	4
	Asuncion	1	7	-2.88	0.90	24.93	0.004	0.83	5
	Agrihan	1	6	-3.22	1.06	29.57	0.006	0.88	4
	Pagan	1	7	-2.66	0.80	17.01	0.009	0.77	5
	Alamagan	1	7	-2.43	0.70	16.34	0.010	0.77	5
	Guguan	1	5	-2.28	1.04	19.70	0.021	0.87	3
	Sarigan	1	7	-3.01	0.83	20.56	0.006	0.80	5
	Saipan	1	5	-4.54	1.26	18.97	0.022	0.86	3
	Tinian	1	5	-4.53	1.33	18.42	0.023	0.86	3
	Aguijan	1	5	-3.94	1.28	21.38	0.019	0.88	3
	Rota	1	7	-3.37	0.83	24.57	0.004	0.83	5
	Guam	1	6	-3.75	0.85	15.75	0.017	0.80	4
Pacific Remote Island Areas (Line Islands)	Wake	1	7	-4.23	1.13	48.54	0.001	0.91	5
	Johnston	1	6	-3.39	1.09	14.12	0.020	0.78	4
	Howland	1	8	-2.24	0.61	16.36	0.007	0.73	6
	Baker	1	7	-3.26	0.97	15.88	0.010	0.76	5
	Kingman	1	5	-6.27	1.82	47.05	0.006	0.94	3
	Palmyra	1	5	-5.22	1.58	51.17	0.006	0.94	3
	Teraina	1	6	-4.44	1.24	39.59	0.003	0.91	4
	Tabuaeran	1	5	-4.95	1.60	37.42	0.009	0.93	3
	Kiritimati	1	7	-3.08	0.89	30.61	0.003	0.86	5
	Jarvis	1	5	-3.81	1.33	38.11	0.009	0.93	3
	Malden	1	6	-4.70	1.42	25.30	0.007	0.86	4
	Starbuck	1	6	-4.42	1.47	54.89	0.002	0.93	4
	Millennium	1	7	-4.53	1.16	30.00	0.003	0.86	5
	Flint	1	5	-4.46	1.27	27.72	0.013	0.90	3
	Vostok	1	6	-3.20	0.94	21.40	0.010	0.84	4

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Chapter 3.

THE NON-LETHAL EFFECTS OF PREDATION ON THE LIFE HISTORY OF CORAL REEF FISHES FROM THE CENTRAL PACIFIC

ABSTRACT

It is widely recognized that removal of apex predators can have broad ecological consequences for terrestrial and aquatic communities. While the direct effects of predator removal have been of principal focus, the non-lethal effects of predator removal are oftentimes less well understood. In marine ecosystems, fisheries exploitation directly alters fish communities by targeting large-bodied predatory species. The direct effect of extraction leads to reductions in species diversity, abundance, and size-structure of the fish assemblage. Reductions of predatory species can lead to compensatory release of non-targeted species. Despite there being well-studied examples of trophic cascades in terrestrial and aquatic systems, comparable effects are less commonly observed in complex systems such as coral reefs. The removal of predatory species may not lead to increased prey abundance or well-defined trophic cascades on coral reefs but may still have important effects that strongly influence the ecology of these systems. We examine the putative effects of fishing and nearshore oceanographic productivity on the condition and life history of fishes across multiple trophic levels. To accomplish this we conducted a large-scale natural experiment across six central Pacific islands, targeting the most abundant (numerical/biomass) coral reef fishes representative of the region and investigated associated patterns in key life history traits of individuals across four major trophic groups (top-predator, mid-level carnivore, planktivore, and herbivore).

We found evidence of fisheries exploitation and oceanographic productivity in structuring the abundance and biomass of key taxa, as well as driving changes in the body condition, growth rates, maximum size and longevity of individuals. These patterns were variable among species and islands though revealed relative consistency among species within trophic groups. At some islands we saw strong biophysical coupling, with gradients in oceanographic productivity resulting in associated changes in the life history traits of certain fishes. In contrast, however, we also saw evidence for a breakdown of this natural coupling at inhabited islands, suggesting local human impacts are capable of homogenizing life history traits of fishes even when strong environmental gradients are present. These results highlight the complex role of human-induced change and natural gradients in environmental regimes in structuring coral reef fish communities.

INTRODUCTION

Predation is widely recognized as one of the most important forces driving evolution and population ecology (Elton 1927, Kerfoot and Sih 1987, Begon et al. 1996) and models describing predator-prey interactions are among the oldest in ecology (Volterra 1926, Gause 1935, Odum et al. 1971). These models can involve simple coupled systems where predators directly alter the population size or density of prey through consumption. In such systems, predator-prey interactions are cyclical and if prey are abundant the population of predators increases until resources (prey) become limited due to consumption. As predator densities decrease, prey populations are released from predation and the cycle resets. Coupled population models have provided invaluable insight into the direct (i.e. lethal) effects of predation through consumption and have been widely used in theoretical and empirical studies (Krebs 2001). The results of these efforts now serve as a foundation for much of our understanding of the lethal effects of predators in population ecology and evolutionary ecology (Murdoch et al. 2003).

In complex aquatic and terrestrial systems involving multiple species, predators occupy the top rung of the trophic ladder and exert strong top-down control over species occupying lower trophic positions. The removal of top predators can destabilize the ecosystem and lead to cascading effects that are evident down to the base of the food chain (Terborgh and Estes 2010, Estes et al. 2011). The process by which the removal of a top-predator indirectly leads to an increase in the food resource of the predator’s prey is widely referred to as a *trophic cascade* (Paine 1980, Terborgh and Estes 2010).

Trophic cascades have been widely documented in terrestrial and aquatic systems (Terborgh and Estes 2010). Perhaps the most well-known examples include the reintroduction of wolves to northern Yellowstone (Ripple et al. 2001, Ripple and Beschta 2012), the effects of the sea star (*Pisaster ochraceus*) in structuring rocky intertidal communities in the Pacific Northwest (Paine 1980), and the role of sea otters as a keystone species in kelp forest communities (Estes and Palmisano 1974, Estes and Duggins 1995). In all examples predators play a critical role in top-down processes and influence the structure and function of communities. Although trophic cascades are often a result of lethal effects of predation which leads to density-mediated alterations of prey, the role that predators play in structuring communities goes beyond consumptive effects (Peckarsky et al. 2008).

There is increasing evidence that the structure and function of ecological communities are not only influenced by lethal effects but are also strongly influenced by non-lethal effects (Schmitz et al. 2004, Preisser et al. 2005, Heithaus et al. 2008, Peckarsky et al. 2008). The non-lethal threat of predation drives prey species to develop or exhibit a diversity of behavioral, morphological, and life-history characteristics to reduce predation risk (Peacor and Werner 2001, Werner and Peacor 2003, Preisser et al. 2005). This development and counter-development of phenotypes across generations has been referred to as an ‘evolutionary arms race’ (Dawkins and Krebs 1979) and can represent costs to a species (Stearns 1976, Stearns 1989, Lima and Dill 1990). The evolutionary timescales by which prey evolve in response to predation can be considerable. However, within each phenotype exists a certain degree of plasticity that allows an organism to modify certain physical characteristics in response to predation (Pettersson and Bronmark 1997, Werner and Peacor 2003). These responses can occur over much shorter timescales and include changes in a species’ behavior (Lima 1998a), foraging (Madin et al. 2010), habitat use (Lima and Dill 1990), reproductive effort (Creel et al. 2007), growth rate (Peacor 2002, Arendt and Reznick 2005), size and age at maturity (Reznick et al. 1990), and morphology (Lively 1986). The costs associated with these responses can be significant and it is now evident through theoretical and empirical studies that the non-lethal indirect effects of predation play a critical role is structuring communities and may contribute to or even initiate trophic cascades (Werner and Peacor 2003, Schmitz et al. 2004, Preisser et al. 2005). Thus, the removal of predators from ecosystems can have important ecological and functional consequences that are manifested across multiple trophic levels.

Opportunities to examine the effects of predators in natural ecosystems have been confounded by the fact that most terrestrial and aquatic systems have witnessed a precipitous decline of predatory species (Jackson et al. 2001, Estes et al. 2011). However, conservation efforts to reintroduce predators in some terrestrial ecosystems over the last several decades has lead to the development of moderately intact animal communities and changes in community structure (Ripple et al. 2001, Ripple and Beschta 2004). Importantly, these conservation efforts have significantly advanced our understanding of the direct and indirect effects of predators in structuring terrestrial communities. Conversely, opportunities to study intact marine communities are limited, and much of our understanding of the role that predators play in structuring marine systems originates from studies that took place in ecosystems that were already significantly altered and where predator densities were far from historical baselines (Dayton et al. 1998, Jackson et al. 2001). This is particularly evident in tropical marine ecosystems where many of the early ecological studies were carried out long after reefs were degraded and predators were removed (Jackson 1997, Sandin et al. 2010).

Over the last decade expeditionary research efforts to explore remote coral reef ecosystems far from human population centers have identified intact ecosystems where predators are abundant (Friedlander and DeMartini 2002, Brainard et al. 2005, DeMartini et al. 2008, Sandin et al. 2008). By examining the differences between remote sites and sites near population centers, researchers have gained an understanding of the broad ecological effects of removing predators from coral reef ecosystems. Unexpectedly, at sites where predators are rare, coral reef fish assemblages have yielded little evidence in support of prey release or trophic cascades (Friedlander and DeMartini 2002, DeMartini et al. 2008, Sandin et al. 2008, Stallings 2009, Williams et al. 2011). Predator-prey interactions found on coral reefs are complex involving multiple species from different trophic levels. The trophic complexity and prevalence of non-linear food chains may suppress sequential prey release commonly exhibited in classical trophic cascades (Sandin et al. 2010). Despite there being little evidence of trophic cascades, these studies show that removal of top-level predators through fisheries exploitation alters the species composition, standing stock (biomass), and size-structure of the fish assemblage (see Chapter 2). Additionally, in systems where predators are abundant, large-bodied species are favored (DeMartini et al. 2008) resulting in the size-structure and longevity of the prey assemblage being shifted toward smaller younger individuals (Ruttenberg et al. 2011). These findings suggest that predators can indirectly affect the prey assemblage even when signs of prey release or trophic cascades are not evident (Ruttenberg et al. 2011). However, few ecological studies have examined the indirect effects of predation on the condition and life history of key species and functional groups in an intact ecosystem and over appropriate spatial scales (Persson et al. 1996). These characteristics are fundamental for assessing the indirect effect of predation and the mechanisms that drive changes in population and community structure.

In addition to the non-lethal effects of predation, coral reefs are exposed to biotic and abiotic forcings that influence the structure and function of the ecosystem (Brown 1997, Done 1999, Gove et al. 2013). Regional and local oceanography can influence patterns of nutrient delivery through upwelling and internal waves (Hatcher 1990, Leichter et al. 1998, Leichter et al. 2003). The strength and frequency of these bottom-up forcings influence primary productivity (chlorophyll-*a*) and thus represent an important flux affecting patterns of production and transfer of resources and energy transfer throughout the ecosystem. Ecological processes including the effects of predators work simultaneously with oceanographic processes to structure coral reef ecosystems in a process known as biophysical coupling.

Here we set out to build on the body of ecological work pertaining to the non-lethal effects of predators by conducting a large-scale natural experiment to examine the effects of predation, while explicitly considering abiotic effects of oceanographic productivity, on the condition and life history of fishes across multiple trophic levels. Based on previous theoretical and empirical ecological studies we set out to answer the question, do growth rates of fishes from lower trophic levels respond to the presence of predators and how do these effects embed within abiotic gradients in productivity? To answer this question we tested three conflicting predictions currently being debated by the ecological community.

First, at sites where predators are abundant, fishes from lower trophic levels may exhibit increased growth due to the increased threat of predation at small size classes. Evidence suggests predation favors rapid growth due to the existence of a refuge in size and the evolution of rapid growth should be ubiquitous in aquatic ecosystems because predatory fishes are often gape limited (Abrams et al. 1996, Arendt and Reznick 2005, Conover 2007). This pattern of rapid growth has been identified in surgeonfishes (Acanthuridae), one of the most common and ecologically important fishes found on coral reefs (Choat and Axe 1996). Second, at sites where predators are abundant, fishes from lower trophic levels may exhibit decreased growth due to trade-offs and life historical costs associated with avoiding predation. There is a growing body of evidence confirming the non-lethal effects of predator avoidance, the most acute and immediate costs being reduced foraging activity and energy uptake, which can result in reduced growth (Stearns 1989, Lima 1998a, Lima 1998b, Urban 2007). However, other factors besides non-lethal effects of predation including resource limitation or productivity (bottom-up) likely influence growth (Arendt and Reznick 2005, Ruttenberg et al. 2005). Third, the threat of predation has little-to-no effect on the growth of species from lower trophic levels. It has been suggested that in systems where a species is preyed upon or competes for resources with many different species, the optimal life history strategy may be to accept a moderate level of risk and adopt foraging behavior that leads to uniform growth (Sih 1992, Munch and Conover 2003). By testing these predictions we provide important insight into the mechanisms that structure marine communities and the direct and indirect effects of removing predators from marine systems. In such cases, we may expect a stronger influence of oceanography conditions on growth patterns.

MATERIALS AND METHODS

Study Area

To examine context specific changes in life history parameters on coral reef fishes, the northern Line Islands (NLI) were chosen as the study region. The NLI are located in the central tropical Pacific Ocean and span 750 km from 6.383° north latitude to 0.367° south latitude (Figure 3.1, Table 3.1). The NLI are comprised of six islands spanning a gradient of human habitation and associated fishing pressure. The unfished and intact islands Kingman, Palmyra, and Jarvis are U.S. territories, protected as U.S. National Wildlife Refuges [designated in 1974 for Jarvis and in 2001 for Kingman and Palmyra (Maragos et al. 2008a)] and are now incorporated as part of the Pacific Marine National Monument (Bush 2009). These designations include a strict ban on fishing activities, but it is likely fishing was rare to non-existent prior to receiving formal protection due to their remoteness (Zgliczynski et al. 2013). In contrast, Teraina, Tabuaeran, and Kiritimati of the Republic of Kiribati are inhabited and support subsistence and commercial fisheries (Sandin et al. 2008).

Although the islands are located within the same biogeographic region, the islands span a gradient of oceanographic productivity (Maragos et al. 2008b, Sandin et al. 2008). Jarvis, Kiritimati, and to a lesser extent Tabuaeran are influenced by upwelled nutrient-rich waters of the westward-flowing South Equatorial Current and the eastward-flowing Equatorial Undercurrent, while Kingman, Palmyra, and Teraina are geographically located in the path of the warmer oligotrophic waters of the North Equatorial Countercurrent. Islands therefore served as replicates and are structured by levels of human habitation (i.e. predator density) and oceanographic productivity.

Quantifying fish abundance and biomass patterns

Efforts to characterize the fish assemblages from the NLI were completed by researchers from SIO and the NOAA Coral Reef Ecosystem Division during expeditions taking place on an annual or biennial basis starting as early as 2000 (see DeMartini et al. 2008, Sandin et al. 2008, Williams et al. 2011). During these expeditions researchers used underwater visual census (UVC) methods to quantify densities and size distributions of non-cryptic diurnally active species. In summary, a pair of divers lays out a 25-m transect line and records the size and species of all fishes on each side of the transect. Each diver records fishes ≥20 cm (TL) within a 4-m wide swath on the outward leg of the transect, and all fishes <20 cm (TL) within a 2-m wide swath during the return leg of the survey. The dive teams typically conduct three belt transect surveys at each station, surveying a 600m^2 area for larger-bodied fishes and 300m^2 area for smaller-bodied fishes. Efforts were made to conduct surveys around each island with survey efforts focusing on fore-reef habitats along the 10-15m isobaths. Data from these surveys were summarized to identify the most abundant species (by number and by weight) observed the NLI (Table 3.2). Our aim was to use the results of visual censuses to select a subset of species representative of each major trophic group (top-predator, mesopredator, mid-level carnivore, planktivore, detritivore, and herbivore) from the central Pacific. Trophic groupings were assigned using online (Fishbase.org) and published sources (Randall 2005).

Eight species were sampled to represent the most abundant species in each trophic group. The twinspot snapper (*Lutjanus bohar*) is a top predator of seaward reefs of low islands and atolls in the Indo-Pacific feeding primarily on reef fishes, crustaceans, and cephalopods (Talbot 1960, Helfrich et al. 1968, Randall 1980, Wright et al. 1986). The darkfin hind (*Cephalopholis urodeta*) is a mesopredator found throughout the Indo-Pacific preying upon small fishes and crustaceans (Randall and Brock 1960). The arc-eye hawkfish (*Paracirrhites arcatus*) is a mid-level predator typically associated with small branching corals throughout the Indo-Pacific and feeds primarily on crustaceans, fish eggs, and small fishes (Randall 2005). The bicolor chromis (*Chromis margaritifer*) is a wide-ranging planktivore found on seaward reefs throughout Oceana. Bartlett's anthias (*Pseudanthias bartlettorum*) is a schooling planktivore inhabiting shallow (10-15m) seaward reefs in the central Pacific (Randall 2005). The bluespotted bristletooth (*Ctenochaetus marginatus*) is a roving detritivore inhabiting seaward reefs in the central and eastern tropical-Pacific. The goldrim surgeonfish (*Acanthurus nigricans*) is an aggressive roving herbivore that feeds on turf and filamentous algae along seaward reefs in the Indo-Pacific. Lastly, the golden Gregory (*Stegastes aureus*) is a territorial herbivorous damselfish endemic to the central Pacific. Together, these fish compromise 30% of the total mean fish abundance and 23% of total mean fish biomass observed during reef assessment and monitoring efforts from the region (Table 3.2).

Collection Methods

A series of land-based and ship-based collections were made from 2005-2011 to gather the requisite samples for this focused life-history study. The majority of fishes included were collected during a 5-week ship-based research cruise that visited 6 of the northern Line Islands October-November 2010 (Figure 3.1). During each expedition, a variety of methods was used to collect individual fish, including hand nets, 3-prong spears (i.e., Hawaiian slings), spearguns, handlines, fishing poles, and fish anesthetic (e.g. clove oil). We recruited assistance of local fishers on inhabited islands whenever possible. Fishes were collected along seaward/exposed reefs at each island/atoll at depths between 5 and 20m with most collections taking place along the 10m isobath. The target number of fish collected for each species-island combination was set based on the results of a power analysis that revealed that at a sample size of 50 would yield parameter estimates within 8% of the true values for 95% of the simulations. Therefore a target of 50 individuals across a range of body sizes for each species-island combination were collected to obtain a representative sample size range of fishes observed in the field and to complete estimates of growth and productivity.

Upon collection all species were stored on ice and brought back to the research ship or field station for initial processing. Each fish was assigned a unique identification tag and basic morphometric information was collected. Fish lengths were collected using digital calipers and included total length (TL), fork length (FL), and standard length (SL). Fishes not dissected in the field were stored individually in plastic bags and frozen.

Frozen fish samples were returned to the Fish Life History Lab at the Scripps Institution of Oceanography. Efforts were made to weigh all frozen fishes upon arrival at the lab prior to beginning the dissection protocol. Dissections included removal and examination of internal organs including gonads, intestines, stomach, and liver. Gonads were weighed and examined to assess reproductive state with assignment into one of 4 categories; immature (F1= no oocytes or spermatocytes present), immature female (F2= some undeveloped oocytes present), mature female (F3= developed oocytes present), and male (M= spermatocytes present).

Estimates of age for each fish were completed by removing sagittal otoliths and following procedures for preparing and reading transverse sections of otoliths as outlined by Choat and colleagues (Choat and Axe 1996, Choat et al. 1996, Choat et al. 2003a). In summary, the pair of sagittae were removed, rinsed and stored dry. One sagitta was weighed and measured across the vertical (dorsal to ventral) and horizontal (rostrum to post-rostrum) axis. The sagittae were mounted on the edge of microscope slides using thermoplastic cement (Crystalbond^{TM}). Sagittae were positioned on the edge of the slide to expose the rostrum but to keep the nucleus of the otolith protected on the slide. The exposed section of the otolith was ground down to the slide edge using a series of wet/dry polishing paper (400 grit [30µm] – 9µm in decreasing order) affixed to a wet grinding-polishing wheel (South Bay Technology INC. Model 900). The otolith was then re-heated on a hotplate and moved to the center of the slide and inverted so that the postrostrum was vertically oriented. The sagitta was then ground and polished to the nucleus using the same sequence as mentioned above. Once it was determined that the transverse section was polished sufficiently to expose increments, a layer of Crystalbond^{TM} was applied to cover and improve optical quality of the section. Sagitta sections were examined under a dissection microscope using transmitted light and the maximum objective to fit the sectioned otolith in the frame. A digital image was captured of each sectioned otolith and a scale bar with unique fish identification number added to each image to facilitate future increment assessment. Images of sectioned sagittae were examined using imaging software (Image J) and opaque bands along the dorsal and ventral axis of the otolith were counted as annuli to estimate age of individuals. Estimates of age were evaluated by two observers using the percentage agreement (PA) method and images were re-examined if readings differed by more than 10%. Otoliths were removed from this assessment if readers could not reach a consensus <10% (or ≤1 year, for age estimates less than 10 years).

Fish fresh frozen-thawed

Due to the difficulty of collecting accurate fish body weight data in the field, specifically when working aboard a moving vessel, the majority of fishes collected for this study were frozen shortly after collection and transported back to the Life History Lab at the Scripps Institution of Oceanography. However, recent efforts to understand the effects of various preservation techniques on the body length and weight of fishes have shown that freezing can lead to changes in weight estimates (Hay 1984, Ajah and Nunoo 2003, Florin and Lingman 2008, Ogle 2009). To account for the effects of freezing on the body weight of the taxa targeted for this study, we compared the fresh weight to post-frozen weight across a variety of individuals collected in land-based field expeditions. Changes in fish weight (g) were expressed in terms of percentage weight loss for each individual specimen and a mean percentage was calculated for each species. Due to high surface-to-volume ratios, smaller fishes lost a greater proportion of weight during the freezing process.

To facilitate weight conversions, a statistical model of weight loss was constructed relative to frozen weight. In particular, the change in weight (weight fresh - weight frozen) was log-transformed and plotted against log-transformed frozen weights, resulting in a robust linear model. All assumptions of linear regression were met. The linear model was fitted through the values and coefficients of determination (R^2), intercept (α_1), and slope (α_2) were estimated for each species based on allometry and the following equation:

$$\ln(\Delta W) = \ln(\alpha_1) + \alpha_2 \ln(W_{Frozen}), \tag{3.1}$$

supporting a power function,

$$\Delta W = \alpha_1 W_{Frozen}{}^{\alpha}{}_2, \tag{3.2}$$

where ΔW is the changes in weight of the fish (grams) and W_{Frozen} is the frozen weight (g) of the fish. No appreciable differences in parameter estimates were observed across species of differing body sizes. Therefore, we re-ran the model incorporating all of the fish species and calculated a mean estimate to be used as the conversion factor for all species across all body weights. We estimated the conversion factors to be: $\alpha_1 = 0.0946$ (SE 0.0063), $\alpha 2 = 0.5620$ (SE 0.0147), and the $R^2 = 0.705$. Thus, fishes collected for this study that lacked initial weights from the field could have their frozen weights converted to initial 'fresh' weights using the following equation:

$$W_{Fresh} = W_{Frozen} + \alpha_1 W_{Frozen}{}^{\alpha}{}_2 \tag{3.3}$$

Data Analyses

Using the output results of *in situ* belt transect surveys, we compared the biomass of major fish trophic groups among reefs, comparing means from inhabited *versus* remote islands using a one-way analysis of variance (ANOVA) with island means serving as replicates. Normality was confirmed using the Anderson-Darling test and homoscedasticity (equal variance among groups) was verified using Bartlett's test. We further examined variations in the mean abundance and biomass of the eight targeted coral reef fish species identified above using a Kruskal-Wallis test (due to the non-normal nature of the data) and subsequent pairwise comparisons using a Kruskal Nemenyi test. All analyses were completed using R 3.1.1 (R Development Core Team, http://www.r-project.org) and the package PMCMR.

To test for an effect of island on differences in fish body condition across our study system, we used a one-way analysis of covariance (ANCOVA) using log-transformed fish mass (g) as the response variable, island as a fixed factor, and log fish length (mm) as the covariate. The ANCOVA performed on log-transformed data thus represents a test of the allometric body function:

$$W = \alpha L^{\beta}, \tag{3.4}$$

where W and L are the weight and length for an individual fish at each island, respectively, and α and β are the island-specific allometric constants. If the ANCOVA reveals a significant interaction between islands and SL, posthoc inspection falls upon values of β. Alternatively, if the are significant island effects with no interaction, posthoc inspection falls on values of α, island-specific allometric constants.

For those species showing no significant interaction between island and the covariate *(C. urodeta, P. arcatus, S. aureus*), we re-calculated the ANCOVA with the interaction term removed. For the remaining five fish species showing significant interactions in the ANCOVA, we report their mean slope values by island from the linear model.

Species-specific growth was estimated for each island using the von Bertalanffy growth function (VBGF):

$$L_t = L_{inf}(1 - \exp([-K(t - t_0)]), \tag{3.5}$$

where L_t is the standard length (SL) at age t, L_{inf} is the theoretical maximum mean (asymptotic) length if species of interest lived indefinitely, K is the growth coefficient that describes the rate at which asymptotic length is attained, t is age in years, and t_0 is the theoretical age for which length is 0 (King 1995, Jennings et al. 2009). Although we made efforts to collect fishes across a range of body sizes, we constrained t_0 to 0 for all species-island combinations due to limited samples, particularly for the smaller size-age classes. We compared species-specific growth rates for each species-island combination and fitting size-at-age data using the VBGF. We also compared the growth parameters K and L_{inf} among islands by plotting 95% confidence ellipses around each parameter estimate (Kimura 1980, Choat et al. 2003b).

RESULTS

Spatial patterns of fish abundance and biomass

Overall fish biomass as estimated by underwater visual censuses was observed to be higher at remote (mean = 338.9 g/m^2) than at inhabited (mean = 120.8 g/m^2) islands ($F_{1,4}$=12.86, p = 0.023) (Figure 3.2, Table 3.3). In particular, sharks were rare at inhabited islands and the mean biomass of top predatory fishes was higher at remote (81.9 g/m^2) than at inhabited (12.6 g/m^2) islands ($F_{1,4}$=67.12, p = 0.001). All other trophic groups (mid-level carnivores, planktivores, and herbivores) did not differ between remote and inhabited islands.

Exploration of underwater visual census data comparing fish abundance and biomass patterns across islands for the eight target fish species yielded varied yet significant effects of island (Table 3.4). The top-predator *L. bohar* was more abundant at Kingman and Palmyra (two of the remote islands) than all other islands, supporting a clear gradient in predatory fish biomass (Figure 3.3). Conversely, the mid-level carnivore *C. urodeta* was least abundant at Kingman and Palmyra and tracked oppositely of *L. bohar*, suggesting mesopredator release (Figure 3.3). Unlike *C. urodeta*, the mid-level carnivore *P. arcatus* showed variable patterns of abundance and biomass, with no clear distinction between remote and inhabited islands. For the planktivore *P. bartlettorum*, abundance and biomass tracked with oceanic productivity, peaking at Kiritimati and Jarvis. Similarly, *C. margaritifer* abundance and biomass also appeared to track with productivity, peaking at Kiritimati but showing low abundance and biomass at Jarvis, suggesting potential competition for resources with the conspecific *P. bartlettorum*. The three herbivore species showed variable patterns in abundance and biomass across islands, without clear signals of productivity or human habitation influencing patterns (Figure 3.3).

Patterns of fish life history parameters

A total of 2807 coral reef fishes representing eight species and six trophic groups were collected across the northern Line Islands (Table 3.2). In each species there were significant and variable patterns of body condition across islands. Of the eight species, three of them (*C. urodeta, P. arcatus, S. aureus*) showed no significant interaction between the factor *island* and the covariate *standard length* (Tables 3.5 and 3.6), but an independent effect of each factor, indicating isometric differences in body condition (as indicated by the model intercepts) across islands (Figure 3.4). Interestingly, these three species represented the smallest body sized fish within each trophic group (*C. urodeta, P. arcatus* - mid-level carnivores; *S. aureus* – territorial herbivore). When the mean body condition of each of the three species was ranked alongside increasing productivity, no clear pattern emerged (Figure 3.4). The remaining five species showed a significant interaction between the factor *island* and the covariate *standard length* (Table 3.5), indicating differences in allometric growth across islands (Figure 3.5). Further examination of the model slopes (β) for each fish species exhibited no systematic pattern across islands However, for three species, a loose scaling appeared present between allometric scaling (a proxy for body condition) and increasing island productivity (Figure 3.5). For the herbivore *A. nigricans* and the planktivore *C. margaritifer*, body condition appeared to track positively with island productivity. Conversely, the planktivore *P. bartlettorum* appeared to track negatively with island productivity. The remaining two species, the top-predator *L. bohar* and the herbivore-detritivore *C. marginatus*, showed no systematic changes in body condition with island productivity.

Of the 2807 fishes collected, 2308 were processed and incorporated into the size-at-age assessments outlined below. Across species, there was a wide variation in potential longevity and body size. The large-bodied top-predator *L. bohar* exhibited the greatest longevity, with some individuals reaching up to 30 years of age (Figure 3.6). The two mid-level carnivores *P. arcatus* and *C. urodeta* were estimated to be up to 14 and 15 years of age, respectively, but *C. urodeta* in general reached a larger length than *P. arcatus* (17.9 versus 10.6 cm maximum SL, respectively) (Figure 3.6). The two planktivore species, *C. margaritifer* and *P. bartlettorum,* reached similar maximum standard lengths (6.3 and 6.6 cm maximum SL, respectively), however the maximum longevity of *C. margaritifer* individuals were estimated to be twice that of *P. bartlettorum* (14 versus 7 years of age). The three herbivores included in the study ranged in body size and age (Table 3.7). The maximum longevity of *S. aureus* and *C. marginatus* was estimated to be 15 and 17 years of age, respectively while *A. nigricans* individuals were estimated to live up to 26 years of age (Table 3.7).

Exploration of the VBGF across all species-island combinations revealed significant differences in growth rates and longevity across islands (Figure 3.7). The top-predator *L. bohar* exhibited similar growth rates and longevity across islands with the exception of Kiritimati, the most densely human populated island in the study system. Here *L. bohar* exhibited the highest growth rates (K), but the overall lowest L_{inf} and longevity (Figure 3.7). The mid-level carnivore *C. urodeta* exhibited similar growth rates (K) and longevity across islands with the exception of Teraina, the least densely populated island of the three inhabited islands. Here *C. urodeta* had the fastest growth rates (K), but the overall lowest L_{inf} and longevity (Figure 3.7). The other mid-level carnivore *P. arcatus* showed little variation in growth rates (K) across islands with the exception of Palmyra, where longevity was reduced, but individuals exhibited the fastest growth rates (K) (Figure 3.7). In contrast, *P. arcatus* exhibited large variation in L_{inf} and longevity across islands. At Jarvis, the most productive island, individuals reached the greatest L_{inf}, however this was not a consistent pattern with island productivity as Kiritimati, also one of the most productive islands, harbored individuals with among the lowest L_{inf} (Figure 3.7).

For the planktivores *P. bartlettorum* and *C. margaritifer*, patterns of growth (K) and L_{inf} tracked opposite across islands. *P. bartlettorum* exhibited the slowest growth but reached a greater L_{inf} at the most productive islands (Jarvis and Kiritimati), while *C. margaritifer* exhibited the lowest L_{inf} and generally a faster growth rate (*K*) at the most productive islands. Patterns in longevity of the two planktivore species were variable across islands with no clear signal of human population status or changes in island productivity (Figure 3.7).

For all three herbivore species *S. aureus, A. nigricans*, and *C. marginatus*, there were no clear differences in longevity of individuals across islands, however differences in growth rates (*K*) and L_{inf} were apparent between remote and inhabited islands. Across remote islands, all three species exhibited slower rates of growth, but greater L_{inf} with increasing island productivity. In contrast, rates of growth and L_{inf} appeared homogenous (clustered) across inhabited islands for all three herbivore species, with no clear effect of either population status or island productivity (Figure 3.7). For all three species, specimens from inhabited islands consistently revealed higher *K* or L_{inf} relative to the estimates from remote islands.

DISCUSSION

The northern Line Islands provide a natural experimental setting in which to examine the putative effects of fishing and nearshore oceanographic productivity on the condition and life history of fishes across multiple trophic levels. Using six islands spanning ~750 km of latitude, we targeted the most abundant (numerically/biomass) coral reef fishes representative of the region and looked at changes in key life history traits of individuals across four major trophic groups (top-predator, mid-level carnivore, planktivore, and herbivore). In short, we found evidence of fisheries exploitation and oceanographic productivity in structuring the abundance and biomass of key taxa, as well as driving changes in the body condition, growth rates, maximum size and longevity of individuals. These patterns were variable among species and islands, highlighting the complex role of human-induced change and natural gradients in environmental regimes in structuring coral reef fish communities. At some islands we saw strong biophysical coupling, with gradients in oceanographic productivity resulting in associated changes in the life history traits of certain fishes. In contrast, we also saw evidence for a breakdown of this natural coupling at inhabited islands, suggesting local human impacts are capable of homogenizing life history traits of fishes even when strong environmental gradients are present.

Fisheries exploitation can have profound impacts to coral reef fish assemblages by altering the species composition, standing stock (biomass), and size-structure of the communities (Friedlander and DeMartini 2002, DeMartini et al. 2008, Sandin et al. 2008, Richards et al. 2012). Because fisheries typically target large-bodied species, even moderate levels of exploitation can result in dramatic changes to the abundance and overall biomass of the assemblage. We found clear and consistent evidence for the top-down effects of fisheries exploitation on the top-predator *Lutjanus bohar*. First, the abundance and biomass of *L. bohar* was significantly reduced at inhabited islands when compared to remote islands. Second, although we found no consistent differences in the body condition of *L. bohar* across islands we found striking evidence of the direct effects of fisheries exploitation on the life history traits of this top-predator. At Kiritimati, the most densely populated island in the archipelago, *L. bohar* were observed to reach a significantly smaller maximum size (L_{inf}) and age compared to other moderately inhabited or remote islands. This finding is further supported by previous efforts to document changes in fish assemblage structure in the Line Islands; DeMartini et al. (2008) found body size frequency distributions of the top-predator *L. bohar* to be dominated by smaller size-classes at Kiritimati with effectively no individuals found above the minimum size for sexual maturity. In addition to *L. bohar*, we observed reduced maximum size (L_{inf}) and longevity of the mid-level carnivore *C. urodeta* at Teraina. Whether this finding is suggestive of direct fisheries exploitation, however, remains unclear. Anecdotal observations suggest that while hook-and-line fishing is ubiquitous across all three inhabited islands, spearfishing is only common on Teraina. Perhaps gear-specificity influences the life history patterns of *C. urodeta*. While targeted top-predatory species, such as *L. bohar*, echoed clear effects of fisheries exploitation, the effects of natural gradients in oceanographic productivity were less apparent. In contrast, we saw little evidence for the effects of fisheries exploitation on fishes from lower trophic levels, but clear evidence for changes in their life history traits as a result of associated shifts in mean oceanographic productivity.

Changes in environmental regimes, specifically oceanographic productivity, can affect food resource availability and influence abundance, biomass, growth, longevity and overall survivorship of reef fishes (Jones 1986, Forrester 1990, Ruttenberg et al. 2005). In this study, we found clear and consistent evidence of such bottom-up, biophysical coupling on both the abundance and biomass patterns as well as life history traits of several fish species examined. The abundance and biomass of the two planktivore species, *Pseudanthias bartlettorum* and *Chromis margaritifer*, generally tracked positively with increasing oceanographic productivity. *P. bartlettorum*, however, was generally more abundant than *C. margaritifer* (with the exception of Kingman) (Figure 3.3). The inter-island variation of *P. bartlettorum* was striking, as the species showed a spike in abundance and biomass at Jarvis, the most productive island, and was near absent at Kingman, the island with the lowest overall productivity. Interestingly, the life history traits of the planktivores were opposite from one another. *P bartlettorum* exhibited slower growth, lower longevity, but reached a greater maximum size (L_{inf}) with increasing productivity, while *C. margaritifer* exhibited faster growth, greater longevity, but reached a smaller maximum size (L_{inf}) across the same gradient. These findings suggest that these planktivores may exhibit a tradeoff between length and condition. As well as the influence of productivity, the basic ecology and behavior of these two planktivores may also influence their life history patterns. *P. bartlettorum* is a gregarious schooling species forming groups of 100s to 1000s of individuals along seaward reefs (Myers 1991, Randall 2005). In contrast, *C. margaritifer* generally forms loose aggregations of 10s of individuals and can become even more dispersed across the reef landscape at larger size classes (Myers 1991, Randall 2005). As such, there are likely density effects, inter-specific competition, and niche partitioning occurring between these two species which may affect species-specific life history responses to oceanic conditions.

In contrast to the predatory and planktivorous fish species, the abundance and biomass of herbivores lacked any consistent or clear effects of fisheries exploitation or natural gradients in oceanic productivity. However, similarly to both planktivore species, all three herbivore species showed strong evidence of biophysical coupling between changing oceanic productivity and key life history traits. Across remote islands, *Stegastes* *aureus*, *Acanthurus nigricans*, and *Ctenochaetus marginatus* all reached a larger maximum size (L_{inf}) at the most productive islands, suggesting positive effects of increased primary productivity. Coral reefs are characteristically oligotrophic and therefore regional or localized increases in resource availability, such as allochthonous food supply, can have considerable influence over the structure and function of these diverse ecosystems (Jones 1986, Forrester 1990).

For example, in the Galapagos, Ruttenberg et al. (2005) showed the damselfish *Stegastes bebei* to exhibit a greater maximum length, to occur at higher densities, and display greater longevity at islands where food resources were more abundant. However, the strong biophysical coupling between oceanic productivity and growth capacity (L_{inf}) of the herbivore species evident across our three remote islands broke down across the three inhabited islands. Here maximum lengths were homogenous across a clear gradient in oceanic productivity; the fishes' life history traits no longer reflected changes in the surrounding background environment. Such a process has been termed biophysical decoupling, whereby local human impacts act to breakdown or change the predictable relationships between aspects of the biological community and the surrounding physical environment (Williams et al. 2015). In this instance, many of the local human impacts that exist across the Line Islands act, either through direct or indirect means, to increase the relative abundance of fleshy macroalgae (Sandin et al. 2008), the key energetic resource for these herbivorous fishes. In the absence of resource limitation, however, changes in oceanic productivity appear to become less important in structuring the life history traits of particular coral reef fishes.

Alternatively, the reductions of the predator assemblage at the inhabited islands could act to release herbivorous prey species from the chronic threat of predation (with associated behavioral and physiological consequences). Such prey release would similarly lead to a release of growth limitations for those species. Regardless of the mechanism, there was consistent evidence across herbivorous species of release of constraints to growth (i.e., increase in K or L_{inf}) on inhabited relative to remote islands. Whether a function of food availability, reduced predation risk, or some unique combination, we see a consistent release of life historical constraints linked to local human activities. To our knowledge, such shifting ecology associated with human activities is a novel observation in studies of life history.

Conclusion

Efforts to understand the influence of the non-lethal effects of predators and environmental variability on the demography and life historical traits of tropical marine fishes have increased over the past decade. However, to date, most ecological studies have been limited to a focus on a single species or conducted over limited spatial scale. We build upon the body of ecological work pertaining to the non-lethal effects of predators and environmental variability by conducting a large-scale (6 islands spanning 750 km) natural experiment examining the effects of predation and oceanographic productivity on the condition and life history of fishes across multiple trophic levels. We observed consistent changes in the body condition, growth rate, maximum size, and longevity of individual species. Importantly, these patterns were not consistent across trophic levels and highlights the complexity of non-lethal effects of predators and environmental variability in structuring the most fundamental characteristics and dynamics of coral reef fish assemblages.

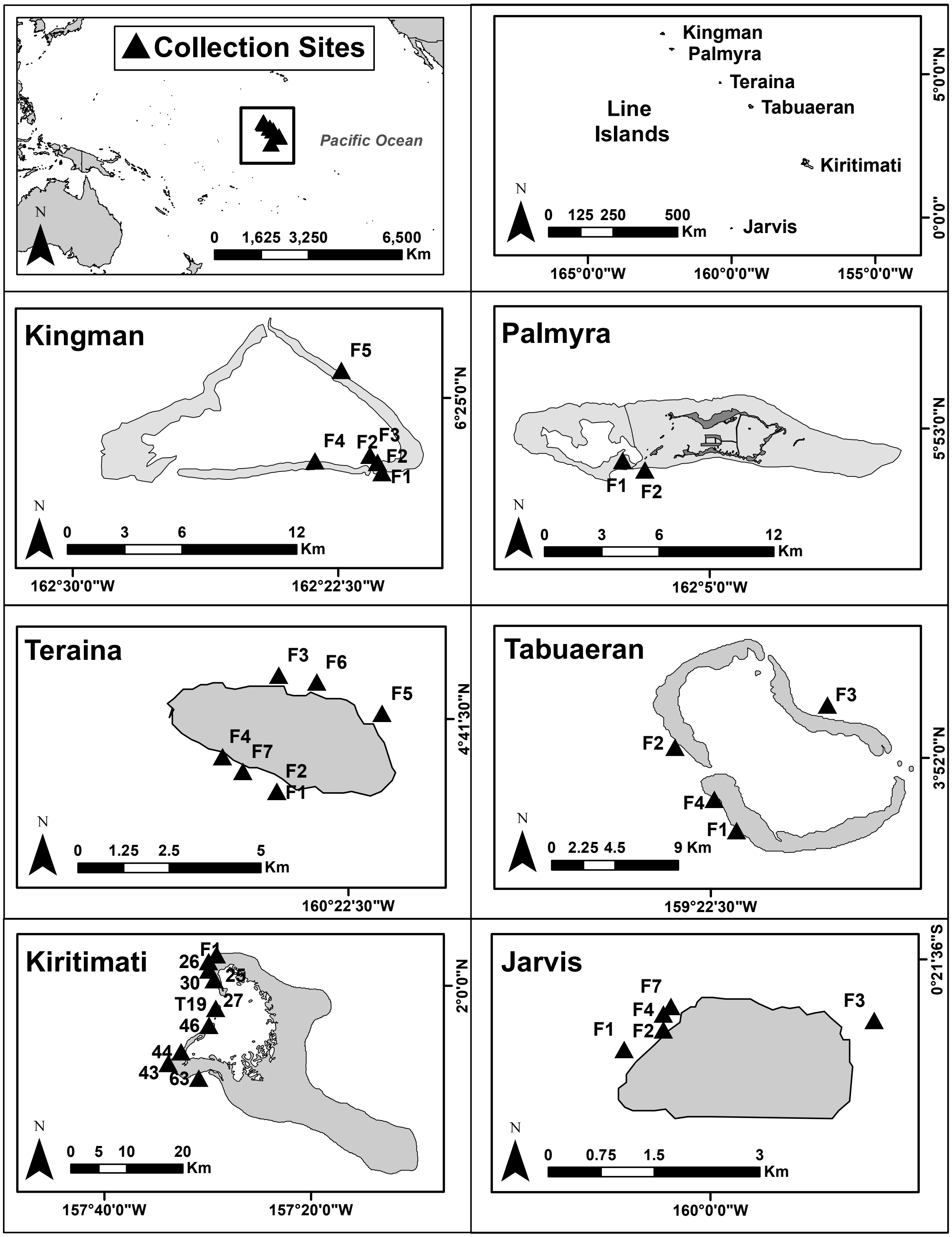

Figure 3.1. Map of the northern Line Islands identifying the dive sites where targeted collections were carried out for this study.

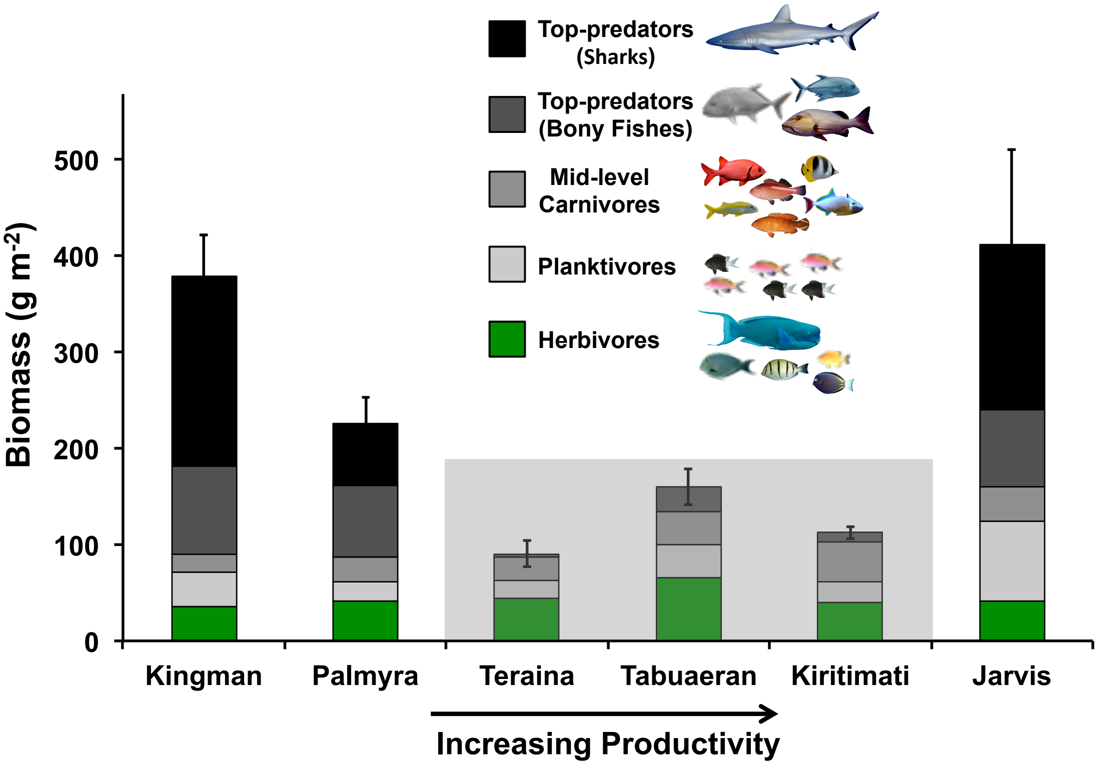

Figure 3.2. Mean fish biomass by trophic group across the northern Line Islands. Vertical bars indicate ± 1 SE (for total biomass). Shaded region of plot indicates inhabited islands. Productivity (chlorophyll-*a*) gradient increases towards the equator from north to south.

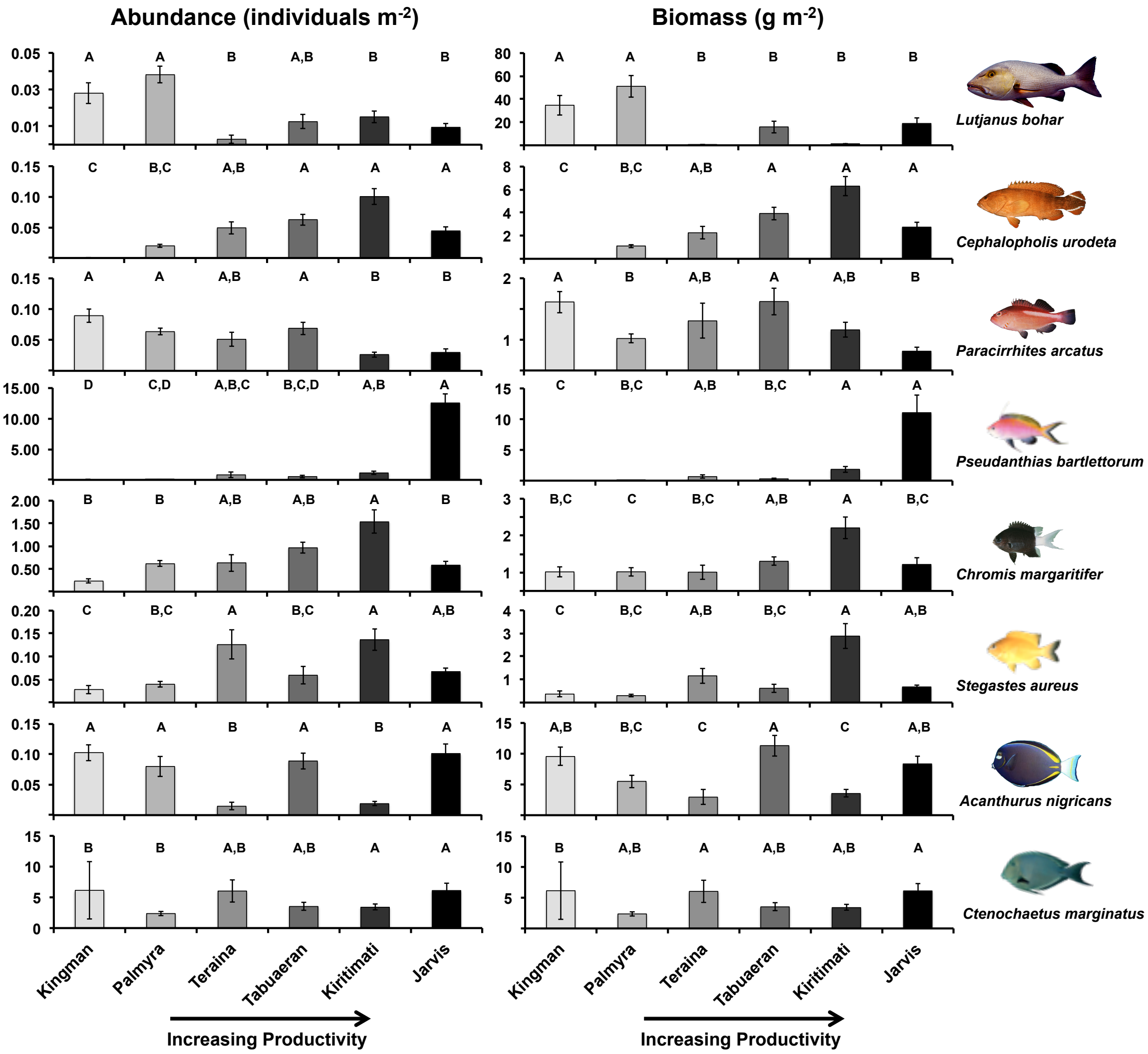

Figure 3.3. Comparisons of fish abundance and biomass for the 8 targeted coral reef species across the 6 northern Line Islands. Data are means with error bars ±SE. Letters above bars indicate island groupings based off of post-hoc analysis. Bars are shaded to indicate gradient on oceanographic productivity (chlorophyll-*a*).

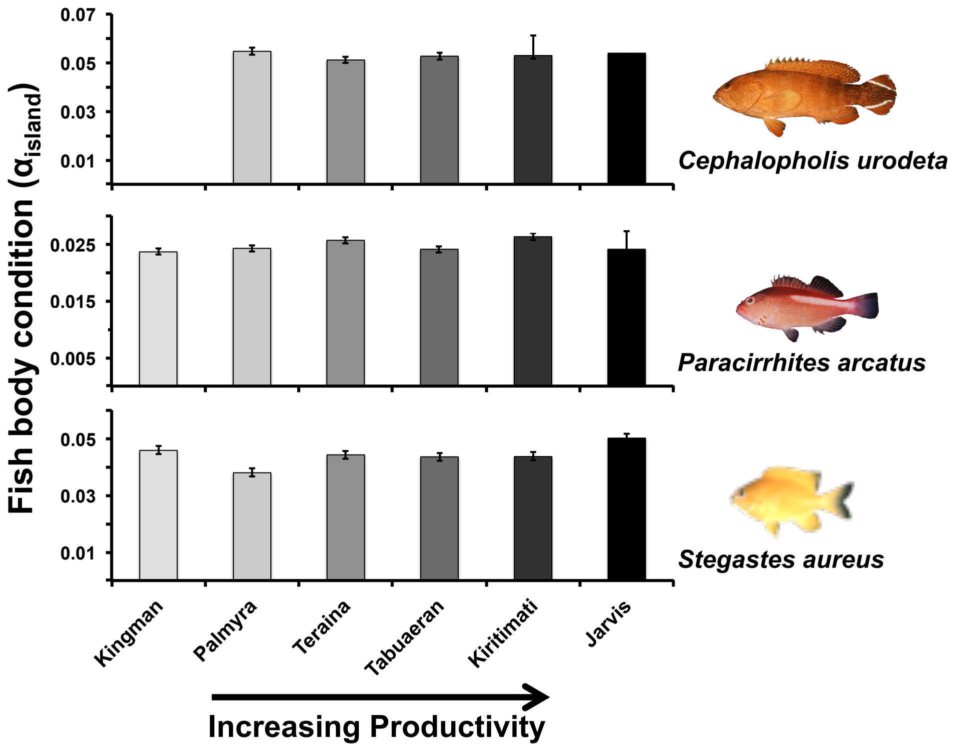

Figure 3.4. Coral reef fish body condition across the 6 northern Line Islands. Data are mean α_{island} values with error bars ±SE for the three species where no interaction was observed (ANCOVA). Bars are shaded to indicate gradient on oceanographic productivity (chlorophyll-*a*).

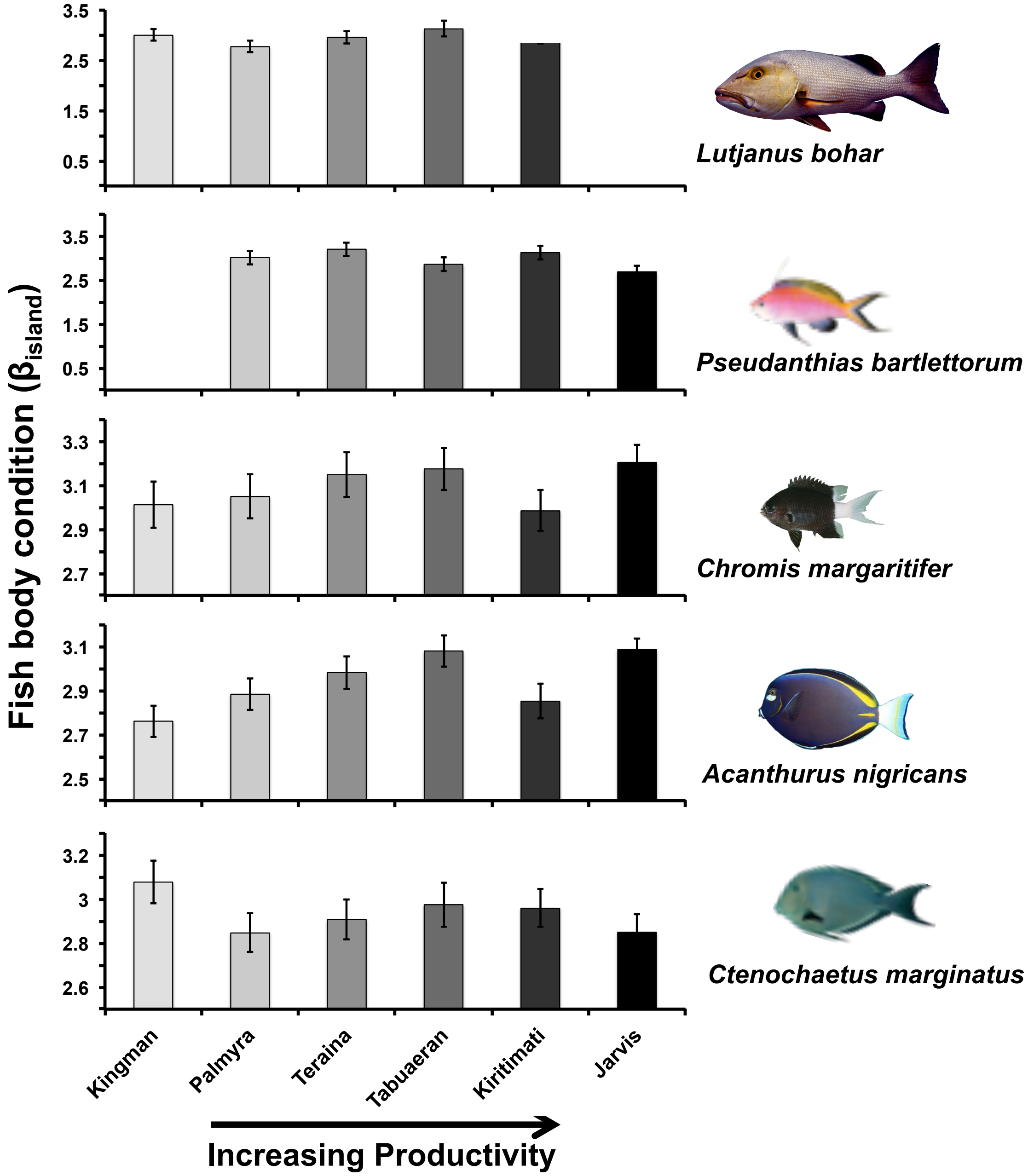

Figure 3.5. Coral reef fish body condition across the 6 northern Line Islands. Data are mean β_{island} values with error bars ±SE. Bars are shaded to indicate gradient on oceanographic productivity (chlorophyll-*a*).

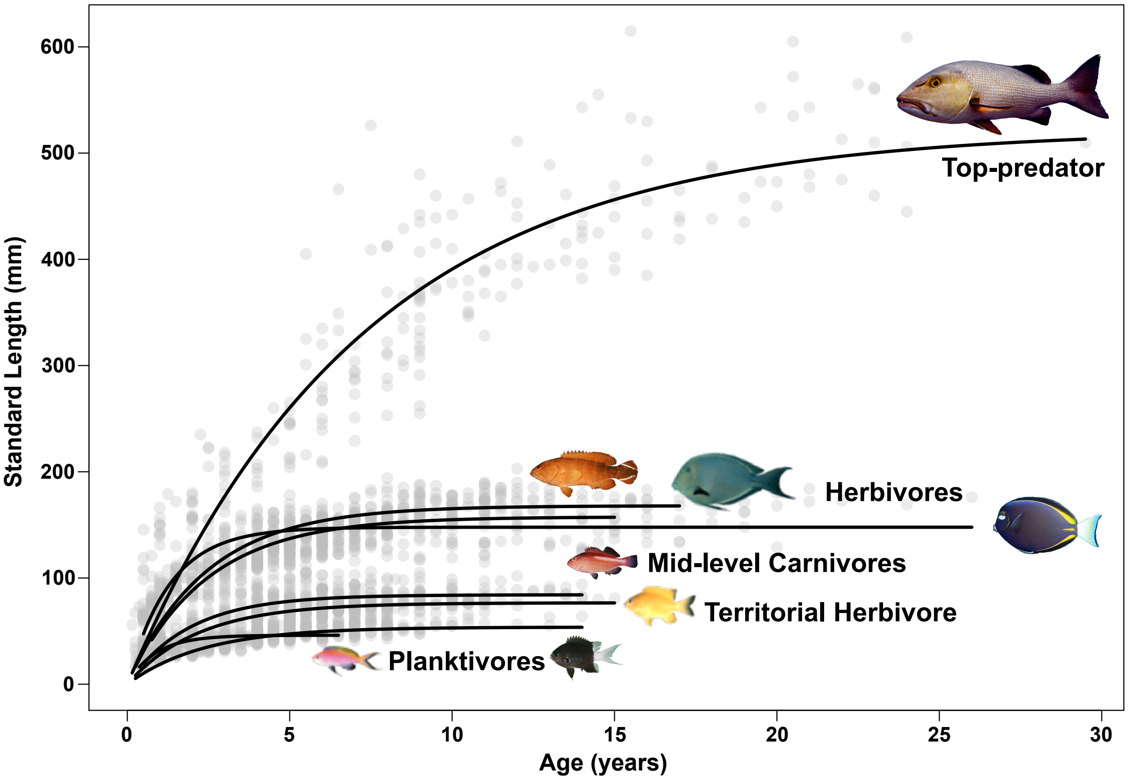

Figure 3.6. Von Bertalanffy growth function (VBGF) fitted to size-at-age data for the 8-targeted coral reef fish species plotted across all 6 northern Line Islands.

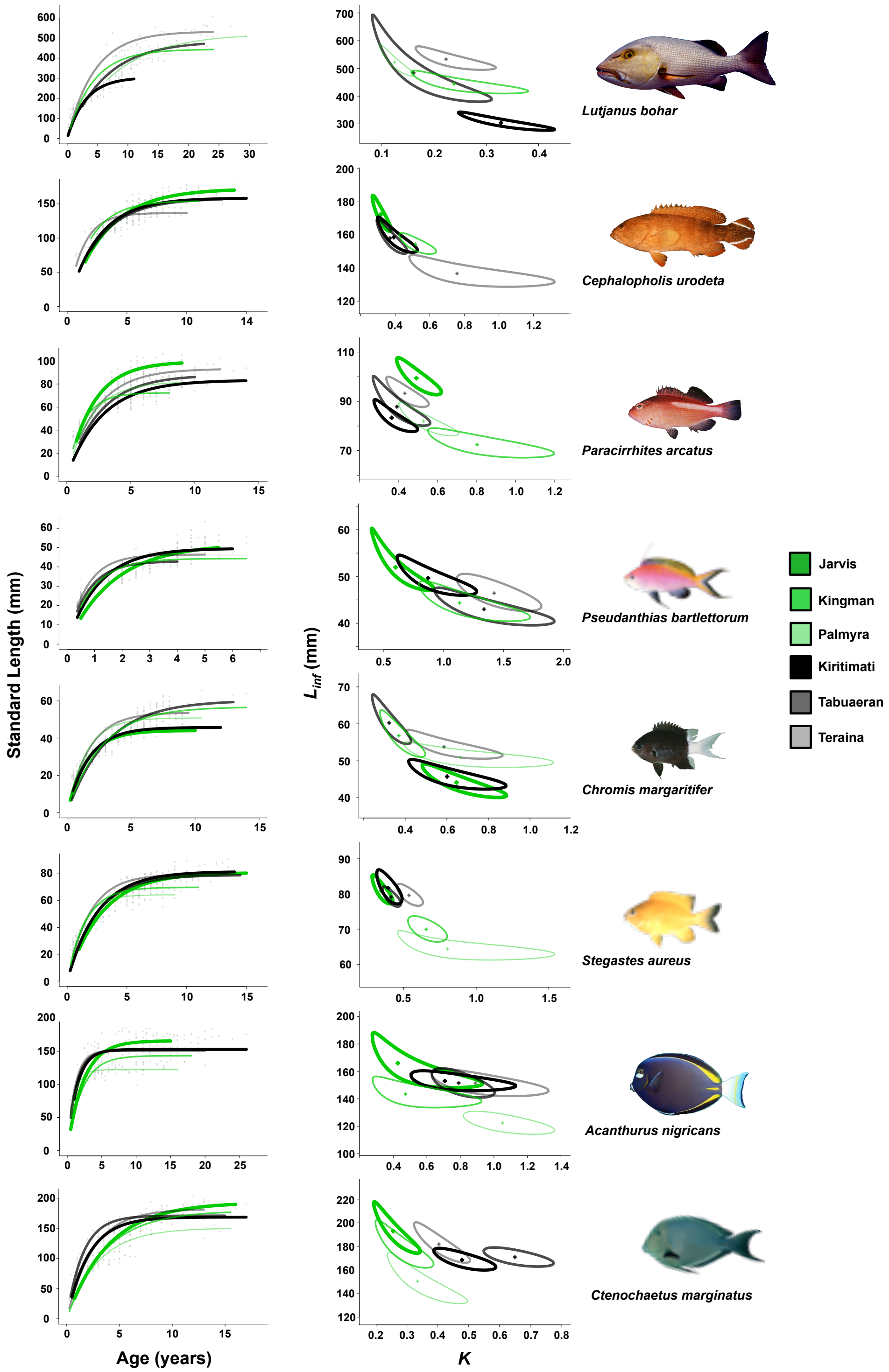

Figure 3.7. Von Bertalanffy growth function (VBGF) fitted to size-at-age data for the 8-targeted coral reef fish species plotted across all 6 northern Line Islands (left panel). Life history parameters, growth coefficient (K) and maximum size (L_{inf}) plotted using 95% confidence ellipses around each parameter estimate following Kimura (1980).

Table 3.1. Island-specific metadata indicating the location of fish collection efforts.

Island	Site Name	Latitude	Longitude
Kingman	F1	6.381	-162.354
	F2	6.386	-162.357
	F3	6.390	-162.360
	F4	6.387	-162.386
	F5	6.430	-162.374
Palmyra	F1	5.871	-162.110
	F2	5.872	-162.111
Teraina	F1	4.674	-160.393
	F2	4.674	-160.393
	F3	4.702	-160.392
	F4	4.682	-160.406
	F5	4.693	-160.367
	F6	4.701	-160.383
	F7	4.679	-160.401
Tabuaeran	F1	3.826	-159.350
	F2	3.876	-159.383
	F3	3.876	-159.309
	F4	3.841	-159.360
Kiritimati	F1	2.026	-157.498
	46	1.936	-157.498
	43	1.875	-157.564
	44	1.894	-157.543
	63	1.852	-157.514
	T19	1.964	-157.487
	25	2.050	-157.486
	27	2.010	-157.489
	30	2.026	-157.498
	26	2.039	-157.499
Jarvis	F1	-0.372	-160.011
	F2	-0.367	-160.006
	F3	-0.368	-159.979
	F4	-0.369	-160.006
	F7	-0.366	-160.005

Table 3.2. Data summary of the most abundant (number and biomass) fish species observed during research expeditions to the Line Islands from 2001-2010. Values are given as means with values outside of parentheses indicating the number of fish collected and the values within parentheses indicating the number of fish otoliths processed for size-at-age comparisons.

									Regional contribution to:	
Trophic Group	**Family**	**Species**	**Jarvis**	**Kiritimati**	**Tabuaeran**	**Teraina**	**Palmyra**	**Kingman**	**Total Fish Adundance (%)**	**Total Fish Biomass (%)**
Top-predator	Lutjanidae	*Lutjanus bohar*	4 (4)	91 (65)	19 (19)	33 (33)	61 (57)	41 (41)	0.31	16.71
Mid-level carnivore	Serranidae	*Cephalopholis urodeta*	54 (51)	83 (64)	56 (55)	49 (49)	71 (62)	11 (11)	0.38	0.91
	Cirrhitidae	*Paracirrhites arcatus*	51 (49)	63 (57)	50 (47)	51 (51)	66 (63)	66 (61)	0.61	0.29
Planktivore	Serranidae	*Pseudanthias bartlettorum*	53 (52)	65 (55)	49 (48)	62 (50)	93 (51)		19.57	0.77
	Pomacentridae	*Chromis margaritifer*	53 (50)	122 (49)	59 (50)	60 (50)	83 (49)	63 (50)	7.92	0.35
Territorial herbivore	Pomacentridae	*Stegastes aureus*	55 (50)	68 (55)	55 (50)	55 (50)	70 (55)	57 (50)	0.56	0.29
Herbivore	Acanthuridae	*Acanthurus nigricans*	52 (50)	75 (69)	55 (48)	57 (50)	72 (43)	61 (49)	0.73	2.63
Herbivore-detritivore		*Ctenochaetus marginatus*	52 (50)	85 (46)	66 (50)	58 (50)	80 (50)	52 (50)	0.43	1.45
		Total	374 (356)	652 (460)	409 (367)	425 (383)	596 (430)	351 (312)	30.50	23.41
		Mean Chlorophyll-*a* (mg m^{-3})	0.2	0.17	0.16	0.15	0.13	0.13		
		Total Reef Fish Abundance (# m^{-2})	27.79 (3.74)	11.82 (0.70)	6.61 (0.61)	7.56 (0.80)	3.52 (0.18)	3.82 (0.32)		
		Total Mean Reef Fish Biomass (g m^{-2})	412.02 (98.08)	112.29 (6.26)	159.51 (18.28)	90.45 (13.98)	225.86 (27.22)	378.82 (42.50)		
		Total Mean Top-predator Biomass (g m^{-2})	256.62	29.53	37.31	12.26	155.55	365.79		
		Mean Percent Algal Cover	39	58	54	52	43	32		

Table 3.3. Analysis of variance (ANOVA) outputs testing for an effect of island (n=6) on the mean biomass (g m^{-2}) of coral reef fishes representing five trophic groups from the northern Line Islands.

Response variable	Factor	DF	Sum.Sq	Mean.Sq	F value	P value
Total fish biomass	Predators	1	71373	71373	12.86	0.023*
	Residuals	4	5548	5548		
Top-predator biomass	Predators	1	7218	7218	67.12	0.001**
	Residuals	4	430	108		

Table 3.4. Kruskal-Wallis outputs testing for an effect of island (n=6) on the abundance and biomass of eight species of coral reef fishes from the northern Line Islands.

Species	Kruskal-Wallis chi-squared	P value
Abundance		
Lutjanus bohar	86.26	<0.001
Cephalopholis urodeta	87.5	<0.001
Paracirrhites arcatus	48.88	<0.001
Chromis margaritifer	16.83	0.004
Pseudanthias bartlettorum	136.79	<0.001
Stegastes aureus	50.2	<0.001
Acanthurus nigricans	56.79	<0.001
Ctenochaetus marginatus	36.75	<0.001
Biomass		
Lutjanus bohar	97.62	<0.001
Cephalopholis urodeta	85.37	<0.001
Paracirrhites arcatus	29.33	<0.001
Chromis margaritifer	25.03	<0.001
Pseudanthias bartlettorum	130.78	<0.001
Stegastes aureus	55.72	<0.001
Acanthurus nigricans	33.97	<0.001
Ctenochaetus marginatus	25.22	<0.001

Table 3.5. Analysis of covariance (ANCOVA) outputs testing for an effect of island (n=6) on the body condition (ln mass) of eight species of coral reef fish from the northern Line Islands while controlling for variations in fish standard length (SL, covariate).

Species	Model	SS	MSS	F	P-value
Lutjanus bohar	Island	0.7	0.2	15.37	<0.0001
	SL	482.4	482.4	39,621.61	<0.0001
	Island:SL	0.4	0.1	7.25	<0.0001
Cephalopholis urodeta	Island	0.15	0.04	1.87	0.1157
	SL	189.87	189.87	9744.69	<0.0001
	Island:SL	0.17	0.04	2.17	0.072
Paracirrhites arcatus	Island	0.52	0.1	7.23	<0.0001
	SL	206.83	206.83	14,326.34	<0.0001
	Island:SL	0.03	0.01	0.46	0.804
Chromis margaritifer	Island	1.3	0.3	11.75	<0.0001
	SL	388.5	388.5	17,159.78	<0.0001
	Island:SL	0.3	0.1	2.36	0.04
Pseudanthias bartlettorum	Island	3.31	0.83	33.97	<0.0001
	SL	217.18	217.18	8922.87	<0.0001
	Island:SL	0.41	0.1	4.23	0.0024
Stegastes aureus	Island	2.2	0.4	21.02	<0.0001
	SL	568.9	568.9	26,767.17	<0.0001
	Island:SL	0.1	0	1.1	0.359
Acanthurus nigricans	Island	1.57	0.31	24.94	<0.0001
	SL	283.58	283.58	22,585.56	<0.0001
	Island:SL	0.41	0.08	6.50	<0.0001
Ctenochaetus marginatus	Island	0.8	0.2	7.45	<0.0001
	SL	678	678	29,906.78	<0.0001
	Island:SL	0.4	0.1	3.2	0.01

Table 3.6. Analysis of covariance (ANCOVA) outputs testing for the independent effects of island (n=6) and fish standard length (SL) on the body condition (ln mass) of eight species of coral reef fish from the northern Line Islands.

Species	Model	SS	MSS	F	P-value
Cephalopholis urodeta	Island	0.15	0.04	1.84	0.12
	SL	189.87	189.87	9596.44	<0.0001
Paracirrhites arcatus	Island	0.52	0.1	7.29	<0.0001
	SL	206.83	206.83	14,442.13	<0.0001
Stegastes aureus	Island	2.2	0.4	20.99	<0.0001
	SL	568.9	568.9	26,727.81	<0.0001

Table 3.7. Von Bertalanffy growth function (VBGF) parameters for the 8 targeted species across all 6 northern Line Islands using length-at-age data and length-weight data. The α values represent the intercept and the β values represent the slope generated from using a linear model and allometric growth equation (3.3) with r^2_{LW} based on fitted line. All fish Standard Length data (SL_{min}, SL_{max}) and L_{inf} values are given in mm and estimated Age_{max} values are given in years.

Species	α	β	r^2_{LW}	SL_{min}	SL_{max}	Age_{max}	L_{inf}	K	r^2_{VBGF}	Total
Lutjanus bohar	0.0317	2.9670	0.99	29.6	609.0	30	509.5	0.14	0.82	249 (219)
Cephalopholis urodeta	0.0536	2.7604	0.97	24.1	179.0	15	156.4	0.42	0.67	324 (292)
Paracirrhites arcatus	0.0235	3.1537	0.97	25.2	106.0	14	84.2	0.53	0.64	347 (328)
Pseudanthias bartlettorum	0.0230	3.1981	0.95	19.7	63.4	7	46.1	1.16	0.73	322 (256)
Chromis margaritifer	0.0418	3.0855	0.98	15.5	65.7	14	53.7	0.43	0.79	440 (298)
Stegastes aureus	0.0386	3.1343	0.98	17.7	91.1	15	76.6	0.46	0.88	360 (310)
Acanthurus nigricans	0.0625	2.9042	0.98	58.0	185.0	26	147.8	0.78	0.70	372 (309)
Ctenochaetus marginatus	0.0558	2.9283	0.99	23.0	203.0	17	168.0	0.41	0.79	393 (296)

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Chapter 4.

THE TROPHIC STRUCTURE OF CORAL REEF FISHES ACROSS GRADIENTS OF OCEANOGRAPHIC PRODUCTIVITY AND PREDATORY FISH BIOMASS

ABSTRACT

Predator-prey interactions and the drivers that influence the structure and function of food webs have long been the focus of ecological studies. Early efforts to understand these interactions organized connections between predators and prey in to a series of links or chains. As the field of ecology advances through the use of novel tools and empirical studies it is becoming increasingly evident that food webs of complex communities are comprised of a framework of interactions involving multiple species across trophic levels rather than a series of links or linear chains. Using stomach contents and stable isotope analyses, we conducted a large-scale natural experiment across six central Pacific coral reefs to investigate the relative importance of predatory fishes and oceanic productivity in structuring a complex marine system. We found trophic overlap between fish species to be somewhat limited and in contrast to the common expectation of a complex topology among trophic groups. Instead, our results showed that different basal sources of energy entering the system can remain isolated on coral reefs, forming distinct trophic pathways up through the food web to top-level carnivores; we term this process *trophic channeling*. Importantly, trophic channeling occurred from two different basal sources of energy, namely allochthonous zooplankton delivery and sunlight fueled primary production. These two energetic pathways contributed unequally to carnivore end-members and this finding was consistent across geographical variations in oceanic

productivity. In fact, our results indicate that the trophic structure of coral reef fish species are more tightly linked to changes in oceanographic productivity than to predatory fish abundance. Further our observations challenge the notion of integrated and distinct trophic roles on coral reefs. In sum our findings provide important insights into the trophic dynamics of a complex marine systems and serve as a catalyst for myriad of additional research questions and field experiments to increase our understanding of marine food webs.

INTRODUCTION

Ecologists have long recognized the importance of predator-prey interactions and consumer-resource relationships in structuring ecological communities. Early efforts to understand these interactions and relationships focused on identifying the trophic connections or diversity of prey items consumed by groups of species (Elton 1927). Organizing these connections into chains or simple food webs based on an individual's trophic niche provided ecologists with important insights into community structure (Paine 1980), the flow of energy (Lindeman 1942), and the importance of top-down and bottom-up control within food webs (Polis and Strong 1996). Many of these classic studies serve as the foundation for our understanding of trophic structure of terrestrial and aquatic systems. However, as the field of ecology evolves, traditional views of food webs, as a series of linear chains with clear distinctions between trophic niches, are put into question (Polis and Strong 1996).

Considering communities across gradients of ecosystem development provides an opportunity to broaden our understanding of trophic dynamics. Ecological theory suggests that as a system matures through successional processes, the food web becomes more complex, heterotrophy and omnivory become more prevalent, and the ecosystem becomes more stable (Odum 1969). It can therefore be predicted that an ecologically mature system would exhibit more complex food webs with less distinction among trophic groups. Recent theoretical models (Bascompte et al. 2005) and food web studies (Thompson et al. 2007) suggest that distinctions between trophic groups (i.e. herbivores feeding on primary producers, predators feeding on grazers, etc.) may be less prevalent in complex systems, and generalist or omnivorous feeding strategies may be more widespread among species than previously expected (Polis and Strong 1996). Further, it has been suggested that a system containing omnivorous species exhibits increased ecosystem stability (Fagan 1997, McCann and Hastings 1997, Holyoak and Sachdev 1998), is more energy efficient (Polis and Strong 1996), and may experience a reduced likelihood of trophic cascades (Bascompte et al. 2005). As such, efforts to examine the trophic dynamics of successionally mature and complex ecosystems provide a critical end-member for understanding trophic interactions among species.

Complex ecosystems, by definition, support a wide range of species with diverse trophic ecologies that can exploit varying basal sources of energy. These sources of energy can travel through food webs via different energetic pathways depending on the number of trophic interactions present within the system. In complex communities where there is high trophic overlap between consumers (i.e. omnivory), there may be few opportunities for isolated trophic pathways to be realized (Thompson et al. 2007). This is particularly the case in communities where food chains are long and consumer species have a greater potential to consume prey items across multiple trophic levels (Thompson et al. 2007). Alternatively, if trophic overlap between consumers is limited, basal signatures of energy can remain isolated and channeled up to top-level carnivores through distinct trophic pathways. For example, McCauley et al. (2012) showed distinct trophic pathways can emerge in the diets of predatory coral reef fishes due to differential resource use across reef habitats (McCauley et al. 2012). While most trophic models are structured principally around size-based models of trophic flow (larger organisms eating smaller organisms), few have considered the potential for structured trophic flow as a function of basal energy source. To address this question, we explore patterns of trophic flow and connections within a series of complex and predator-rich replicate ecosystems – coral reef fish assemblages of the remote central Pacific.

Coral reefs as a model ecosystem –

Coral reefs are among the most complex and biodiverse ecosystems on the planet, and therefore provide invaluable opportunities for ecologists to study food web structure and trophic dynamics of a complex community. However, there are several challenges associated with studying the trophic ecology of complex coral reef ecosystems. First, coral reefs are comprised of species assemblages that exhibit broad flexibility in diet, and omnivory can be found ubiquitously across trophic levels (Randall 1967). The lack of discrete trophic levels among species makes it difficult to identify true trophic connections and create a detailed, topological depiction of trophic linkages. For example, many top-predatory fishes subsidize a piscivorous diet with invertebrate prey or may forage in multiple habitats beyond shallow coral reefs (McCauley et al. 2012). Additionally, many mid-to-low-trophic level carnivores may opportunistically or incidentally feed across traditional trophic boundaries while feeding on micro-invertebrates that seek refuge in algal turfs or coralline algae (Randall 1967). Similarly, subtle distinctions among fish species that forage upon the same benthic habitats can result in diets classified as principally herbivorous through to principally detritivorous (Choat et al. 2002, Crossman et al. 2005).

Second, coral reefs span vast geographic ranges and are exposed to diverse biotic and abiotic forcings that influence the structure and function of the ecosystem (Brown 1997, Done 1999, Gove et al. 2013). For example, local oceanographic conditions, such as currents and internal waves, can deliver important sources (via upwelling) of allochthonous nutrients and planktonic resources (Hatcher 1990, Leichter et al. 1998, Leichter et al. 2003). Additionally, nearshore water flow patterns can influence the recycling of autochthonous sources of nutrients and plankton to the reef including detritus, eggs, and larvae (Andrews and Gentien 1982, Pineda 1991, Wolanski and Delesalle 1995, Leichter et al. 1998, Leichter et al. 2003). The magnitude and frequency of these events directly affects primary productivity and the strength of bottom-up forces that structure coral reef communities (Polis and Strong 1996). Together these bottom-up forces can vary temporally and spatially, and confound efforts to describe the trophic dynamics of coral reef communities.

Lastly, it has been widely documented that coral reefs have been significantly impacted through a host of anthropogenic activities (Jackson et al. 2001, Pandolfi et al. 2005, Knowlton and Jackson 2008, Munday et al. 2008). Fisheries alone have had a profound effect on the trophic dynamics of coral reefs (Jennings and Polunin 1996, Jennings and Kaiser 1998, Pauly et al. 1998, Dulvy et al. 2004). Fisheries are often size-selective targeting the large-bodied species that typically occupy higher trophic levels (Roberts 1995, Polunin and Roberts 1996, Graham et al. 2005). Therefore, even moderate levels of exploitation can have marked effects by reducing the size-structure and trophic composition of the fish assemblage. Ecological theory suggests that reductions in top predators on coral reefs should lead to the release of prey species in response to reduced predation, resulting in direct shifts in density of prey species (i.e., prey release) or in the more extreme alternating shifts in density of prey and the prey’s prey (i.e. trophic cascade) (Sandin et al. 2010). Beyond evidence of direct effects of predators, there are many examples of indirect, top-down effects influencing the trophic dynamics of coral reefs. For example, reductions in predatory species by fisheries exploitation can lead to changes in foraging ecology (Madin et al. 2010a, Madin et al. 2010b) or the trophic niche (Layman et al. 2007) of species from lower trophic levels. Thus, the mere presence or absence of predators can alter the trophic dynamics of the system; and fished reefs provide an altered depiction of food web structure.

Here we conduct a large-scale natural experiment to examine the trophic structure of key coral reef fish species representing multiple trophic groups across six islands in the remote central Pacific. The Northern Line Islands represent an ideal study system to explore the quantitative shifts in trophic dynamics across strong gradients in predator abundance, ranging from unfished and thus late-successional through to fished and thus less predator-heavy and trophically complex. Further, these islands span a gradient of oceanic productivity, from moderately oligotrophic through to relatively nutrient-rich. Using stable isotope techniques ($\delta^{13}C$ and $\delta^{15}N$), we investigate the relative importance of predators (top-down) and oceanographic productivity (bottom-up) in structuring a complex marine system (Figure 4.2). Importantly, we included analysis of eight locally abundant fish species that represent a large proportion of the total fish assemblage, and thus we report on not only species-specific patterns but also patterns of trophic coupling across these islands. We demonstrate that the isotopic composition of coral reef species are more tightly linked to changes oceanographic productivity than to abundance of predators, though we find that the relative isotopic position (and putative trophic relationships) remains consistent across contexts. Further we challenge the notion that coral reef food webs are well-mixed, but instead we demonstrate a pattern of ‘trophic channeling' which represents coherent yet discrete patterns of flow permeating the trophic structure of reef fish assemblages.

MATERIALS AND METHODS

Study Sites

To examine the trophic dynamics of key species across gradients of predatory fish biomass and oceanographic productivity, we conducted a large-scale natural experiment across six northern Line Islands located more than 1500 km south of the Hawaiian Archipelago in the central equatorial Pacific (Figure 4.3). Teraina, Tabuaeran, and Kiritimati are part of the Republic of Kiribati and contain human population densities ranging from several hundred to several thousand people (DeMartini et al. 2008, Sandin et al. 2008). Fishing serves as the primary source of livelihood for island residents with hook and line, spearfishing, and hand-nets (Kiritimati supports multiple aquarium fish exporters) being the most common methods. In contrast, Kingman, Palmyra and Jarvis are uninhabited U.S. possessions protected from fishing as part of the U.S. Pacific Remote Islands Marine National Monument and the U.S. Fish and Wildlife Service Pacific Reefs National Wildlife Refuge Complex (Maragos et al. 2008a, Bush 2009). As such these protected islands contain some of the most intact coral reef ecosystems in the Pacific (DeMartini et al. 2008, Sandin et al. 2008). Efforts to compare coral reef fish assemblages across the northern Line Islands have revealed stark differences between inhabited and uninhabited islands (DeMartini et al. 2008, Sandin et al. 2008). At uninhabited islands, total fish biomass is 2-4 times higher than at inhabited islands, with top-predators comprising the highest proportions of fish biomass (Table 4.1). Conversely, fish assemblages at inhabited islands are comprised of smaller-bodied species from lower-trophic levels. Importantly, there is only limited evidence of prey release associated with changes in top-predator density (DeMartini et al. 2008). Thus, the gradient in top-predator abundance observed across the northern Line Islands provides an ideal setting to examine the trophic structure and function of a complex system in response to changes in predator density and influence.

The northern Line Islands are also exposed to a latitudinal gradient of oceanographic productivity, whereby sea surface temperature increases and nutrient concentrations decrease with increasing latitude (Figure 4.1, Table 4.1) (Altabet 2001, Maragos et al. 2008b, Sandin et al. 2008, Gove et al. 2013). At the regional scale, Jarvis, Kiritimati, and to a lesser extent Tabuaeran, are influenced by upwelled nutrient-rich waters of the westward-flowing South Equatorial Current and the eastward-flowing Equatorial Undercurrent, while Kingman, Palmyra, and Teraina are geographically located in the path of the warmer oligotrophic flow of the North Equatorial Countercurrent. Additionally, Jarvis and Kiritimati are influenced by localized upwelling events as a result of the eastward flowing Equatorial Undercurrent coming into contact with steep island topography (Gove et al. 2006). By including variations in oceanography across the six northern Line Islands we evaluate the role of oceanography in structuring the trophic dynamics of coral reef fish assemblages.

Fish Collections

To examine context-specific changes in the trophic dynamics of fishes from the northern Line Islands, we collected samples of eight of the most abundant coral reef species representing each major trophic group (top-predator, mid-level carnivore, planktivore, detritivore, and herbivore). Sample collections took place during a five-week research cruise to the northern Line Islands between October and November 2010. Target species were identified based on the results of underwater visual censuses (belt-transect surveys) to characterize fish assemblages (abundance, biomass, and size-structure) during previous expeditions across the northern Line Islands (DeMartini et al. 2008, Sandin et al. 2008). Based on these surveys we selected the following species (with trophic group): *Lutjanus bohar* (Top-predator), *Cephalopholis urodeta* (Mid-level carnivore), *Paracirrhites arcatus* (Mid-level carnivore), *Chromis margaritifer* (Planktivore), *Pseudanthias bartlettorum* (Planktivore), *Stegastes aureus* (Territorial herbivore), *Acanthurus nigricans* (Herbivore), and *Ctenochaetus marginatus* (Herbivore-detritivore). Together these 8 species provide an overall representation of the fish assemblages from the region as they account for 30% of total fish abundance and 23% of the total fish biomass (Table 4.1). A target number of 10 individuals across a range of body sizes were collected at each island to obtain a representative sample for each species-island combination. In some cases targeted species were collected during previous research expeditions (Ruttenberg et al. 2011, Walsh et al. 2012), and in an effort to minimize impacts to coral reef communities, we made use of these samples.

Collections were designed to minimize effects of environmental noise and ontogentic variation on the inter-island comparisons. To limit the confounding effects of habitat and wave exposure on species distributions and trophic dynamics, we made efforts to collect a majority of specimens along leeward forereef habitats of all islands at depths between 8-15 m. Infrequently and due to the challenges associated with conducting remote fieldwork, sea conditions prevented access to leeward sites and the team was forced to complete collections at patch reef or backreef habitats until sea conditions subsided. To minimize potential changes in isotopic signal with body size, efforts were made to constrain the size classes of individual species-island combinations in order to control for ontogenetic dietary shifts by selecting samples based off of the regional median total length (TL) for each species using the results of underwater visual censuses. A section of muscle tissue was removed from the left dorsal region of each fish for stable isotope analysis. Tissue sample consisted of 0.05-1.0 grams of muscle tissue (weight of sample depended on fish size) and was stored dry in a microcentifuge tube and frozen until stable isotope analysis could be completed.

Stomach Contents Analysis

To evaluate the relative contribution of prey items to the diet of each targeted species we used stomach content analyses. For the carnivores (*L. bohar*, *C. urodeta*, and *P. arcatus*), we removed all stomach contents and weighed each food item individually to create a mean weight of item consumed (all food items combined). To characterize diet composition, we estimated what proportion of this total weight was made up of different prey items. Prey items were defined as broad taxonomic groups. For the planktivores (*C. margaritifer* and *P. bartlettorum*), diet composition was based on the relative abundance of food items in the stomach, again assigned to broad taxonomic groups. For the herbivores (*S. aureus, A. nigricans*, and *C. marginatus*), diet composition was, like the planktivores, based on relative abundance of food items in the stomach. However, due to the difficulty of identifying algae that have undergone partial digestion to a high taxonomic resolution, all algae were assigned to one of three functional group categories, namely early stage algae (e.g. low-lying turf algae), late stage algae (e.g. upright fleshy seaweeds), and calcified algae (e.g. encrusting algae that contained $CaCO_3$). Additionally for herbivores, food items were also classified into the invertebrate and sand categories.

Stable Isotope Analysis

Approaches used to identify trophic position or niche width in marine systems have traditionally relied on stomach content analysis (Hyslop 1980, Bearhop et al. 2004), which offers an invaluable tool for identifying the types of prey and the general feeding habits of a consumer (Randall 1967). However, this approach provides only a snapshot of feeding habits and may reflect inaccurately the diet or trophic position of target species, especially for carnivores that switch prey sources frequently or that consume items that are digested at different rates (Jennings et al. 2002a). To address some of the challenges associated with studying the trophic ecology of coral reef fishes, stable isotope analysis has become increasingly popular for estimating trophic niche and describing the flow of energy through ecological communities (Peterson and Fry 1987).

Here we use stable isotopes to evaluate and describe changes in trophic structure of key coral reef species across gradients of oceanography and predator density across the northern Line Islands. Stable isotope ratios in the muscle tissues (proteins) of consumers reflect the isotopic values of the food consumed (Hobson 1999). The ratio of nitrogen isotopes (^{15}N to ^{14}N) exhibits an stepwise enrichment with each trophic level and can be used to estimate an organisms trophic position (Fry 2006), as the tissues of consumers tend to be between 2.5 and 4.0 per mil ($^{0}/_{00}$) greater than those of their diets (Peterson and Fry 1987). Ratios of carbon isotopes (^{13}C to ^{12}C) change little with trophic transfers and can therefore be used to identify sources of dietary carbon (Post 2002, Bearhop et al. 2004). However, our aim in this assessment was to examine the trophic structure of coral reef fishes and therefore our interpretation solely focuses on the $\delta^{15}N$ values; $\delta^{13}C$ values are only graphically reported. Presenting mean signatures of $\delta^{13}C$ - $\delta^{15}N$ of an organism or population in bi-plot space can provide important information regarding trophic position, food web structure, and niche width (Post 2002, Layman et al. 2005, Layman et al. 2007).

Frozen tissue samples from the 8 fish species-island combinations served as the source for stable isotope data. Sample analysis followed standard protocols (Post 2002, Post et al. 2007, Michener and Lajtha 2008) and was completed at the Boston University Stable Isotope Laboratory or the Scripps Institution of Oceanography Mass-Spectrometry Lab. In summary, frozen tissue samples were first freeze-dried for 24 hours to remove moisture and then ground to a fine powder using a mechanical grinder mill (Wig-L-Bug®). A 1.0-1.25 mg sample of powdered tissue was weighed out (to nearest 0.01 mg) in a tinfoil cup using a precision microelectric balance and subsequently encapsulated in their respective tinfoil cup. Individual samples were then flash combusted at 1800ºC in a Eurovector Carbon and Nitrogen elemental analyzer and the combustion products (CO_2, N_2 and H_2O) were separated chromatographically and introduced into GVI IsoPrime isotope ratio mass spectrometer, with water removed using a magnesium perchlorate water trap. Stable isotope ratios of nitrogen (^{15}N to ^{14}N) and carbon (^{13}C to ^{12}C) were expressed as the relative per mil (‰) difference between the samples and international standards (Vienna PDB carbonate and N_2 in air, respectively). Values were reported in δ notation where δ^{15}N or δ^{13}C ratios were expressed by the equation:

$$\delta^{15}\text{N or }\delta^{13}\text{C} = \left[\frac{R_{sample}}{R_{stondard}} - 1\right] \times 1000, \tag{4.1}$$

where R is $^{15}N/^{14}N$ or $^{13}C/^{12}C$, respectively. To increase sample accuracy, one replicate per 10 samples as well as any initial anomalous results were rerun. To ensure consistent combustion among sample replicates, a known standard (e.g. peptone, a hydrolyzed animal protein from Sigma Chemical Company, glycine, or citrus leaves, SRM 1572) was run after every 15 consecutive samples. If the known standard yielded results 0.15 ‰ above or below the documented standard value, the samples preceding the standard were rerun.

Marine macroalgal samples served to characterize the base of nearshore coral reef habitat. We selected *Halimeda* sp. as the focal algal group for analysis because it is both the most abundant macroalgal taxon found in the northern Line Islands (Sandin et al 2008) and is the only group found in high densities consistently across the islands. Samples were collected from each island/atoll in the vicinity of the fish collection sites and brought back to the research vessel to be dried and stored individually in labeled sample bags. To prepare samples for stable isotope analysis, a small segment (~ 1.0 g) of each sample was cut near the tip of new growth. A total of 20 individual segments were collected from each island. For analysis, *Halimeda* sp. samples were placed in pre-labeled cleaned (acid washed using 5% HCl) 15 ml falcon tubes. Samples were then de-calcified by adding ~5 ml of 5% HCl to each falcon tube. After 24 hrs the HCl solution was decanted and an additional 5 ml of 5% HCl was added to each falcon tube to ensure de-calcification of samples had taken place. The HCl solution was again decanted and samples were rinsed by adding ~10 ml of DI water to each falcon tube, capped, and gently shaken. The DI water was decanted and the process was repeated 3 times to ensure most of the HCl solution had been removed. Samples were then placed on labeled clean (combusted at 450°C for 12 hrs) aluminum weigh boats and placed in drying oven at 60°C for 72 hours. Samples were then removed from the drying oven and ground to a fine powder using a mechanical grinder mill (Wig-L-Bug®). A 1.4-1.6 mg sample of powdered *Halimeda* sp. was weighed out (to nearest 0.01 mg) in a tinfoil cup using a precision microelectric balance and subsequently encapsulated in their respective tinfoil cup. Individual samples were then processed through a mass spectrometer as outlined above to obtain stable isotope values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$).

Estimates of Oceanographic Productivity - Satellite derived data

Satellite-derived data were used to estimate island-specific measures of productivity (chlorophyll-*a*) following methods outlined by Gove et al (2013). In summary, we calculated mean chlorophyll-*a* (mg m^{-3}) for each island using freely available satellite derived data using Moderate Resolution Imaging Spectroradiometer (MODIS; http://modis.gsfc.nasa. gov/). Means were calculated by averaging eight-day chlorophyll-*a* values for each island over the time period 2002-2014. A masking routine was used to estimate the nearshore chlorophyll-*a* values along the 30 m isobath or a distance of 250m from the reef crest around each island and to omit any contaminated data associated with island or lagoon reflectance inshore of the 30-m isobath or directly adjacent to each pixel (Gove et al. 2013).

Data Analyses

Stable isotope data (means and standard deviation) were plotted in $\delta^{13}C$ - $\delta^{15}N$ bi-plot space for each island-species combination as well as macroalgae to visualize measures trophic structure. To test for an effect of the presence of predators and variations in oceanic productivity on the $\delta^{15}N$ signatures of each fish species we used a one-way analysis of covariance (ANCOVA), with predators as a fixed factor (two levels: abundant/not abundant) and oceanic chlorophyll-*a* (measured in mg/L) as a continuous covariate. Normality of the data was verified using the Anderson-Darling test and homoscedasticity (equal variance among groups) verified using Bartlett's test. To test whether the relative $\delta^{15}N$ signal for species within trophic groups remained consistent across islands (relative to the putative source), we used a two-factor analysis of variance (ANOVA), treating island and species as fixed factors. This was done for the three species within the herbivore guild and three species within the carnivore guild (top-predators and mid-level carnivores combined) but not the planktivore guild; it was decided *a priori* that the planktivore guild had a lack of power to separate these effects due to low replication (only two species were present and one species-island combination was absent due to the lack of *P. bartlettorum* present at Kingman).

To examine stable isotope patterns of the three consumer species (*L. bohar*, *C. urodeta*, and *P. arcatus*) and the five species from lower trophic levels (*C. margaritifer, P. bartlettorum*, *S. aureus, A. nigricans*, and *C. marginatus*) we created stable isotope vector bi-plots using the mean values of $\delta^{13}C$ - $\delta^{15}N$ for each species-island combination. By plotting a vector between these two points for each island-species combination we were able to visualize differences in mean stable isotope values between the consumers and the species from lower trophic levels as well as any consistent patterns observed across islands for each species.

All the above analyses were performed using R version 3.1.2 (R Development Core Team, http://www.r-project.org).

RESULTS

Systematic stomach content analysis of the 8 targeted species provided a snapshot of the diet composition for species as well as the size range of prey items consumed by the three carnivores, *Lutjanus bohar*, *Cephalopholis urodeta,* and *Paracirrhites arcatus* (Table 4.2). The mean size of prey was positively related to the size of the carnivore and mean prey size scaled approximately an order of magnitude between each respective carnivore species (Table 4.2). Although the $\delta^{15}N$ stable isotope signatures varied little among carnivores within islands (Figure 4.2), diet composition varied among carnivores across islands (Figure 4.3, Table 4.2). For example, the diet of *L. bohar* varied greatly among islands, while the diet of *C. urodeta* was heavily dominated by crustaceans and small-bodied fish across all islands and was dominated by small-bodied crustaceans across all islands for *P. arcatus*. These results indicate that species of carnivores ingest a distinct collection of prey items, despite the similarity of trophic position as indicated by similarity of stable isotopic signatures.

The diet composition of the herbivores *Stegastes aureus*, *Acanthurus nigricans*, and *Ctenochaetus marginatus* varied among species but species-specific diet remained consistent across islands (Table 4.2). The diet of the territorial herbivore *S. aureus* was comprised primarily of early stage algae (Growth form: Filamentous, Cyanobacteria, Net-like), invertebrates, and sand while the diet of *A. nigricans* consisted primarily of early algae and late algae (Growth form: Complex Cylinder, Foliose, Thick & Leathery) (Table 4.2). Lastly, the diet of the herbivore-detritivore *C. marginatus* was comprised primarily of sand and early algae (Table 4.2).

Graphical analysis revealed consistency in the relative positions of some species in stable isotopic space across islands (Figure 4.4). Pairwise comparisons of the stable isotope values between consumers and species from lower trophic levels revealed consistent patterns for some species-island combinations. In particular, both mid-level carnivores (*C. urodeta* and *P. arcatus*) and the top-predator *L. bohar* were elevated similarly in δ^{15}N relative to the planktivores *Pseudanthias bartlettorum* and *Chromis margaritifer* across islands. In contrast, there was limited evidence of δ^{15}N enrichment between the three consumers and each of the herbivores *A. nigricans*, *C. marginatus*, and *S. aureus* (Figure 4.4). Across islands, there was no evidence of systematic isotopic enrichment between consumers and any of the herbivorous / detritivorous species. The only consistency in relative isotopic signatures was between each of the consumers and *C. marginatus* in units of δ^{15}N, with the detritivorous species showing consistently similar values of δ^{15}N relative to consumer species across islands (Figure 4.4).

Comparisons of the trophic structure for a subset of the most abundant coral reef fishes from the Line Islands revealed a significant effect of productivity (chlorophyll-*a*) on the δ^{15}N stable isotope signature of the top-predator *L. bohar*, the mid-level carnivores *C. urodeta* and *P. arcatus*, and the planktivore *C. margaritifer* (Table 4.3). In all these cases, fishes collected from islands further from the equator and in more nutrient-replete waters had more elevated δ^{15}N levels (Figure 4.5) (See Figures 4.2 and 4.3 for island-specific and species-specific trends). The increasing $\delta^{15}N$ stable isotope signatures for the top-predator *L. bohar*, the mid-level carnivores *C. urodeta* and *P. arcatus*, and the planktivore *C. margaritifer* closely tracked concurrent increases in $\delta^{15}N$ for the basal energy sources, namely particulate organic matter (POM) (Figure 4.5). Additionally, when estimating the stepwise enrichment (2.5-4.0 $^{0}/_{00}$) of the putative prey for the three carnivore species, we observed consistent overlap between carnivores and planktivores (Figure 4.5). In contrast, no significant effect of productivity was observed for the planktivore *P. bartlettorum* and the herbivores *S. aureus, A. nigricans*, and *C. marginatus* (Table 4.3, Figure 4.5), however all three herbivore species again appeared to track the basal energy source, namely macroalgae (Figure 4.5). There was no significant effect of the presence of predators on the $\delta^{15}N$ stable isotope signatures of any of the species included in this study, as noted by there being no support for the binary "predator" factor (i.e., high predator biomass *versus* low predator biomass) in the ANCOVA (Table 4.3). Comparisons of $\delta^{15}N$ within the herbivore guild revealed a significant interaction between island and species making interpretation challenging (Table 4.4). In contrast, comparisons of $\delta^{15}N$ within the carnivore guild (top-predators and mid-level carnivores) revealed a significant effect of island and species with no significant interaction between the two fixed factors (Table 4.4).

DISCUSSION

By conducting a large-scale natural experiment across six Pacific coral reef islands, we found trophic overlap between fish species to be somewhat limited, in contrast to the common expectation of a complex topology among trophic groups.

Instead, our results showed that different basal sources of energy entering the system can remain isolated on coral reefs, forming distinct trophic pathways up through the food web to top-level carnivores; we term this process *trophic channeling* (Figure 4.6). Importantly, trophic channeling occurred from two different basal sources of energy, namely allochthonous zooplankton delivery and sunlight fueled primary production. These two energetic pathways contributed unequally to carnivore end-members and this finding was consistent across geographical variations in oceanic productivity.

Most trophic models of coral reef fish assemblages assume that size almost exclusively determines the potential prey of carnivores, with large-bodied carnivores consuming larger prey types than their small-bodied prey (Jennings et al. 2002b, Jennings and Warr 2003, Mumby et al. 2006). Our data suggest instead that prey following distinct energetic pathways (i.e., those tracking planktonic *versus* benthic algal basal sources) contribute unequally to carnivore trophic demands. Quantitatively, the planktonic pathways appear to provide the majority of the isotopic signature, and thus likely energy contribution, to these teleost carnivores. An outstanding question remains – what is the fate of the sunlight-derived energy on a coral reef? Perhaps herbivorous fishes on coral reefs are principally vulnerable to other groups of predators, in this case to the predatory reef sharks and large-bodied ambush predators like groupers (Figure 4.6). Importantly, though, the predators examined in this study compose almost 50% of the biomass of apex predators, with *L. bohar* being by far the largest biomass contributor to the guild, with reef sharks as the next most massive group and large-bodied groupers being relatively uncommon. Alternatively, it is possible that predation of herbivores is much less common than is predation of planktivores. If true, we may expect that the average longevity of herbivores would be longer than that of planktivores, especially when considered in units of mass (i.e., how long does a unit of energy from benthic photosynthesis remain in fish consumers relative to a unit of energy from plankton?). If the results from this study are consistent across other carnivore species, we may expect a stark distinction in longevity, with profound implications for modeling the trophic dynamics of reef ecosystems.

For this study we targeted among the most abundant species across multiple trophic groups to gain valuable insights into the trophic structure fish assemblages from the central Pacific (Table 4.1). Because trophic position often scales with body size (Peters 1986, Jennings et al. 2001, Layman et al. 2005) we predicted that the three carnivores would occupy distinct trophic positions in δ^{15}N isotopic space based on their respective body sizes, with larger-bodied carnivores being more enriched in isotopic space than smaller-bodied species. Specifically, we selected three carnivores representing a range of body sizes and feeding ecologies to examine the role of predatory species in structuring food webs. *Lutjanus bohar* are aggressive top-predators, often competing with reef sharks (Family: Carcharhinidae), that forage opportunistically on fishes and to a lesser extent crustaceans and cephalopods (Myers 1999, Randall 2005). *Cephalopholis urodeta* are classified as a medium-sized mid-level carnivore that reside amongst the reef structure and makes use of their large gape size to ambush small-to-medium sized fishes and crustaceans (Myers 1999, Randall 2005). Lastly, *Paracirrhites arcatus* are small-bodied mid-level carnivores that reside on branches of live coral from the genera *Pocillopora* and *Acropora* and ambush prey including fishes and crustaceans (Randall 1985, DeMartini 1996, Randall 2005). Systematic stomach content analysis of the three carnivore species supported our prediction and showed that average prey size scaled with carnivore body size and the individual diet of each carnivore species varied in taxonomic diversity and proportion of food items consumed (Table 4.2). However, the results of our stable isotope analyses, offering a more integrated history of diets, were striking and indicated that all three carnivores shared isotopically similar diets (Figure 4.5). These findings were unexpected but are consistent with trophic channeling. The diets of carnivores were comprised of different food items and scaled with body size, but the trophic pathways from basal sources of productivity up through the web to each respective carnivore were heterogeneous and may involve different turnover rates (Rooney et al. 2006, Layman et al. 2007).

Across islands, we observed a significant effect of productivity (chlorophyll-*a*) on the isotopic signatures of four of the eight species included in this study (Table 4.3). In all four cases, productivity was positively related to the δ^{15}N isotopic signatures of each carnivore or planktivore. The stable isotope signature of the planktivore *Pseudanthias bartlettorum* also appeared to be influenced by productivity but did not yield statistically significant results ($p<0.1$), most likely as a result of not being observed at Kingman Reef (thus resulting in a five-island design with associated reduction in statistical power). Interestingly, all the three carnivores and the two planktivore species exhibited consistent groupings across islands based on their respective trophic position. However, we did incorporate satellite-derived measures of productivity (annual means of chlorophyll-*a* for each island) as well as measures of POM previously documented from for the central Pacific (Altabet 2001). In all cases the isotopic signatures of the two planktivores scaled consistently with productivity and POM. Patterns observed for the three carnivores (*L. bohar*, *C. urodeta* and *P. arcatus*) were consistent with the planktivores suggesting that the major contribution to their diet originated from an allochthonous zooplankton basal source. These findings were further supported with stomach content analysis whereby the diet composition of the planktivores varied little among species across island and copepods comprised a majority (>65%) of the diet.

In contrast to the carnivores, the isotopic signatures of the three-herbivore species did not scale with productivity most likely as a result of the complexity of energy transfer and fractionation between basal sources of the food web. These findings indicate that the herbivores included in this study have distinct feeding ecologies which is reflected in their diet and stable isotope signatures (Figure 4.5, Table 4.2). For example the stable isotope signatures of *Stegastes aureus* and *Ctenochaetus marginatus* exhibit greater enrichment in δ15N space as a result of diet items including invertebrates and detritus respectively (Figure 4.5, Table 4.2) In the case of *C. marginatus*, δ15N isotopic signatures tracked consistently with the isotopic signatures of the carnivores consistent with a feeding ecology including coprophagy (Figure 4.5, Table 4.2).

Stable isotope values were consistent across islands and indicated a pattern of trophic structure and consistency across a heterogeneous collection of coral reef ecosystems. Importantly, rather than describing a fully integrated and trophically-linked food web, our observations support the notion of trophic channeling, whereby energy is transferred via discrete isolated channels up through the food web to carnivore end members (Figure 4.6). We demonstrate two forms of channeling – *source-based trophic channeling*, in which dominant teleost carnivores derive the majority of their resources from the plankton-fueled channel without quantitatively important contributions from the sunlight-fueled channel, and *size-based trophic channeling*, in which species of carnivores derive resources from distinct size classes of prey despite these prey residing at comparable trophic levels above the planktonic source. Complex food webs like those on coral reefs thus reveal clear topological constraints, which come into focus only when joining views of foundational energy sources and size-structured predation. Together these findings provide important insight into the trophic dynamics of coral reef fish assemblages and set up myriad additional research questions and field experiments to increase our understanding of one of the most complex ecosystems on the planet.

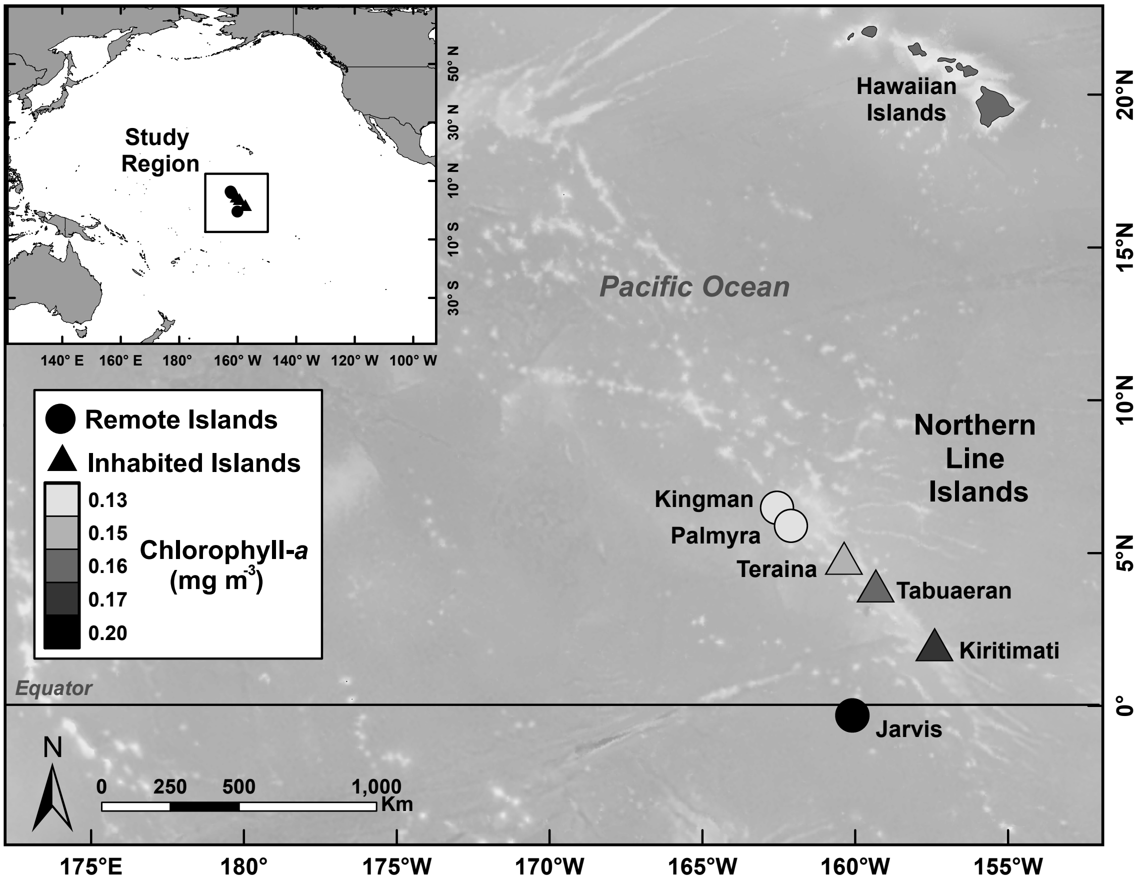

Figure 4.1. The northern Line Islands identifying three remote islands (Kingman, Palmyra and Jarvis) and three inhabited islands (Teraina, Tabuaeran, and Kiritimati) that served as study sites. Mean nearshore oceanic productivity (chlorophyll-*a*) is provided for each island and scales with black-white shading.

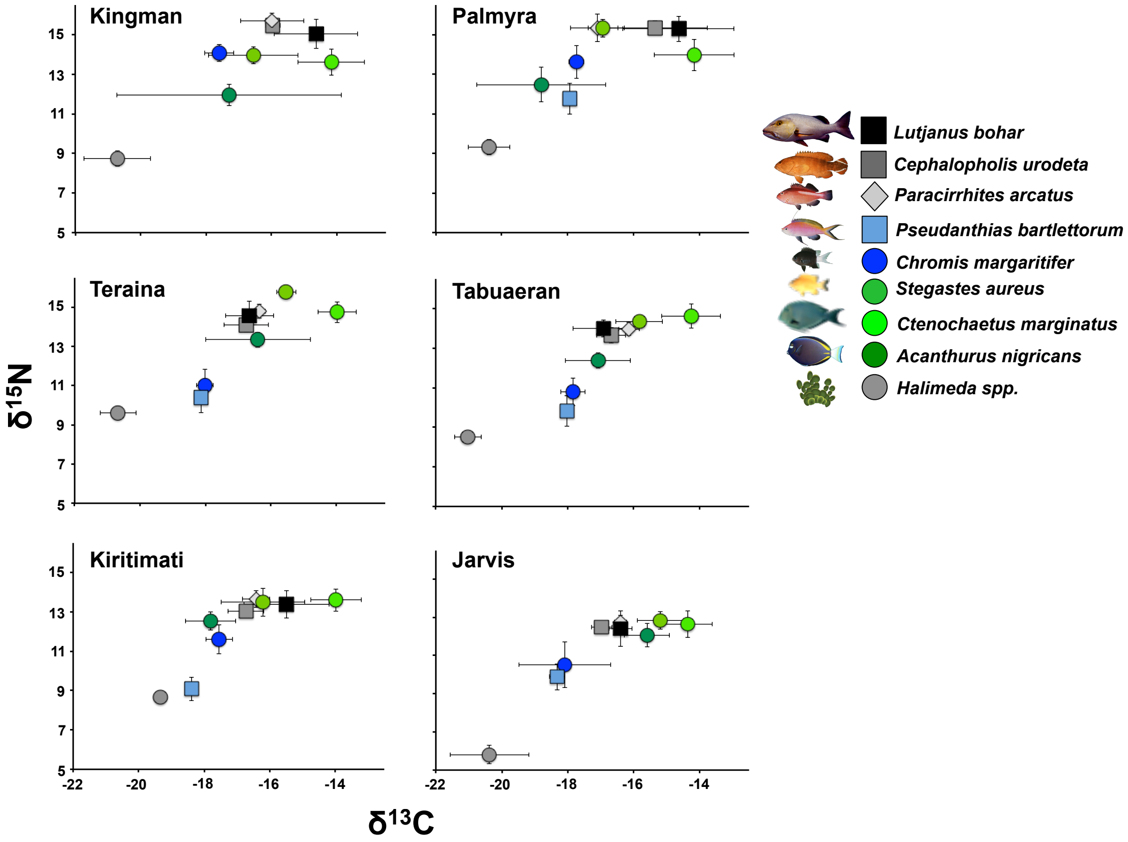

Figure 4.2. Stable isotope bi-plots ($\delta^{13}C$ - $\delta^{15}N$) for 8 species of coral reef fishes and 1 species of macroalgae (*Halimeda* sp.) plotted for each island. All values are mean and ± standard deviation.

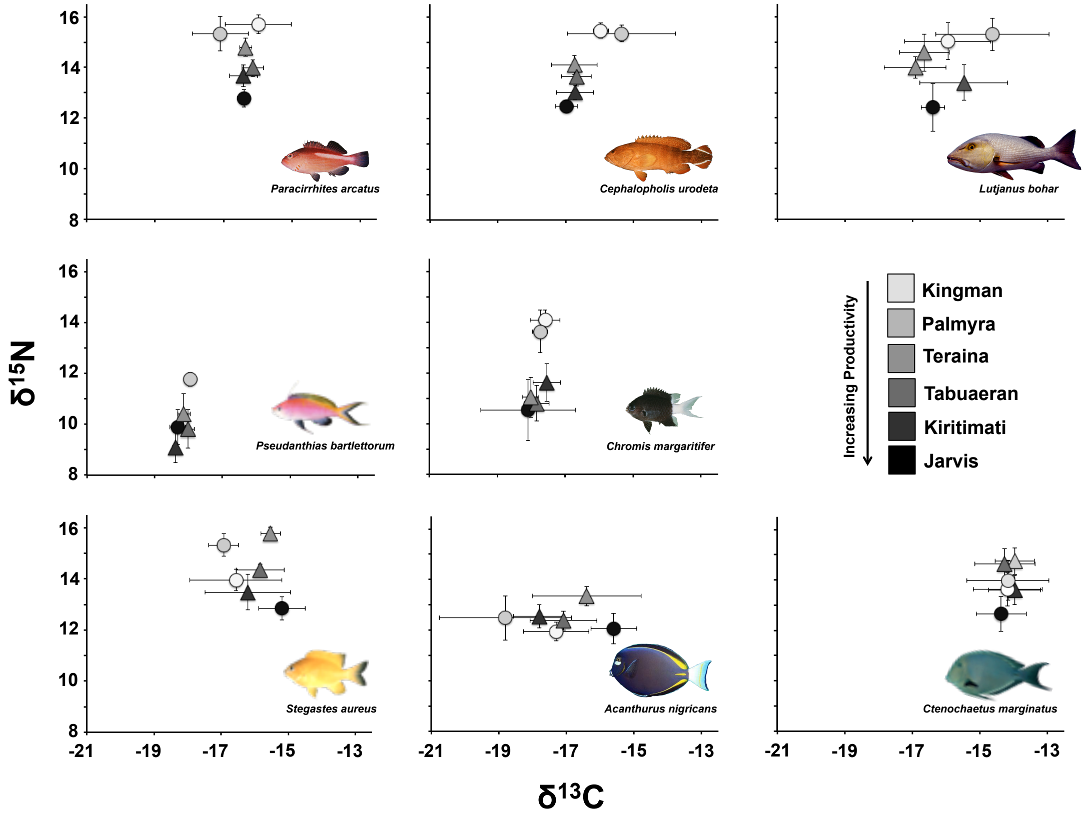

Figure 4.3. Stable isotope bi-plots ($\delta^{13}C$ - $\delta^{15}N$) for 8 species of coral reef fishes plotted across the 6 islands for each panel. Symbols represent island and shading represents scale of productivity. All values are mean and ± standard deviation.

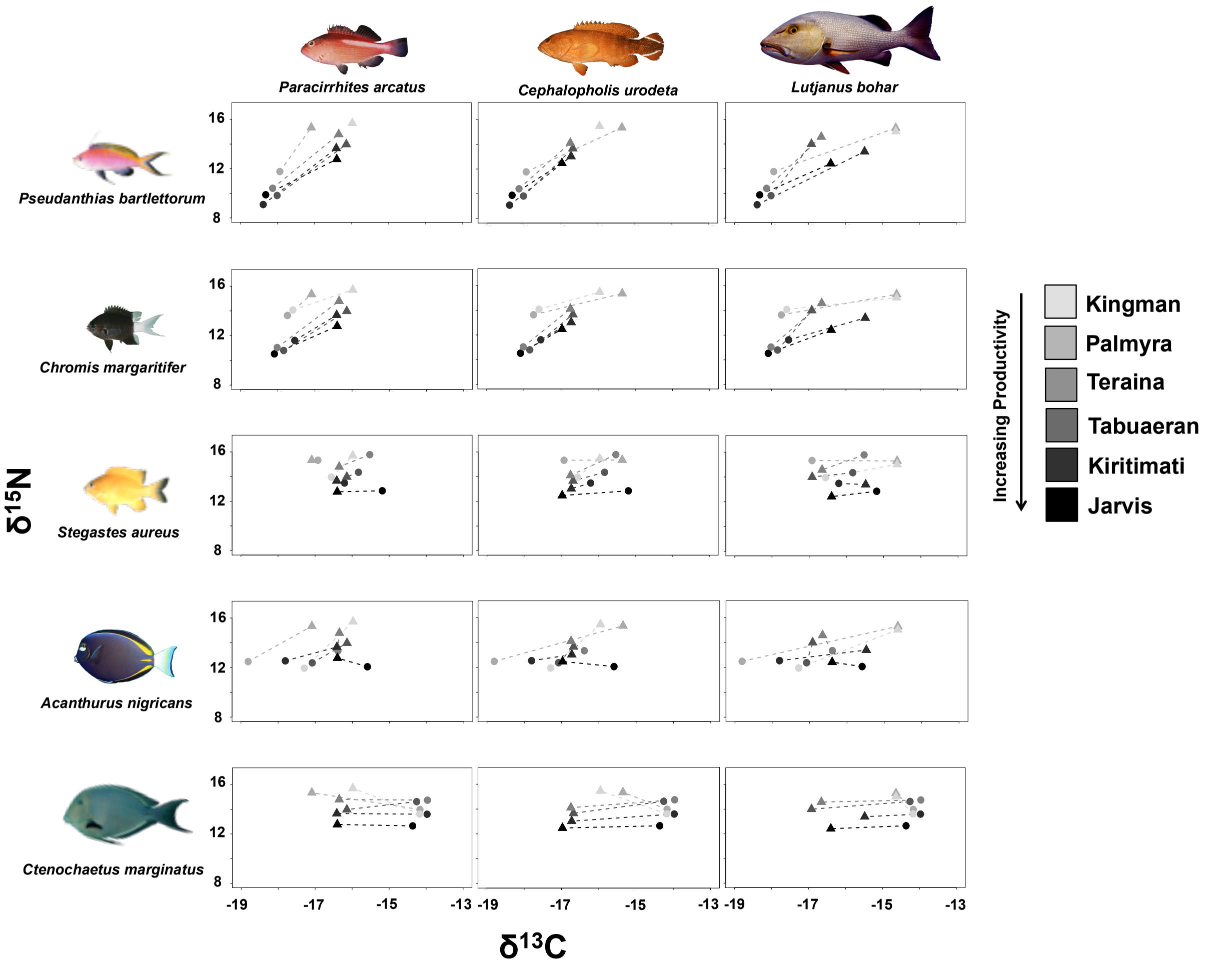

Figure 4.4. Pair-wise comparisons of stable isotope values ($\delta^{13}C$ - $\delta^{15}N$) between three consumers and five species from lower trophic levels (two planktivores and three herbivores) across islands. Triangle points represent the consumer species and circle points represent the planktivores and herbivores. Shading of points indicates island and scale of productivity. Standard deviation values are provided for these species in Figures 4.2 and 4.3.

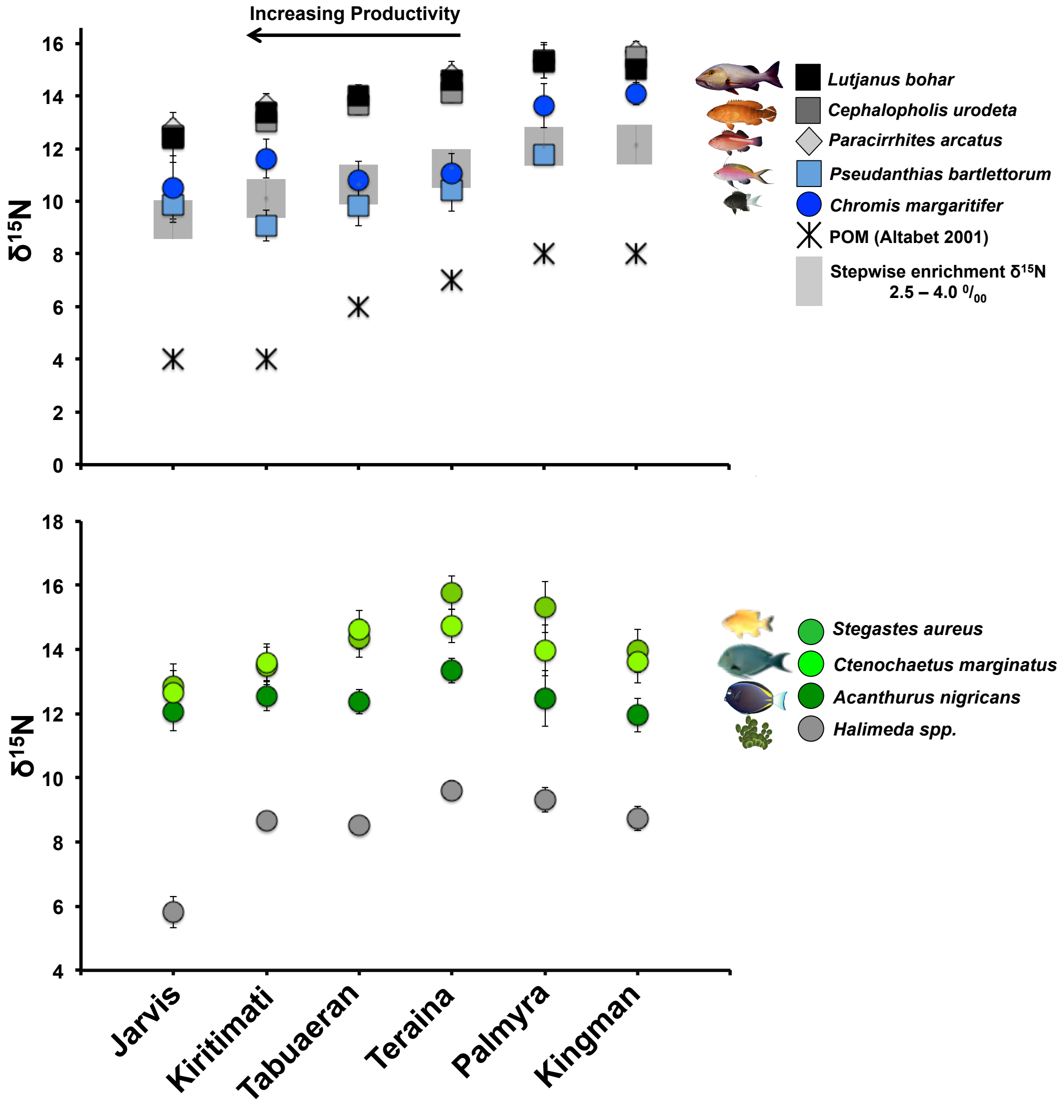

Figure 4.5. Values of $\delta^{15}N$ for each species plotted across islands in south-north orientation and gradient of oceanic productivity. All values are mean and ± standard deviation. Shaded areas in top plot represent estimated stepwise enrichment calculated based on the $\delta^{15}N$ means of the carnivore species subtracting 2.5-4.0 $^{0}/_{00}$. Latitudinal estimated mean Particulate Organic Matter (POM) taken from Altabet (2001).

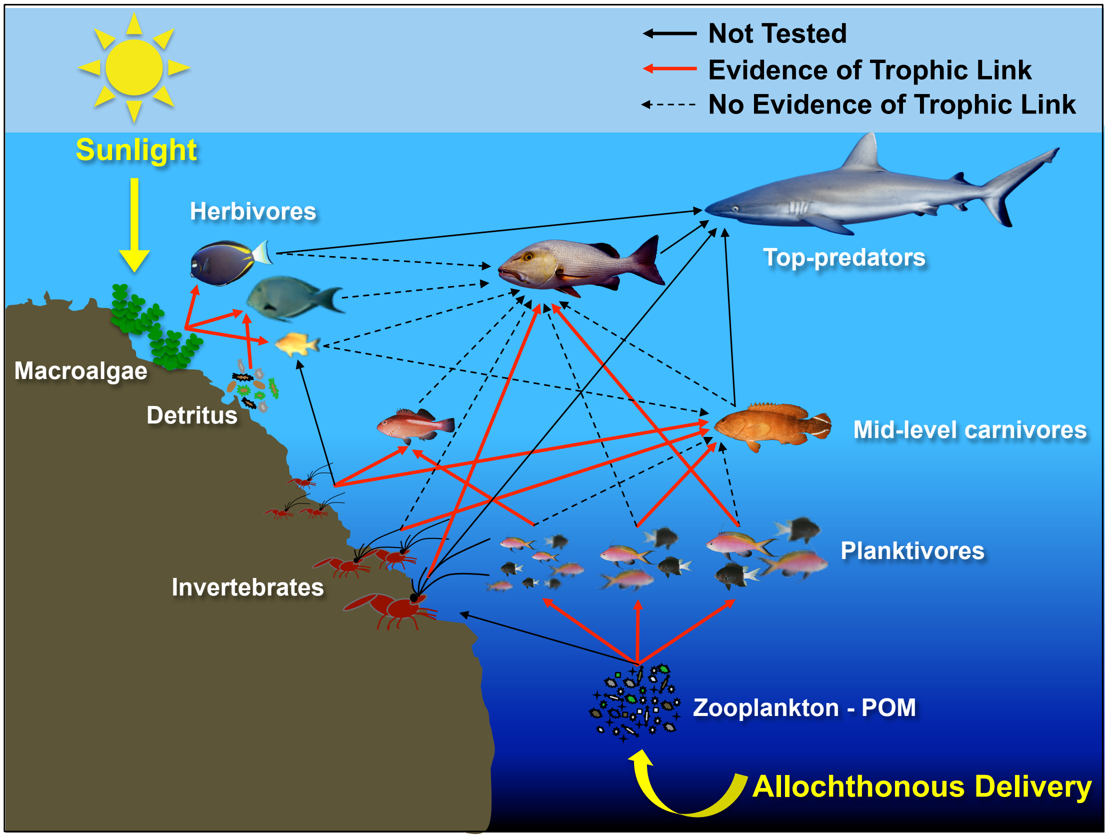

Figure 4.6. Conceptual illustration depicting *trophic channeling* on coral reefs, the process whereby different basal sources of energy (sunlight *versus* allochthonous delivery) entering the system can remain isolated, forming distinct trophic pathways up through the food web to top-level carnivores. All lines (solid and dashed) indicate classical topological expectation of a coral reef food web. Solid black lines indicate putative trophic linkages that were not tested in this study. Red lines indicate trophic connections where we observed strong evidence of consistent pairwise relationships. Dashed black lines indicate no evidence of strong consistent linkages.

Table 4.1 Characteristics of the 8 targeted coral reef species included in this study identifying sample size by island and the regional contribution of each species to total mean fish abundance and biomass given as a percentage (%). Satellite derived estimates of productivity (chlorophyll-*a*) are provided for each island. Values for chlorophyll-*a*, abundance, and biomass are means with standard error given in parentheses.

									Regional contribution to:	
Trophic Group	**Family**	**Species**	**Jarvis**	**Kiritimati**	**Tabuaeran**	**Teraina**	**Palmyra**	**Kingman**	**Total Fish Adundance (%)**	**Total Fish Biomass (%)**
Top-predator	Lutjanidae	*Lutjanus bohar*	3	51	10	10	30	10	0.31	16.71
Mid-level carnivore	Serranidae	*Cephalopholis urodeta*	10	10	10	10	10	10	0.38	0.91
	Cirrhitidae	*Paracirrhites arcatus*	10	49	10	10	51	10	0.61	0.29
Planktivore	Pomacentridae	*Chromis margaritifer*	10	51	10	10	46	10	7.92	0.35
	Serranidae	*Pseudanthias bartlettorum*	10	10	10	10	10	NP	19.57	0.77
Territorial herbivore	Pomacentridae	*Stegastes aureus*	10	10	10	10	10	10	0.56	0.29
Herbivore	Acanthuridae	*Acanthurus nigricans*	10	49	10	10	25	10	0.73	2.63
Herbivore-detritivore		*Ctenochaetus marginatus*	10	10	10	10	10	10	0.43	1.45
		TOTAL	73	240	80	80	192	70	30.50	23.41
		Mean Chlorophyll-*a* (mg m^{-3})	0.2	0.17	0.16	0.15	0.13	0.13		
		Total Reef Fish Abundance (# m^{-2})	27.79 (3.74)	11.82 (0.70)	6.61 (0.61)	7.56 (0.80)	3.52 (0.18)	3.82 (0.32)		
		Total Mean Reef Fish Biomass (g m^{-2})	412.02 (98.08)	112.29 (6.26)	159.51 (18.28)	90.45 (13.98)	225.86 (27.22)	378.82 (42.50)		
		Total Mean Top-predator Biomass (g m^{-2})	256.62	29.53	37.31	12.26	155.55	365.79		

Table 4.2. Results of the systematic stomach analyses for the 8 targeted species across 6 survey islands. Sample size is given as number analyzed and numbers in parentheses indicates the number of samples with items present in stomach. All data obtained from MSc. Thesis of E. Cordner (2013).

Species			**Kingman**	**Palmyra**	**Teraina**	**Tabuearan**	**Kiritimati**	**Jarvis**
Lutjanus bohar		Sample size	24	20	8	7		
			(19)	(11)	(6)	(4)		
		Mean Prey Size (g)	4.16	13.29	13.11	1.78		
	Diet Composition (% Weight)	Crustacean	50	29	50	25		
		Fish	43	53	17	50		
		Other	8	17	33	25		
Cephalopholis urodeta		Sample Size	17	61	45	55	37	54
			(12)	(19)	(13)	(9)	(13)	(14)
		Mean Prey Size (g)	0.55	0.59	0.37	2.29	0.56	0.54
	Diet Composition (% Weight)	Crustacean	63	49	70	39	50	63
		Fish	31	43	24	46	39	29
		Other	7	8	7	9	4	4
Paracirrhites arcatus		Sample Size	26	29	47	49		48
			(15)	(18)	(19)	(26)		(18)
		Mean Prey Size (g)	0.05	0.03	0.06	0.05		0.05
	Diet Composition (% Weight)	Crustacean	91	81	80	80		89
		Fish	4	9	9	9		1
		Other	4	9	11	11		11
Pseudanthias bartlettorum		Sample Size		20	20	20	9	20
		Copepods		71	75	65	73	72
	Diet Composition (%)	Fish eggs		2	6	10	12	14
		Larvaceans		5	1	1	3	3
		Forams		16	11	17	4	6
		Other		7	6	8	9	4
Chromis margaritifer		Sample Size	20	20	20	22		20
		Copepods	81	76	88	86		70
	Diet Composition (%)	Fish eggs						
		Larvaceans	14	6	6	4		4
		Forams		7	2	4		17
		Other	5	12	4	6		8
Stegastes aureus		Sample Size	26	26	26	26	24	26
		Early Algae	25	33	25	43	12	36
	Diet Composition (%)	Late Algae	8	8	9	13	10	18
		Calcified Algae		1	1	2	1	1
		Inverts	21	16	23	23	12	12
		Sand	46	42	41	18	65	32
		Other	1	1	1			
Acanthurus nigricans		Sample Size	26	15	26	25		26
		Early Algae	25	45	35	41		33
	Diet Composition (%)	Late Algae	50	44	50	43		56
		Calcified Algae	4	3	4	13		2
		Inverts	17	4	4			5
		Sand	3	4	6	3		4
		Other	1	1	1			1
Ctenochaetus marginatus		Sample Size	26	26	26	26	26	26
		Early Algae	30	27	19	38	17	21
	Diet Composition (%)	Late Algae	11	9	8	17	11	19
		Calcified Algae	3	2	1	3	2	2
		Inverts	15	10	12	7	9	9
		Sand	41	52	58	31	59	49
		Other	1		1	3	2	

Table 4.3. Output results of analysis of covariance (ANCOVA) for the 8 targeted species across all islands use the factors of productivity (chlorophyll-*a*; [Chl-*a*]), predatory fish biomass (Predators), and their interactions.

Trophic Group	**Species**	**Factor**	***F*-value**	***P*-value**
Top-predator	*Lutjanus bohar*	Chl-*a*	214.40	**0.005**
		Predators	0.34	0.621
		Chl-*a*:Predators	0.50	0.555
Mid-level carnivores	*Cephalopholis urodeta*	Chl-*a*	201.34	**0.005**
		Predators	10.23	0.085
		Chl-*a*:Predators	0.0	1.000
	Paracirrhites arcatus	Chl-*a*	112.61	**0.009**
		Predators	0.54	0.540
		Chl-*a*:Predators	0.30	0.641
Planktivores	*Chromis margaritifer*	Chl-*a*	38.32	**0.025**
		Predators	11.54	0.077
		Chl-*a*:Predators	6.15	0.131
	Pseudanthias bartlettorum	Chl-*a*	43.34	0.096
		Predators	31.45	0.112
		Chl-*a*:Predators	2.57	0.355
Territorial herbivore	*Stegastes aureus*	Chl-*a*	7.22	0.115
		Predators	3.39	0.207
		Chl-*a*:Predators	0.92	0.438
Herbivore	*Acanthurus nigricans*	Chl-*a*	0.30	0.640
		Predators	4.45	0.169
		Chl-*a*:Predators	2.52	0.254
Herbivore-detritivore	*Ctenochaetus marginatus*	Chl-*a*	5.30	0.148
		Predators	10.11	0.086
		Chl-*a*:Predators	1.01	0.420

Table 4.4. Output results of analysis of variance (ANOVA) testing the effect of two fixed factors (Island and Species) on the $\delta^{15}N$ signatures of key coral reef fish trophic groups. Herbivores trophic group includes *Stegastes aureus, Acanthurus nigricans*, and *Ctenochaetus marginatus*. The top-predator and mid-level carnivores trophic group includes *Lutjanus bohar*, *Cephalopholis urodeta,* and *Paracirrhites arcatus*.

Trophic Group	**Factor**	**DF**	***F*-value**	***P*-value**
Herbivores	Island	5	55.9	<0.001
	Species	2	205.4	<0.001
	Island:Species	10	8.1	**<0.001**
Top-predator and mid-level carnivores	Island	5	179.2	**<0.001**
	Species	2	8.4	**<0.001**
	Island:Species	10	1.6	0.099

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