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AN ABSTRACT OF THE THESIS of Andrew W. Jarrett for the Master of Science in Biology  
presented August 23, 2018

Title: FACTORS DRIVING ICHTHYOLOGICAL VARIATION ACROSS THE  
REPUBLIC OF THE MARSHALL ISLANDS

Approved: \_\_\_\_\_

Peter C. Houk, Chair, Thesis Committee

Coral reef fish communities across the Pacific offer invaluable societal and ecological functions. Although they support ecosystems, economies, and cultures throughout the region, coastal fisheries are being increasingly jeopardized by human activities. Sustainability of these fisheries is vital, but currently restricted by a lack of understanding about how natural environments and human factors interact to shape reef fish populations. Understanding the influence of each environmental and anthropogenic variable, across multiple spatial scales, is a fundamental step to establishing meaningful conservation measures. The Republic of the Marshall Islands (RMI) in eastern Micronesia is an ideal location to observe these relationships because it consists of 29 atolls and 5 islands that vary greatly in morphology as well as human population. This study focused on assessing differences in reef fish communities between and within 10 atolls and 1 low-lying coral island. Fish data was collected using a modified stationary point count (SPC) method at 150 sites across environmental regimes. Using linear models, we recorded substantial shifts in fish biomass and assemblage structure in relation to increasing human population density. Further sensitivity analysis revealed that large-bodied piscivores and planktivores declined more steeply than any other groups. Additionally, within each

trophic guild we discovered major differences in community composition across the country, with smaller-bodied faster growing taking up a significantly greater proportion of the biomass on the more populous atolls. Furthermore, we calculated an aggregate metric of fish assemblage characteristics for each site, and learned that the inner reef sites of our three most densely populated atolls were substantially worse than those on all other atolls. To examine variation within each atoll, we ran linear mixed effects models which provided evidence of localized human footprints. From the models developed in this study, we have the ability to predict fish assemblage traits for other atolls across the country based on environmental and anthropogenic data. This gives resource managers the ability to make educated decisions and begin conservation measures before in-situ data becomes available. In conclusion, the Republic of the Marshall Islands possesses extraordinary marine resources but there is still an obvious need for management to sustain these reef fish populations long-term.

TO THE OFFICE OF GRADUATE STUDIES

The members of the committee approve the thesis of Andrew W. Jarrett presented on August 23, 2017.

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**FACTORS DRIVING ICTHYOLOGICAL VARIATION ACROSS THE  
REPUBLIC OF THE MARSHALL ISLANDS**

**BY**

**Andrew W. Jarrett**

**A thesis submitted in partial fulfillment of the requirements for  
the degree of**

**MASTER OF SCIENCE  
IN  
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## **Introduction**

Pacific coral reefs are among some of the most diverse, complex, and dynamic ecosystems in the world. Coastal fisheries in the Pacific provide valuable ecosystem services that maintain economies, societies, and cultures throughout the region. Long-term sustainability of these fisheries is imperative, yet limited by a lack of understanding about how natural environments and human pressures interact to shape fish populations, and the reefs they support. Comprehending the leverage of these natural and anthropogenic influences is the first step to creating meaningful conservation decisions. For the benefit of coral reefs and the people that depend on them, researchers must recognize the regional and local forces driving reef fisheries.

Of course many of the processes acting upon fish communities are scale dependent. At the regional scale, key environmental factors include water temperature, primary productivity, latitude, island geomorphology, habitat space, island connectivity, and proximity to the Indo-West Pacific diversity center (Choat 1991; Knowlton 2001; Floeter et al. 2004; Hillebrand 2004; Sale 2004; Parravicini et al. 2013; Taylor et al. 2015; Williams et al. 2015; Duffy et al. 2016; Heenan et al. 2016). Locally, factors like wave exposure, reef habitat type, and human stressors are more influential (MacNeil et al. 2009; Parravicini et al. 2013). Independently, each of these variables can influence many attributes of coastal fisheries, including species carrying capacities, species diversity, and assemblage structure (Galzin et al. 1994; Sale 2004; Heenan et al. 2016). However, these factors are not independent of one another, and studies highlighting their interactive influences are increasingly prevalent as larger datasets become available (Parravicini et al. 2013; Stuart-Smith et al. 2013; Edwards et al. 2014; Williams et al. 2015; Heenan et al. 2016). Understanding natural drivers of variation in coral reef fisheries is an essential prerequisite to assessing change in key fisheries metrics, and linking



biological changes with human footprints (Jennings et al. 1995; Stevenson et al. 2007; DeMartini et al. 2008; Cinner et al. 2013; Heenan et al. 2016).

### ***Geography (Location, Location, Location)***

Of the factors that shape a reef fish population, its geographic location is the most fundamental. The region in which a reef resides dictates the environmental conditions and also the potential species pool available to recruit from neighboring populations.

Latitude is a proxy for changes in many of the environmental factors that influence reef fish assemblages. In the tropics, variation in temperature, day length, productivity, and light attenuation all increase with latitude. The environmental differences found along latitudinal gradients are often reflected in the fish communities. Fish diversity, biomass, and abundance typically peak near the equator where warmer temperatures support greater rates of primary production, and metabolic activity (Hillebrand 2004; Stuart-Smith et al. 2013; Duffy et al. 2016). However, low latitudes also suffer from pronounced oceanic thermoclines that prevent many nutrients from reaching surface waters, while reefs at higher latitudes receive episodic fertilization of cool nutrient rich water from upwelling events that temporarily boost productivity. Despite potential nutrient limitations, primary consumers often benefit from the stability of equatorial environments. In fact, many herbivores depend on the warm temperatures found at low latitudes to make eating a nutrient poor diet energetically feasible (Choat 1991; Floeter et al. 2004). This places strict latitudinal constraints on many species and leads to dramatic shifts in species composition (Meekan and Choat 1997; Ferreira et al. 2004; Floeter et al. 2004). Fish species belonging to higher trophic levels are less affected by latitude due to greater thermal tolerances and range sizes, and yet local standing stock biomass of these groups remains greater in equatorial waters (Williams et al. 2015).



A biogeographical gradient also exists longitudinally. The Indo-West Pacific is home to the greatest reef fish diversity on Earth. This is largely the result of the region's favorable position straddling the Indian and Pacific Oceans, abundance of reef habitat, and history of periodic isolation that occurred with sea level fluctuations (Cowman and Bellwood 2013). Across the Pacific, reef fish diversity has been found to decline with distance from this center (Choat 1991; Bellwood and Hughes 2001; Mora et al. 2003; Pinca et al. 2012; Parravicini et al. 2013). Although it is important to note that many biogeographical trends only appear at broad scales, with localized factors playing a greater role in structuring reef fish assemblages around individual islands (Bellwood and Hughes 2001; Knowlton 2001).

Clearly geography dictates regional species diversity, however, the invisible connection a reef has with its neighbors via surface currents is a key driver of local species composition and population replenishment (Abesamis et al. 2016). Isolation limits species diversity and foreign recruitment to only those species with the capable dispersal range (Hobbs et al. 2012). However, the reduced species richness does not necessarily mean there is a reduction in the function of the system as many reef fish species tend to fulfill similar ecological roles (Mouillot et al. 2014). Although certain functional groups benefit from the additional species buffering potential that comes with increased diversity, around 38% of all reef fish functional groups are occupied by a single species even on the most speciose reefs (Bellwood et al. 2003; Mouillot et al. 2014; Duffy et al. 2016). In addition, being geographically or even just hydrologically isolated can reduce the resilience of a reef to disturbances such as storms or fishing pressure due to a heavy reliance on local stocks for juvenile recruitment (Hughes et al. 2010). In this way, connectivity between islands is both a regional and a local scale factor that can explain not only current characteristics of a fish community, but future population dynamics as well.

## ***Geomorphology***

Pacific fish communities depend on the coral reefs that form on and around high islands, low islands or atolls, and seamounts. Most Pacific islands begin as volcanic seamounts that emerge from the water and slowly grow skyward to form high islands. These are geologically young volcanic land masses that usually develop fringing reef systems. As high islands slowly subside and the fringing reefs grow seaward, lagoons and barrier reef systems form and provide greater habitat space and diversity for fish and other marine organisms. Consequently, the greatest species richness of reef fish is found on complex high islands with lagoons (Allen 2007; Taylor et al. 2014).

Conversely, atolls provide large amounts of reef habitat relative to land area, but the diversity of habitats is limited. Despite this, atolls achieve high levels of productivity because lagoons act as oceanic lakes, slowing water movement and promoting phytoplankton growth, resulting in high concentrations of chlorophyll- $\alpha$  (Gove et al. 2016). The enhanced productivity and coral growth supports larger biomasses and abundances of reef fish, albeit less diverse, than high islands (Littler et al. 1991; Cinner et al. 2013). The limited habitat and species diversity of atolls is actually favorable for studying reef fish ecology because processes and factors governing populations can be assessed comprehensively and compared across atolls without many of the confounding factors of other island types.

More individual aspects of island morphology, including size and shape, also contribute to defining local fish assemblages. The physical size of an island or atoll directly determines the amount of habitat available for a fish community. While this has been quantified a variety of ways, the results consistently show that species richness increases with island size (Galzin et al. 1994; MacNeil et al. 2009; Parravicini et al. 2013). Beyond size, the shape of an island dictates the flow of surface currents, as well as the amount of reef habitat

that is exposed to wind generated wave energy. Consequently, island geometry also determines the distribution of nutrients and pelagic larvae within the system, and can have a major local impacts on productivity and variation within the fish populations (Hamner and Wolanski 1988; Charpy et al. 1997).

### ***Local factors***

The influences of oceanographic and geomorphological factors establish the regional species pool available to an island system, but local factors ultimately determine the species composition of a fish community (Bellwood and Hughes 2001; Mora et al. 2003). Naturally, the strongest of these factors would be reef type and wave energy, but human disturbances, including fisheries exploitation, place additional selective pressures on reef fish populations. Across an island, fish populations can vary dramatically due to heterogeneity in these variables and it is important to account for their independent influences prior to drawing conclusions about the ecological functioning or 'health' of a system or population.

Classically, reefs have been categorized into three groups; outer, inner, and patch reefs. Each type is associated with a distinct abiotic environment. The primary differences found between these environments is in water quality, solar attenuation, and protection from wave energy. Outer reefs are the group most influenced by wave energy, and major differences in species diversity and abundance have been documented between leeward and windward facing reefs (Friedlander et al. 2003; McLean et al. 2016; Bejarano et al. 2017). Ocean swells can also limit the height and three-dimensional complexity of windward reefs, decreasing the habitat available for fish, which results in lower abundance and diversity (Friedlander et al. 2003). However, low coral complexity makes feeding easier for many herbivore species and Heenan et al. (2016) showed maximal abundances of grazers at intermediate levels of wave exposure,

balancing the shelter of complex habitats with the grazing efficiency of more exposed areas. Energetic environments also exert direct pressures on fish populations by limiting the species composition and size structure to those physiologically capable of swimming in rough conditions (Fulton et al. 2005; Bejarano et al. 2017). In contrast, protected reef habitats offer greater potential for fish population growth due to greater retention and access to productive water. Therefore, in the absence of human interference, the highest fish abundances are expected to occur on outer leeward facing reefs. Yet, reefs protected from wave energy are more vulnerable to fisheries exploitation due to increased accessibility (McLean et al. 2016).

### ***Fishing impacts***

Recently, humans have become the single largest factor influencing reef fish populations worldwide (Friedlander and DeMartini 2002; Williams et al. 2011; Cinner et al. 2013). Even moderate levels of fishing significantly alter reef fisheries, reducing overall biomass and abundance of large individuals (Jennings and Polunin 1997; Dulvy et al. 2004; Houk and Musburger 2013). The tendency for fisherman to fish down the food web leads to the reduction of large piscivores and other keystone species that are crucial to the functioning of a reef. Although there is functional redundancy amongst fish species on a reef, declines in function are ultimately driven by the systematic depletion of upper trophic levels and the reduction of the overall size structure of a fish community. Large individuals provide a disproportionate amount of the beneficial services that maintain the function of a reef, regardless of a specie's trophic position. Lokrantz et al. (2008) found that a single "functionally-mature" parrotfish is responsible for as much grazing and bioerosion on a reef as 75 immature counterparts. This functional disparity is especially alarming when considering that large parrotfish become almost nonexistent when human densities reach 16 individuals



per kilometer (Bellwood et al. 2012). Even the overfishing of generalist predators can lead to changes in herbivore composition by altering competitive interactions, eventually decreasing the stability of the entire community (Britten et al. 2014). Unfortunately, overfishing is a chronic problem that plagues coral reefs worldwide, and as a result, reef fish biomasses have been accurately predicted globally based solely on their distance from a commercial market (Cinner et al. 2013).

### ***Republic of the Marshall Islands***

The RMI is the easternmost nation in Micronesia and consists of paralleling archipelagic chains with a total of 29 atolls and 5 islands that span 9 degrees in latitude. Although portions of the country are developing, many residents maintain a primarily subsistence lifestyle with reef fish providing an essential source of protein and income. As is true for most of the world, many of those living in rural or remote areas are choosing to relocate to the more industrious islands. This urbanization movement within the RMI has created a distinct gradient in human populations. When coupled with the geographic and environmental variation found across the country, the RMI presents a unique opportunity to study the processes controlling the abundance, diversity, and biomass of reef fish assemblages across multiple spatial scales. Therefore, the objective for this research was to quantify the variation between populations, identify the role each natural factor had in creating that variation, and use any remaining unexplained variance to investigate the influence of human activities, both within and between atolls.

## **Methods**

### ***Study Sites***

This study examined reef fish populations across 10 atolls and 1 low-lying coral island in the Republic of the Marshall Islands. Atolls were included from both of the two island chains locally known as the Ratak and Ralik, or “sunrise” and “sunset”, representing their respective positions east and west. Additionally, their latitudinal positions ranged from 4.5 to 14.7 degrees. From north-to-south the atolls surveyed were Rongelap, Utrik, Mejit, Wotho, Wotje, Ujae, Lae, Maololap, Aur, Majuro, and Namdrik. Each is unique in its size, shape, and human population density (Table 1). Lagoon sizes range between 8.42 km<sup>2</sup> and 1004.32 km<sup>2</sup>, while human population densities vary between 0.07 and 94.21 people per reef area km<sup>2</sup>. Notably, Rongelap represents the largest atoll and also the lowest human population density (79 people, 0.07 people per km<sup>2</sup>). All residents of Rongelap were evacuated in 1954 following the Castle Bravo test of the nuclear bomb in nearby Bikini atoll which caused massive amounts of radioactive fallout to blanket the island. There has been sparse human population on Rongelap ever since, allowing it to serve as a near pristine reference for other atolls. Conversely, Majuro, being the capitol and urban center for the country, constitutes the highest human population density of any atoll in the study with 94.21 people km<sup>-1</sup>. Underwater visual census surveys were conducted opportunistically between 2011 and 2017 (Table 1).

Table 2. Summary of island geographic, environmental, and anthropogenic statistics.

Island	Number of Sites	Latitude	Lagoon Size (km <sup>2</sup> )	Chlorophyll-a estimate	S.S.T.	Total Reef Area (km <sup>2</sup> )	Human Population (2011)
Aur	13	8.27	239.78	0.054	28.9	47.41	499
Lac	13	8.93	17.66	0.045	29.0	11.80	317
Majuro	35	7.13	295.05	0.065	29.2	57.43	27797
Maloclap	18	8.70	972.72	0.053	28.8	95.44	682
Mejit	4	10.28	3.73	0.041	28.5	4.50	348
Namdrik	8	5.61	8.12	0.068	29.6	9.92	508
Rongelap	10	11.22	1004.32	0.044	28.4	135.24	79
Ujae	16	9.06	185.94	0.047	28.9	63.31	364
Utrik	7	11.23	57.73	0.043	28.3	39.64	435
Wotho	12	10.11	94.92	0.042	28.7	14.09	97
Wotje	15	9.43	624.34	0.051	28.6	88.84	859



### ***Survey Design***

Sites for underwater visual censuses were selected using a standardized set of criteria (Houk et al. 2015). First, sites were divided amongst the two major habitats, outer barrier reefs and inner patch/back reefs. Sites were then distributed along distance gradients from human populations, both inside and outside any site-based management, and across major environmental regimes such as wave energy when conditions permitted. This design provided a representative snapshot of fish assemblages for each atoll that was suitable for comparative analysis. A total of 150 sites were included in the analysis.

### ***Fish data collection***

Fisheries data were collected by four calibrated observers, utilizing a modified stationary point count (SPC) method (Bannerot and Bohnsack 1986; Houk et al. 2015). Following the 10m depth contour, a single observer stopped at ~20m intervals along a series of 5, 50m transects laid end to end, partitioned by short separations. During each 3 minute observational period, fish observers recorded the identity and estimated the fork length for all food fish greater than 10 cm long within a 5m radius. This resulted in 12 replicate SPC stations per site. Fish lengths were later binned into 5 cm size classes prior to analyses. Biomass estimates were calculated using length-weight relationships gathered from fisheries-dependent studies in Micronesia, or FishBase ([www.fishbase.org](http://www.fishbase.org)) (Kulbicki et al. 2005; Cuetos-Bueno and Houk 2018; Cuetos-Bueno et al. 2018; Houk et al. 2018). Fish data were aggregated by several taxonomic and functional grouping categories: (i) families, (ii) genus, (iii) genus plus body-size (e.g., small and large-bodied parrotfishes, see Houk et al. 2017 for specific criteria), and (iv) trophic levels (Table 2). Finally, in order to understand local processes more clearly, we also calculated a previously defined fish condition score for each site that was derived from a group

Table 3. Summary of fish species groupings and Length-Weight ratios used.

Trophic Group	Functional Group	Species	LW_a	LW_b
Herbivore	Large-bodied acanthurid	<i>Acanthurus blochii</i>	0.02506	3.032
Herbivore	Large-bodied acanthurid	<i>Acanthurus dussumieri</i>	0.04256	2.8683
Herbivore	Large-bodied acanthurid	<i>Acanthurus xanthopterus</i>	0.02673	2.984
Herbivore	Large-bodied parrotfish	<i>Cetoscarus bicolor</i>	0.029265239	2.887848184
Herbivore	Large-bodied parrotfish	<i>Chlorurus frontalis</i>	0.027972548	2.907018223
Herbivore	Large-bodied parrotfish	<i>Chlorurus microrbinos</i>	0.015214273	3.099015775
Herbivore	Large-bodied parrotfish	<i>Hipposcarus longiceps</i>	0.022961873	2.929937799
Herbivore	Large-bodied parrotfish	<i>Scarus altipinnis</i>	0.009040059	3.250312707
Herbivore	Large-bodied parrotfish	<i>Scarus festivus</i>	0.0234	2.956
Herbivore	Large-bodied parrotfish	<i>Scarus forsteni</i>	0.03365	2.918
Herbivore	Large-bodied parrotfish	<i>Scarus ghobban</i>	0.008899	3.126
Herbivore	Large-bodied parrotfish	<i>Scarus rubroviolaceus</i>	0.023788333	2.963532937
Herbivore	Large-bodied parrotfish	<i>Scarus xanthopleura</i>	0.0234	2.956
Herbivore	Naso lituratus	<i>Naso lituratus</i>	0.068167175	2.661608318
Herbivore	Naso unicornis	<i>Naso unicornis</i>	0.039370491	2.795422791
Herbivore	Rabbitfish	<i>Siganus argenteus</i>	0.039711356	2.741984707
Herbivore	Rabbitfish	<i>Siganus puellus</i>	0.009282224	3.273064957
Herbivore	Rabbitfish	<i>Siganus punctatus</i>	0.019924094	3.051196494
Herbivore	Rabbitfish	<i>Siganus spinus</i>	0.01502	3.093
Herbivore	Rabbitfish	<i>Siganus vulpinus</i>	0.078505031	2.549788208
Herbivore	Rudderfish	<i>Kyphosus cinerascens</i>	0.115278172	2.527519171
Herbivore	Rudderfish	<i>Kyphosus sp (Kyphosidae)</i>	0.0129	3.151
Herbivore	Rudderfish	<i>Kyphosus vaigiensis</i>	0.013186648	3.180259197
Herbivore	Small-bodied acanthurid	<i>Acanthurus achilles</i>	0.028	2.983
Herbivore	Small-bodied acanthurid	<i>Acanthurus guttatus</i>	0.028	2.983
Herbivore	Small-bodied acanthurid	<i>Acanthurus leucocheilus</i>	0.028	2.983
Herbivore	Small-bodied acanthurid	<i>Acanthurus lineatus</i>	0.068343762	2.694853417
Herbivore	Small-bodied acanthurid	<i>Acanthurus nigricans</i>	0.028	2.983
Herbivore	Small-bodied acanthurid	<i>Acanthurus nigricauda</i>	0.140773768	2.467422208
Herbivore	Small-bodied acanthurid	<i>Acanthurus nigrofuscus</i>	0.02637	3.028
Herbivore	Small-bodied acanthurid	<i>Acanthurus nigraris</i>	0.028	2.983
Herbivore	Small-bodied acanthurid	<i>Acanthurus olivaceus</i>	0.028	2.983
Herbivore	Small-bodied acanthurid	<i>Acanthurus pyroferus</i>	0.028	2.983
Herbivore	Small-bodied acanthurid	<i>Ctenochaetus binotatus</i>	0.03916	2.875
Herbivore	Small-bodied acanthurid	<i>Ctenochaetus cyanocheilus</i>	0.0237	3.056
Herbivore	Small-bodied acanthurid	<i>Ctenochaetus flavicauda</i>	0.0237	3.056
Herbivore	Small-bodied acanthurid	<i>Ctenochaetus hawaiiensis</i>	0.02239	2.97
Herbivore	Small-bodied acanthurid	<i>Ctenochaetus striatus</i>	0.02313	3.063
Herbivore	Small-bodied acanthurid	<i>Ctenochaetus strigosus</i>	0.0237	3.056
Herbivore	Small-bodied acanthurid	<i>Zebrasoma scopas</i>	0.02905	2.993
Herbivore	Small-bodied acanthurid	<i>Zebrasoma veliferum</i>	0.03425	2.866

Herbivore	Small-bodied parrotfish	<i>Calotomus carolinus</i>	0.01049	3.146
Herbivore	Small-bodied parrotfish	<i>Chlorurus bleekeri</i>	0.027972548	2.907018223
Herbivore	Small-bodied parrotfish	<i>Chlorurus japanensis</i>	0.01281	3.113
Herbivore	Small-bodied parrotfish	<i>Chlorurus sordidus</i>	0.01281	3.113
Herbivore	Small-bodied parrotfish	<i>Scarus bleekeri</i>	0.0234	2.956
Herbivore	Small-bodied parrotfish	<i>Scarus dimidiatus</i>	0.0234	2.956
Herbivore	Small-bodied parrotfish	<i>Scarus flavipectoralis</i>	0.0234	2.956
Herbivore	Small-bodied parrotfish	<i>Scarus frenatus</i>	0.0234	2.956
Herbivore	Small-bodied parrotfish	<i>Scarus fuscocaudalis</i>	0.0234	2.956
Herbivore	Small-bodied parrotfish	<i>Scarus globiceps</i>	0.0234	2.956
Herbivore	Small-bodied parrotfish	<i>Scarus niger</i>	0.028048665	2.938715328
Herbivore	Small-bodied parrotfish	<i>Scarus oviceps</i>	0.014411706	3.139911718
Herbivore	Small-bodied parrotfish	<i>Scarus psittacus</i>	0.0201	3.007
Herbivore	Small-bodied parrotfish	<i>Scarus schlegeli</i>	0.05001	2.843
Herbivore	Small-bodied parrotfish	<i>Scarus sp</i>	0.0234	2.956
Herbivore	Small-bodied parrotfish	<i>Scarus spinus</i>	0.0234	2.956
Planktivore	Large-bodied acanthurid	<i>Acanthurus mata</i>	0.180381122	2.343910383
Planktivore	Naso other	<i>Naso annulatus</i>	0.05103	2.715
Planktivore	Naso other	<i>Naso brevirostris</i>	0.01065	3.243
Planktivore	Naso other	<i>Naso caesius</i>	0.0085	3.25
Planktivore	Naso other	<i>Naso hexacanthus</i>	0.02017	2.956
Planktivore	Naso other	<i>Naso vlamingii</i>	0.0085	3.25
Planktivore	Small-bodied acanthurid	<i>Acanthurus thompsoni</i>	0.028	2.983
Planktivore	Squirrel-Cardinal-Soldier	<i>Priacanthus hamrur</i>	0.02997	2.801
Secondary	Batfish	<i>Platax orbicularis</i>	0.0443	2.951
Secondary	Batfish	<i>Platax teira</i>	0.0443	2.951
Secondary	Cheilinus undulatus	<i>Cheilinus undulatus</i>	0.01131	3.136
Secondary	Goatfish	<i>Mulloidichthys flavolineatus</i>	0.01197	3.101
Secondary	Goatfish	<i>Mulloidichthys vanicolensis</i>	0.0074	3.293
Secondary	Goatfish	<i>Parupeneus barberinoides</i>	0.0145	3.13
Secondary	Goatfish	<i>Parupeneus barberinus</i>	0.070679547	2.585884177
Secondary	Goatfish	<i>Parupeneus bifasciatus</i>	0.0145	3.13
Secondary	Goatfish	<i>Parupeneus cyclostomus</i>	0.0145	3.13
Secondary	Goatfish	<i>Parupeneus insularis</i>	0.0145	3.13
Secondary	Goatfish	<i>Parupeneus multifasciatus</i>	0.01136	3.221
Secondary	Goatfish	<i>Parupeneus pleurostigma</i>	0.0145	3.13
Secondary	Hawkfish	<i>Paracirrhites spp.</i>	0.00912	3.07
Secondary	Large-bodied emperor	<i>Gymnocranius microdon</i>	0.0302	2.909
Secondary	Large-bodied emperor	<i>Gymnocranius sp</i>	0.0302	2.909
Secondary	Large-bodied emperor	<i>Lethrinus erythracanthus</i>	0.014682113	3.0542221
Secondary	Large-bodied emperor	<i>Lethrinus olivaceus</i>	0.02936	2.851
Secondary	Large-bodied emperor	<i>Lethrinus xanthurus</i>	0.02007	2.964
Secondary	Large-bodied emperor	<i>Monotaxis grandoculis</i>	0.038482789	2.837921466
Secondary	Large-bodied grouper	<i>Aethaloperca rogae</i>	0.063722877	2.675775018
Secondary	Large-bodied snapper	<i>Lutjanus gibbus</i>	0.023208297	2.857425253



Secondary	Large-bodied snapper	<i>Lutjanus monostigma</i>	0.02218	2.913
Secondary	Large-bodied snapper	<i>Macolor macularis</i>	0.032679015	2.889810171
Secondary	Large-bodied snapper	<i>Macolor niger</i>	0.032679015	2.889810171
Secondary	Mullet	<i>Moolgarda sebeli</i>	0.0179	2.95
Secondary	Ray	<i>Aetobatus narinari</i>	0.00586	3.13
Secondary	Small-bodied emperor	<i>Gnathodentex aureolineatus</i>	0.01804	3.063
Secondary	Small-bodied emperor	<i>Lethrinus erythropterus</i>	0.0165	3.043
Secondary	Small-bodied emperor	<i>Lethrinus harak</i>	0.009	3.123
Secondary	Small-bodied emperor	<i>Lethrinus obsoletus</i>	0.01733	3.026
Secondary	Small-bodied emperor	<i>Lethrinus sp. (Lethrinidae)</i>	0.0165	3.043
Secondary	Small-bodied snapper	<i>Lutjanus fulvus</i>	0.02106	2.974
Secondary	Small-bodied snapper	<i>Lutjanus kasmira</i>	0.00842	3.247
Secondary	Small-bodied snapper	<i>Lutjanus semicinctus</i>	0.037429332	2.789692953
Secondary	Spinecheck	<i>Pentapodus caninus</i>	0.0157	3.054
Secondary	Spinecheck	<i>Scolopsis sp.</i>	0.0157	3.054
Secondary	Squirrel-Cardinal-Soldier	<i>Myripristis adusta</i>	0.025679441	2.992349207
Secondary	Squirrel-Cardinal-Soldier	<i>Myripristis amaena</i>	0.01576	3.261
Secondary	Squirrel-Cardinal-Soldier	<i>Myripristis berndti</i>	0.02769	3.003
Secondary	Squirrel-Cardinal-Soldier	<i>Myripristis kuntee</i>	0.00991	4.468
Secondary	Squirrel-Cardinal-Soldier	<i>Myripristis sp (Holocentridae)</i>	0.0276	3.059
Secondary	Squirrel-Cardinal-Soldier	<i>Neoniphon sammara</i>	0.02762	2.888
Secondary	Squirrel-Cardinal-Soldier	<i>Neoniphon sp (Holocentridae)</i>	0.0288	2.867
Secondary	Squirrel-Cardinal-Soldier	<i>Pempheris ovalensis</i>	0.01331	3
Secondary	Squirrel-Cardinal-Soldier	<i>Sargocentron caudimaculatum</i>	0.0219	3.047
Secondary	Squirrel-Cardinal-Soldier	<i>Sargocentron spiniferum</i>	0.094581913	2.564566801
Secondary	Squirrel-Cardinal-Soldier	<i>Sargocentron tiere</i>	0.0219	3.047
Secondary	Sweetlips	<i>Plectorhinchus picus</i>	0.01151	3.089
Secondary	Trevally/Jack	<i>Selar crumenophthalmus</i>	0.01003	3.18
Secondary	Triggerfish	<i>Balistapus undulatus</i>	0.0057	3.393
Secondary	Triggerfish	<i>Balistoides viridescens</i>	0.02442	3.018
Secondary	Triggerfish	<i>Cantherhines dumerilii</i>	0.0057	3.393
Secondary	Triggerfish	<i>Melichthys niger</i>	0.0057	3.393
Secondary	Triggerfish	<i>Melichthys vidua</i>	0.0057	3.393
Secondary	Triggerfish	<i>Pseudobalistes flavimarginatus</i>	0.0057	3.393
Secondary	Triggerfish	<i>Sufflamen bursa</i>	0.0324	2.929
Secondary	Triggerfish	<i>Sufflamen chrysopteron</i>	0.0324	2.929
Secondary	Wrasse	<i>Bodianus axillaris</i>	0.0108	3.173
Secondary	Wrasse	<i>Cheilinus digrammus</i>	0.0155	3.058
Secondary	Wrasse	<i>Cheilinus fasciatus</i>	0.0155	3.058
Secondary	Wrasse	<i>Cheilinus trilobatus</i>	0.01623	3.059
Secondary	Wrasse	<i>Cheilinus unifasciatus</i>	0.0155	3.058
Secondary	Wrasse	<i>Coris aygula</i>	0.00266	3.489
Secondary	Wrasse	<i>Epibulus insidiator</i>	0.01614	3.081
Secondary	Wrasse	<i>Halichoeres trimaculatus</i>	0.02749	2.736
Secondary	Wrasse	<i>Hemigymnus fasciatus</i>	0.02423	2.923

Secondary	Wrasse	<i>Hemigymnus melapterus</i>	0.02423	2.923
Secondary	Wrasse	<i>Oxycheilinus digramma</i>	0.0155	3.058
Secondary	Wrasse	<i>Oxycheilinus unifasciatus</i>	0.0155	3.058
Secondary	Wrasse	<i>Tbalassoma hardwickii</i>	0.01783	2.978
Tertiary	Large-bodied grouper	<i>Amyperodon leucogrammicus</i>	0.00142	3.548
Tertiary	Large-bodied grouper	<i>Cephalopholis argus</i>	0.00929	3.181
Tertiary	Large-bodied grouper	<i>Epinephelus cyanopodus</i>	0.01105	3.114
Tertiary	Large-bodied grouper	<i>Epinephelus fuscoguttatus</i>	0.01335	3.057
Tertiary	Large-bodied grouper	<i>Epinephelus bowlandi</i>	0.060692156	2.611042432
Tertiary	Large-bodied grouper	<i>Epinephelus lanceolatus</i>	0.0173	3
Tertiary	Large-bodied grouper	<i>Epinephelus maculatus</i>	0.017660311	2.930226261
Tertiary	Large-bodied grouper	<i>Epinephelus polyphekadion</i>	0.013949417	3.041713628
Tertiary	Large-bodied grouper	<i>Epinephelus tawina</i>	0.017677396	2.968599504
Tertiary	Large-bodied grouper	<i>Plectropomus areolatus</i>	0.011232925	3.077009777
Tertiary	Large-bodied grouper	<i>Plectropomus laevis</i>	0.00591	3.238
Tertiary	Large-bodied grouper	<i>Plectropomus leopardus</i>	0.01175	3.06
Tertiary	Large-bodied grouper	<i>Plectropomus oligacanthus</i>	0.015474026	2.972052707
Tertiary	Large-bodied grouper	<i>Pariola louti</i>	0.021194765	2.942862683
Tertiary	Large-bodied reef-pelagic	<i>Elagatis bipinnulata</i>	0.011708047	3
Tertiary	Large-bodied reef-pelagic	<i>Grammatorcynus bilineatus</i>	0.00661	3.01
Tertiary	Large-bodied reef-pelagic	<i>Gymnosarda unicolor</i>	0.0105	3.065
Tertiary	Large-bodied reef-pelagic	<i>Scomberoides lysan</i>	0.01122	2.87
Tertiary	Large-bodied reef-pelagic	<i>Scomberomorus commerson</i>	0.01617	2.856
Tertiary	Large-bodied reef-pelagic	<i>Sphyræna barracuda</i>	0.00813	2.93
Tertiary	Large-bodied reef-pelagic	<i>Sphyræna forsteri</i>	0.00534	3.034
Tertiary	Large-bodied reef-pelagic	<i>Sphyræna jello</i>	0.0058	3.013
Tertiary	Large-bodied reef-pelagic	<i>Sphyræna genie</i>	0.0058	3.013
Tertiary	Large-bodied reef-pelagic	<i>Tuna sp (Scombridae)</i>	0.00481	3.368
Tertiary	Large-bodied snapper	<i>Aprion virescens</i>	0.02297	2.886
Tertiary	Large-bodied snapper	<i>Lutjanus bohar</i>	0.01563	3.059
Tertiary	Reef-pelagic	<i>Decapterus marnadsi</i>	0.0119	3
Tertiary	Reef-pelagic	<i>Sphyræna helleri</i>	0.0058	3.013
Tertiary	Shark	<i>Carcharhinus albimarginatus</i>	1e-04	4.268
Tertiary	Shark	<i>Carcharhinus amblyrhynchos</i>	0.00227	3.373
Tertiary	Shark	<i>Carcharhinus melanopterus</i>	0.0013	3.508
Tertiary	Shark	<i>Nebrius ferrugineus</i>	0.00417	3.07
Tertiary	Shark	<i>Stegostoma varium</i>	0.00389	3.12
Tertiary	Shark	<i>Trienodon obesus</i>	0.0018	3.344
Tertiary	Small-bodied grouper	<i>Cephalopholis leopardus</i>	0.0115	3.109
Tertiary	Small-bodied grouper	<i>Cephalopholis spiloparaea</i>	0.0115	3.109
Tertiary	Small-bodied grouper	<i>Cephalopholis urodeta</i>	0.02822	2.818
Tertiary	Small-bodied grouper	<i>Epinephelus fasciatus</i>	0.01383	3.041
Tertiary	Small-bodied grouper	<i>Epinephelus hexagonatus</i>	0.0122	3.053
Tertiary	Small-bodied grouper	<i>Epinephelus merra</i>	0.01584	2.966
Tertiary	Small-bodied grouper	<i>Epinephelus spilotoceps</i>	0.0122	3.053

Tertiary	Small-bodied grouper	<i>Gracila albomarginata</i>	0.0134	3.031
Tertiary	Small-bodied snapper	<i>Aphareus furca</i>	0.0167	3.022
Tertiary	Trevally/Jack	<i>Alectis ciliaris</i>	0.0083	3.197
Tertiary	Trevally/Jack	<i>Carangoides ferdau</i>	0.03683	2.851
Tertiary	Trevally/Jack	<i>Carangoides oblongus</i>	0.0361	2.812
Tertiary	Trevally/Jack	<i>Carangoides orthogrammus</i>	0.01559	3.026
Tertiary	Trevally/Jack	<i>Caranx ignobilis</i>	0.0151	3.086
Tertiary	Trevally/Jack	<i>Caranx lugubris</i>	0.0198	2.986
Tertiary	Trevally/Jack	<i>Caranx melampygus</i>	0.0234	2.918
Tertiary	Trevally/Jack	<i>Caranx sexfasciatus</i>	0.0198	2.986
Tertiary	Trevally/Jack	<i>Trachinotus baillonii</i>	0.0083	3.197
Tertiary	Trevally/Jack	<i>Trachinotus blochii</i>	0.0083	3.197

of regional scientists (Houk et al. 2015). This score combined total fish biomass, predator biomass, mean size including sharks, species evenness, and assemblage heterogeneity into a single metric believed to reflect attributes of a given reef fish community that are beneficial for ecosystem functioning. Additionally, having a combined metric assists researchers in assessing differences across locales with uncertain disturbance histories. For instance, disturbances that result in increased algal growth are expected to encourage the population growth of small herbivores (Halford et al. 2004). A situation like this would effectively increase the overall biomass, but decrease the mean size.

### ***Environmental data***

Data for a number of environmental factors was acquired from several open access sources online. Geomorphological information for each atoll was extracted from a dataset of satellite derived maps of global coral reefs (UNEP-WCMC, 2010, <http://data.unep-wcmc.org/datasets/1>). Geographical measurements of atoll sizes were provided by a 2011 census conducted by the RMI Economic Policy and Planning Statistics Office (EPPSO, 2011). Boat-based access was estimated by calculating the shortest path distance between each site and each human population center within an atoll, without crossing land or shallow reef. This calculation required using a suite of mapping packages for R: *sp*, *raster*, *rgeos*, and *gdistance* (Pebesma & Bivand, 2005; Hijmans, 2017; Bivand & Rundel, 2017; van Etten, 2018). In addition, a second measure of human access was calculated by taking straight line distances for sites within 2 kilometers of any populated island. These reefs were considered to be accessible from land based upon discussions with fishers. Because some atolls had more than one populated island, the final distance metric was integrated over all possible human population centers, and weighted by the size of the human population.



$$Final\ Access\ Value = \sum Distance * (island\ population / total\ atoll\ population)$$

Since this variable no longer reflected just a measurable distance, it had to be scaled within each atoll in order to be comparable. Monthly mean sea surface temperature data (0.025° resolution) from NASA's Aqua MODIS satellite was sourced from the NOAA's Bloomwatch 180 website (<https://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW180.jsp>) for all available months from January 2011 to January 2018. Coordinates that fell within the lagoon or were too close to land were discarded. The exclusion zone was half of the diagonal distance between points (~1,943m) as explained in Gove et al. 2013. The long-term average for islands was considered to be the average of all remaining points within 4 exclusion zones (1943-7772m). For site level comparisons, the long-term average was calculated for the pixel closest to each survey site. Similar averages were derived for chlorophyll- $\alpha$  (0.025° resolution) to serve as a proxy for the natural oceanic productivity associated with each atoll and outer reef site. Site-level wave energy data was calculated from 10 year wind records, fetch distances, and angles of exposure, following previous studies (Quikscat wind dataset 1999-2009; Ekeboom et al. 2003; Houk et al. 2014; Houk et al. 2015). Wave energy estimates represented an estimate of natural flushing as well as fishing accessibility, and is therefore both a natural and human factor.

### ***Statistical Analysis***

Statistical analyses were conducted using the latest version of R (Version 3.4.0, R Core Team, 2017). The statistical approach aimed to comprehensively quantify relationships between reef fish assemblages, natural environmental factors, and proxies for fishing pressure across the RMI at two spatial scales, across all atolls and within each atoll.

This study first examined inter-atoll variation in fish assemblages for each major reef type separately. Data were aggregated at the site level, then the site averages were taken to represent individual atolls. Due to differing island geomorphology and logistical constraints, some atolls didn't have data available for both reef types, or had insufficient replication ( $n=1$ ) to include in the analysis. In total, these criteria yielded 10 atolls for examining fish assemblages on both inner and outer reef types. While the number of atolls remained constant, atoll identity differed for each reef type examination

Forward, step-wise multiple regressions were first used to examine only natural environmental factors against the dependent biological variables. This process began by identifying the predictor variable with the best fit to the observed data. Forward steps were only taken when the model fit was improved (AIC), and residual normality and leverage were verified. In addition to checking whether the predictor variables explain the data significantly more than can be expected by chance ( $p<0.05$ ), all models were visually checked for residual normality using a Q-Q plot. If any questionable patterns were found during the visual inspection, the residuals were then run through a Shapiro-Wilkes test. Models found to have significantly non-normal residuals ( $p<0.05$ ) during the Shapiro-Wilkes test were discarded. Furthermore, residuals were assessed for leverage using a plot of Cook's distance. Models with points that had a Cook's D higher than 0.5 were then run again without the leveraging point. If the resulting model remained significant without the point, the original model was deemed acceptable. Given that data existed for 10 atolls, only models with single terms were included, although terms could include interactions.

Dependent variables included for the inter-atoll analyses included total fish biomass, as well as the respective biomass for sharks, herbivores, planktivores, secondary consumers and tertiary consumers. Independent predictor variables were the environmental factors noted

above and several derived human factors. The human population factors included total human population and three different measures of human population density with human population divided by lagoon area, total reef area, or patch reef area. Each predictor variable was centered and scaled, mean of zero and standard deviation of 1, prior to any modelling. Biomass was log transformed,  $\log(x+1)$ , in order to normalize the data. To avoid collinearity within the models, we ensured that predictor variables were not overly correlated ( $r > 0.5$ ), by producing a correlation matrix for all factors each time the scale of investigation changed. All correlations that were found between predictors were discussed and no related variables were included in the model simultaneously. The residual variance left unaccounted for by natural factors was then examined with respect to human factors following the same procedures. In order to identify groups of conservation interest, the analyses were repeated at the functional group and species level. However instead of using biomass, we chose to use the percent contribution each group had to the overall biomass in order to capture demographic differences between these communities. Finally, in order to appreciate inter-atoll differences using another measure we assessed the distribution of site-level fish condition scores. Because the condition scores were scaled within reef type groups the values from different reefs within an atoll cannot be compared. A single tailed Wald's t-test was used to determine if the distribution of scores within an atoll was significantly less than or greater than the distribution of all other sites.

For intra-atoll analyses, linear mixed effects models were performed using the *lme4* package for R (Bates et al. 2015) to test the local relationship between fish community condition scores, defined above, and the suite of independent variables. There are fewer predictor variables available for site-level analyses, therefore the modeling was constrained to reef type and travel distance to nearest human population. The calculated wind/wave energy (from above), and chlorophyll- $\alpha$  estimates were available as additional predictors for models

on outer reef subsets. Due to the inherently grouped nature of the sites, island was treated as a random effect. Reef type was also a random effect but was nested within each island. Lastly, inter-observer variation is real and unavoidable so observers were treated as a fixed effect in all the models. Two null models were created for comparative purposes, one with a fixed slope across groups and one that allowed the slope to vary within each group. Significance was then obtained via a likelihood ratio test between the null model and the full model that included the distance factor. The residuals of all models were visually examined for heteroscedasticity, of which none was found.

## **Results**

### ***Inter-Atoll Models***

Across the 10 study atolls, average fish biomass varied greatly between 4.01 kg/SPC to a maximum of 43.63 kg/SPC (Table 3). Our most undisturbed atoll, Rongelap consistently outperformed the inner reefs of all other atolls. In addition to having the highest average total biomass across inner reefs (34 kg/SPC), it also had the greatest biomass for sharks (60.957 kg/SPC), tertiary consumers (10.06 kg/SPC), secondary consumers (8.16 kg/SPC), and planktivores (9.379 kg/SPC). Unfortunately, only a single site was sampled outside the lagoon which prevented us from using it as a reference for analyses of outer reefs. Shark biomass varied more than any other functional group with the highest value representing an average of 65 kg of shark biomass per SPC and the lowest values recorded no sharks. Biomass estimates for other groups were more consistent. The average biomass of tertiary consumers on outer reefs was highest on Wocho at 12.9 kg/SPC and lowest on Mejit with only 0.86 kg/SPC. Across inner reefs the biomass ranged from 10.06 kg/SPC on Rongelap to 0.05 kg/SPC on Lae. Planktivore biomass on outer reefs varied from 2.45 kg/SPC on Maloelap to 0.057



Table 4. Average fish biomass (kg) per SPC across several groups. Sharks were removed from all calculations of tertiary and total biomass.

Island	Reef Type	Total Biomass	Shark	Tertiary	Planktivore	Secondary	Herbivore
<b>Aur</b>	Inner	12.09 ± 5.6	2.06 ± 2.5	2.21 ± 2.4	4.31 ± 1.6	1.23 ± 0.9	4.3 ± 2.2
	Outer	11.07 ± 4.6	26.34 ± 43	1.18 ± 2.4	1.35 ± 1.2	3.3 ± 2.4	4.27 ± 2.6
<b>Lae</b>	Inner	4.01 ± 1.5	0.88 ± 1.8	0.05 ± 0.1	0.25 ± 0.3	1.03 ± 1.4	2.68 ± 0.9
	Outer	18.64 ± 14	5.32 ± 8.7	2.09 ± 2.5	0.07 ± 0.1	3.71 ± 5.1	14.41 ± 9.7
<b>Majuro</b>	Inner	6.08 ± 5.4	1.93 ± 4.7	0.54 ± 1	0.6 ± 2.8	1.81 ± 2.4	3.37 ± 2.4
	Outer	7.21 ± 4.2	0.31 ± 0.7	0.67 ± 1.7	0.04 ± 0.1	1.18 ± 1	4.02 ± 3.5
<b>Maloelap</b>	Inner	11.22 ± 8.1	4.04 ± 5.5	1.38 ± 1.5	2.71 ± 3.5	2.53 ± 2.7	5.39 ± 2.7
	Outer	20.74 ± 19.3	20.92 ± 112.2	3.36 ± 2.1	2.45 ± 1.8	7.75 ± 1.8	14.92 ± 16.1
<b>Mejit</b>	Outer	6.4 ± 1.2	0.06 ± 0.1	0.86 ± 0.2	0.2 ± 0.2	1.23 ± 0.2	4.11 ± 1.5
<b>Nandrik</b>	Inner	5.55 ± 4.7	0 ± 0	0.15 ± 0	0 ± 0	1.66 ± 1.4	3.74 ± 3.3
	Outer	5.55 ± 4.2	3.12 ± 2.7	0.94 ± 0.7	0.06 ± 0	1 ± 0.5	3.54 ± 3.5
<b>Rongelap</b>	Inner	34.84 ± 17.3	60.96 ± 89.2	10.06 ± 6.6	9.38 ± 7.9	8.16 ± 9.5	4.2 ± 3.5
<b>Ujae</b>	Inner	5.47 ± 4.3	1.71 ± 2.4	1.96 ± 3.2	0.12 ± 0.2	1.48 ± 1.3	1.92 ± 0.3
	Outer	43.65 ± 28.1	17.96 ± 31.8	11.72 ± 12	1.04 ± 4.5	19.18 ± 22.7	8.06 ± 6.8
<b>Utrik</b>	Inner	5.63 ± 6.1	0 ± 0	2.74 ± 3.9	0.03 ± 0	1.45 ± 1.1	1.42 ± 1.1
	Outer	6.6 ± 4.6	2.98 ± 2	1.99 ± 1.8	0.32 ± 0.4	1.85 ± 1.2	2.43 ± 1.7
<b>Wotho</b>	Inner	18.4 ± 7.4	22.97 ± 24.3	5.43 ± 4.4	1.07 ± 1.6	3.25 ± 2.4	8.65 ± 3
	Outer	28.59 ± 16.1	11.83 ± 12.8	12.94 ± 10.8	1.06 ± 1.3	8.49 ± 7.6	6.1 ± 7.5
<b>Wotje</b>	Inner	8.53 ± 4.9	4.7 ± 6.2	2.04 ± 2.1	1.09 ± 2	1.54 ± 1.5	2.48 ± 3.1
	Outer	9.01 ± 3.7	5.54 ± 3.9	2.1 ± 0.8	0.68 ± 1.1	1.84 ± 1.1	4.39 ± 2.8

kg/SPC on Majuro. Rongelap again, as stated above, had the highest average planktivore biomass for inner reefs at 9.379 kg/SPC, while there were no planktivores recorded on Namdrik's inner reefs. Secondary consumers on outer reefs had average values between 19.18 kg/ SPC on Ujae and 1.00 on Namdrik. On inner reefs Rongelap had the most secondary consumers at 8.16 kg/SPC while Lae had the least at 1.03 kg/SPC. Finally, herbivore biomass was lowest on Utrik for both inner and outer reefs (1.42 & 2.43 kg/SPC, respectively). The highest herbivore biomass was found on the outer reefs of Maloelap (14.92 kg/SPC) and the inner reefs of Wotho (8.65 kg/SPC).

Regression analyses found little support for natural environmental factors driving variation in fish biomass at the island scale. In fact, only tertiary consumers (inner reefs) and planktivores (inner and outer reefs) had significant relationships ( $p < 0.05$ ) with any of the natural factors and also did not exhibit unacceptable amounts of model leveraging (Table 4). Sea surface temperature had a negative relationship with tertiary consumer biomass on inner reefs, while latitude and total reef area both had positive associations. All three predictors explained roughly 50 percent of the variation in tertiary consumer biomass on inner reefs ( $R^2 = 0.54^{**}$ ,  $0.5^*$ , &  $0.48^*$  respectively)<sup>1</sup>. Latitude and sea surface temperature were found to be strongly correlated ( $R = -0.968$ ) with one another so in actuality they only represent a single relationship. The only other significant relationship found was larger lagoon size and total reef area promoted higher planktivore biomass ( $R^2 = 0.4^*$  &  $0.35^*$ , respectively), both of which are measures of habitat space. In summary, we rejected the hypothesis that natural factors were strong predictors of biomass within any fish trophic level.

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<sup>1</sup> Significance of linear models (\*  $< 0.05$ , \*\*  $< 0.01$ , \*\*\*  $< 0.001$ ).

Table 4. Single variable linear model results.

Dep. Variable	Transformation	Ind. Variable	Adj. R-squared	p-value	Std.err.	AIC	Shapiro-p	Significance	
<b>Inner</b>	Herbivore	log	pop.density.patch	0.248	0.081	0.346	10.944	0.242	NS
		log	Patch Reef area	0.053	0.255	0.389	13.251	0.325	NS
		log	pop.density	-0.015	0.379	0.402	13.946	0.851	NS
		log	pop.density.total	-0.043	0.451	0.408	14.222	0.963	NS
		log	Human Population	-0.058	0.496	0.411	14.361	0.982	NS
		log	lagoon.area.m	-0.089	0.622	0.417	14.652	0.836	NS
		log	Total Reef Area km2	-0.110	0.750	0.421	14.842	0.944	NS
		log	island.avg.SST	-0.114	0.784	0.422	14.877	0.886	NS
		log	latitude	-0.114	0.789	0.422	14.881	0.908	NS
		log	island.10.year.avg.chla	-0.124	0.922	0.424	14.964	0.959	NS
		none	pop.density.patch	0.072	0.228	2.003	46.042	0.482	NS
		none	pop.density	-0.101	0.688	2.183	47.758	0.169	NS
		none	lagoon.area.m	-0.102	0.695	2.184	47.767	0.049	NS
		none	Patch Reef area	-0.103	0.698	2.184	47.772	0.115	NS
	none	pop.density.total	-0.113	0.774	2.194	47.863	0.187	NS	
	none	island.10.year.avg.chla	-0.114	0.784	2.195	47.873	0.313	NS	
	none	Human Population	-0.116	0.802	2.197	47.888	0.184	NS	
	none	Total Reef Area km2	-0.116	0.804	2.197	47.890	0.114	NS	
	none	latitude	-0.125	0.960	2.206	47.969	0.194	NS	
	none	island.avg.SST	-0.125	0.974	2.206	47.971	0.183	NS	
	Planktivore	log	pop.density	0.489	0.015	0.551	20.245	0.531	*
		log	lagoon.area.m	0.409	0.028	0.593	21.704	0.337	*
		log	Total Reef Area km2	0.319	0.052	0.637	23.120	0.509	NS
		log	pop.density.patch	0.294	0.061	0.648	23.479	0.509	NS



Reef Type	Dep. Variable	Transformation	Ind. Variable	Adj. R-squared	p-value	Std.err.	AIC	Shapiro-p	Significance
		log	pop.density.total	0.231	0.090	0.676	24.331	0.284	NS
		log	island.avg.SST	0.061	0.243	0.748	26.330	0.714	NS
		log	Patch Reef area	0.033	0.286	0.759	26.625	0.029	NS
		log	latitude	0.014	0.320	0.766	26.822	0.623	NS
		log	Human Population	-0.021	0.394	0.780	27.170	0.229	NS
		log	island.10.year.avg.chla	-0.093	0.640	0.807	27.847	0.265	NS
		none	Total Reef Area km2	0.460	0.019	2.163	47.574	0.309	*
		none	lagoon.area.m	0.386	0.033	2.305	48.845	0.457	*
		none	pop.density.patch	0.153	0.144	2.708	52.069	0.053	NS
		none	island.avg.SST	0.064	0.240	2.847	53.073	0.115	NS
		none	latitude	0.052	0.257	2.865	53.198	0.166	NS
		none	pop.density	-0.005	0.357	2.949	53.778	0.007	NS
		none	island.10.year.avg.chla	-0.067	0.527	3.038	54.374	0.012	NS
		none	pop.density.total	-0.083	0.591	3.061	54.523	0.003	NS
		none	Human Population	-0.096	0.655	3.079	54.643	0.002	NS
		none	Patch Reef area	-0.110	0.750	3.100	54.772	0.003	NS
	Secondary	log	pop.density	0.410	0.027	0.339	10.520	0.474	*
		log	pop.density.total	0.345	0.043	0.357	11.573	0.073	*
		log	pop.density.patch	0.313	0.054	0.366	12.049	0.154	NS
		log	Total Reef Area km2	0.214	0.100	0.391	13.391	0.119	NS
		log	lagoon.area.m	0.144	0.151	0.409	14.242	0.063	NS
		log	Human Population	0.094	0.202	0.420	14.820	0.227	NS
		log	island.avg.SST	0.060	0.245	0.428	15.185	0.217	NS
		log	latitude	0.057	0.249	0.429	15.216	0.137	NS
		log	island.10.year.avg.chla	-0.030	0.417	0.448	16.103	0.091	NS

Table 4. Single variable linear model results. (continued)

Reef Type	Dep. Variable	Transformation	Ind. Variable	Adj. R-squared	p-value	Std.err.	AIC	Shapiro-p	Significance
		log	Patch Reef area	-0.057	0.492	0.454	16.352	0.003	NS
		none	Total Reef Area km2	0.467	0.018	1.549	40.899	0.832	*
		none	lagoon.area.m	0.342	0.044	1.722	43.013	0.418	*
		none	latitude	0.132	0.163	1.978	45.788	0.110	NS
		none	island.avg.SST	0.074	0.226	2.042	46.429	0.045	NS
		none	pop.density.patch	0.059	0.247	2.059	46.594	0.004	NS
		none	island.10.year.avg.chla	-0.022	0.395	2.145	47.414	0.003	NS
		none	pop.density	-0.063	0.514	2.188	47.810	0.001	NS
		none	pop.density.total	-0.100	0.680	2.226	48.153	0.000	NS
		none	Human Population	-0.108	0.733	2.234	48.223	0.000	NS
		none	Patch Reef area	-0.119	0.844	2.246	48.326	0.000	NS
Shark		log	pop.density.patch	0.707	0.001	0.712	25.350	0.154	**
		log	pop.density	0.573	0.007	0.860	29.136	0.239	**
		log	pop.density.total	0.418	0.026	1.004	32.236	0.810	*
		log	Total Reef Area km2	0.335	0.046	1.073	33.559	0.165	*
		log	lagoon.area.m	0.298	0.059	1.102	34.097	0.012	NS
		log	latitude	0.175	0.126	1.195	35.713	0.711	NS
		log	Patch Reef area	0.166	0.134	1.202	35.832	0.017	NS
		log	island.avg.SST	0.134	0.161	1.225	36.205	0.258	NS
		log	Human Population	0.100	0.195	1.249	36.588	0.702	NS
		log	island.10.year.avg.chla	0.085	0.213	1.259	36.758	0.993	NS
		none	Total Reef Area km2	0.388	0.032	14.998	86.305	0.597	*
		none	lagoon.area.m	0.228	0.092	16.842	88.624	0.207	NS
		none	latitude	0.197	0.111	17.182	89.024	0.158	NS
		none	island.avg.SST	0.115	0.179	18.034	89.993	0.052	NS

Table 4. Single variable linear model results. (continued)

Table 4. Single variable linear model results. (continued)

Reef Type	Dep. Variable	Transformation	Ind. Variable	Adj. R-squared	p-value	Std.err.	AIC	Shapiro-p	Significance
		none	pop.density.patch	0.106	0.189	18.131	90.100	0.004	NS
		none	island.10.year.avg.chla	0.053	0.255	18.657	90.671	0.007	NS
		none	pop.density	-0.029	0.412	19.448	91.502	0.001	NS
		none	pop.density.total	-0.084	0.598	19.963	92.025	0.000	NS
		none	Human Population	-0.095	0.651	20.062	92.124	0.000	NS
		none	Patch Reef area	-0.119	0.845	20.285	92.345	0.000	NS
	Tertiary	log	pop.density	0.691	0.002	0.409	14.287	0.606	**
		log	pop.density.total	0.675	0.002	0.420	14.799	0.952	**
		log	pop.density.patch	0.600	0.005	0.465	16.851	0.016	**
		log	island.avg.SST	0.543	0.009	0.498	18.192	0.914	**
		log	latitude	0.508	0.012	0.516	18.932	0.606	*
		log	Total Reef Area km2	0.419	0.026	0.561	20.593	0.863	*
		log	island.10.year.avg.chla	0.326	0.049	0.604	22.080	0.084	*
		log	Human Population	0.261	0.075	0.633	22.995	0.225	NS
		log	lagoon.area.m	0.232	0.090	0.645	23.392	0.467	NS
		log	Patch Reef area	-0.025	0.403	0.746	26.275	0.809	NS
		none	latitude	0.418	0.026	2.318	48.959	0.453	*
		none	Total Reef Area km2	0.381	0.034	2.390	49.570	0.517	*
		none	island.avg.SST	0.338	0.046	2.472	50.245	0.161	*
		none	pop.density.patch	0.220	0.097	2.683	51.889	0.051	NS
		none	island.10.year.avg.chla	0.215	0.099	2.691	51.944	0.075	NS
		none	lagoon.area.m	0.149	0.147	2.802	52.752	0.415	NS
		none	pop.density	0.113	0.181	2.861	53.172	0.018	NS
		none	pop.density.total	-0.017	0.383	3.063	54.536	0.024	NS
		none	Human Population	-0.044	0.454	3.104	54.802	0.020	NS



Table 4. Single variable linear model results. (continued)

Reef Type	Dep. Variable	Transformation	Ind. Variable	Adj. R-squared	p-value	Std.err.	AIC	Shapiro-p	Significance
Total		none	Patch Reef area	-0.108	0.733	3.197	55.393	0.014	NS
		log	pop.density.patch	0.576	0.007	0.390	13.321	0.947	**
		log	pop.density	0.560	0.008	0.397	13.679	0.453	**
		log	pop.density.total	0.400	0.030	0.464	16.793	0.611	*
		log	Total Reef Area km2	0.339	0.045	0.487	17.755	0.383	*
		log	lagoon.area.m	0.305	0.057	0.499	18.255	0.069	NS
		log	island.avg.SST	0.123	0.171	0.561	20.583	0.968	NS
		log	Patch Reef area	0.096	0.200	0.570	20.887	0.117	NS
		log	Human Population	0.086	0.212	0.573	20.998	0.639	NS
		log	latitude	0.083	0.215	0.573	21.025	0.713	NS
		log	island.10.year.avg.chla	-0.028	0.409	0.607	22.164	0.886	NS
		none	Total Reef Area km2	0.448	0.020	6.918	70.830	0.323	*
		none	lagoon.area.m	0.311	0.055	7.733	73.058	0.227	NS
		none	pop.density.patch	0.214	0.101	8.261	74.378	0.046	NS
		none	latitude	0.159	0.139	8.543	75.051	0.455	NS
		none	island.avg.SST	0.128	0.166	8.700	75.415	0.338	NS
		none	island.10.year.avg.chla	0.014	0.319	9.250	76.611	0.044	NS
		none	pop.density	0.003	0.341	9.302	76.752	0.014	NS
		none	pop.density.total	-0.079	0.577	9.678	77.544	0.009	NS
		none	Human Population	-0.094	0.647	9.744	77.680	0.007	NS
none	Patch Reef area	-0.124	0.934	9.876	77.949	0.004	NS		
Outer	Herbivore	log	pop.density	0.002	0.342	0.510	18.678	0.562	NS
		log	lagoon.area.m	-0.053	0.481	0.524	19.218	0.357	NS
		log	pop.density.total	-0.068	0.531	0.528	19.355	0.262	NS

Reef Type	Dep. Variable	Transformation	Ind. Variable	Adj. R-squared	p-value	Std.err.	AIC	Shapiro-p	Significance
		log	Total Reef Area km2	-0.096	0.656	0.534	19.614	0.200	NS
		log	island.avg.SST	-0.106	0.720	0.537	19.706	0.137	NS
		log	Human Population	-0.107	0.728	0.537	19.716	0.293	NS
		log	island.10.year.avg.chla	-0.114	0.786	0.539	19.779	0.242	NS
		log	latitude	-0.124	0.940	0.541	19.870	0.176	NS
		none	lagoon.area.m	0.080	0.219	4.289	61.268	0.135	NS
		none	pop.density	-0.010	0.369	4.494	62.202	0.071	NS
		none	Total Reef Area km2	-0.067	0.526	4.617	62.743	0.020	NS
		none	pop.density.total	-0.084	0.596	4.654	62.903	0.027	NS
		none	Human Population	-0.097	0.663	4.683	63.025	0.025	NS
		none	island.10.year.avg.chla	-0.104	0.708	4.698	63.090	0.019	NS
		none	island.avg.SST	-0.117	0.819	4.725	63.207	0.007	NS
		none	latitude	-0.125	0.963	4.741	63.274	0.007	NS
	Planktivore	log	pop.density	0.747	0.001	0.205	0.417	0.817	***
		log	pop.density.total	0.452	0.020	0.301	8.146	0.425	*
		log	lagoon.area.m	0.401	0.029	0.315	9.046	0.661	*
		log	Total Reef Area km2	0.353	0.041	0.327	9.818	0.960	*
		log	Human Population	-0.022	0.395	0.411	14.382	0.564	NS
		log	island.avg.SST	-0.040	0.441	0.415	14.557	0.219	NS
		log	latitude	-0.051	0.474	0.417	14.665	0.276	NS
		log	island.10.year.avg.chla	-0.107	0.725	0.428	15.181	0.210	NS
		none	lagoon.area.m	0.503	0.013	0.543	19.951	0.278	*
		none	Total Reef Area km2	0.421	0.025	0.587	21.480	0.862	*
		none	pop.density	0.297	0.060	0.646	23.407	0.249	NS
		none	pop.density.total	0.049	0.261	0.751	26.433	0.128	NS

Table 4. Single variable linear model results. (continued)



Reef Type	Dep. Variable	Transformation	Ind. Variable	Adj. R-squared	p-value	Std.err.	AIC	Shapiro-p	Significance
Secondary		none	Human Population	-0.023	0.399	0.780	27.169	0.146	NS
		none	island.avg.SST	-0.076	0.563	0.799	27.669	0.073	NS
		none	latitude	-0.108	0.735	0.811	27.962	0.037	NS
		none	island.10.year.avg.chla	-0.114	0.790	0.814	28.021	0.049	NS
		log	pop.density	0.422	0.025	0.580	21.248	0.646	*
		log	pop.density.total	0.403	0.029	0.589	21.570	0.618	*
		log	Total Reef Area km2	0.122	0.172	0.715	25.432	0.726	NS
		log	lagoon.area.m	0.070	0.232	0.736	26.008	0.525	NS
		log	Human Population	0.054	0.253	0.742	26.173	0.618	NS
		log	island.10.year.avg.chla	-0.008	0.364	0.766	26.813	0.686	NS
		log	latitude	-0.034	0.425	0.776	27.063	0.428	NS
		log	island.avg.SST	-0.112	0.770	0.804	27.795	0.111	NS
		none	pop.density	0.132	0.162	5.277	65.414	0.017	NS
		none	Total Reef Area km2	0.012	0.324	5.631	66.712	0.028	NS
		none	pop.density.total	-0.025	0.403	5.734	67.076	0.005	NS
		none	island.10.year.avg.chla	-0.042	0.449	5.783	67.245	0.015	NS
	none	Human Population	-0.065	0.523	5.846	67.463	0.006	NS	
	none	latitude	-0.099	0.678	5.939	67.778	0.004	NS	
	none	lagoon.area.m	-0.108	0.733	5.961	67.852	0.002	NS	
	none	island.avg.SST	-0.125	0.958	6.006	68.003	0.001	NS	
Shark		log	pop.density	0.718	0.001	0.692	24.773	0.522	**
		log	pop.density.total	0.519	0.011	0.904	30.119	0.509	*
		log	lagoon.area.m	0.279	0.067	1.106	34.167	0.192	NS
		log	Total Reef Area km2	0.265	0.073	1.117	34.360	0.608	NS
		log	Human Population	0.046	0.265	1.273	36.970	0.763	NS

Table 4. Single variable linear model results. (continued)

Reef Type	Dep. Variable	Transformation	Ind. Variable	Adj. R-squared	p-value	Std.err.	AIC	Shapiro-p	Significance
		log	latitude	-0.120	0.850	1.379	38.574	0.965	NS
		log	island.avg.SST	-0.124	0.934	1.382	38.613	0.941	NS
		log	island.10.year.avg.chla	-0.125	0.959	1.382	38.619	0.938	NS
		none	lagoon.area.m	0.535	0.010	13.694	84.486	0.385	**
		none	Total Reef Area km2	0.293	0.061	16.886	88.677	0.716	NS
		none	pop.density	0.140	0.155	18.618	90.630	0.007	NS
		none	pop.density.total	-0.020	0.391	20.281	92.341	0.002	NS
		none	Human Population	-0.065	0.521	20.720	92.770	0.002	NS
		none	island.avg.SST	-0.122	0.880	21.264	93.288	0.001	NS
		none	island.10.year.avg.chla	-0.123	0.903	21.275	93.298	0.002	NS
		none	latitude	-0.124	0.928	21.285	93.307	0.001	NS
	Tertiary	log	pop.density.total	0.461	0.018	0.541	19.871	0.273	*
		log	pop.density	0.353	0.041	0.593	21.708	0.403	*
		log	Human Population	0.116	0.178	0.693	24.825	0.459	NS
		log	Total Reef Area km2	0.086	0.211	0.705	25.155	0.070	NS
		log	island.10.year.avg.chla	0.071	0.230	0.711	25.320	0.288	NS
		log	latitude	0.025	0.299	0.728	25.803	0.095	NS
		log	lagoon.area.m	-0.011	0.371	0.742	26.172	0.018	NS
		log	island.avg.SST	-0.086	0.604	0.768	26.881	0.015	NS
		none	pop.density	0.115	0.179	4.280	61.226	0.039	NS
		none	island.10.year.avg.chla	0.054	0.254	4.427	61.901	0.054	NS
		none	pop.density.total	-0.031	0.418	4.621	62.758	0.002	NS
		none	latitude	-0.032	0.420	4.622	62.765	0.006	NS
		none	Human Population	-0.069	0.536	4.705	63.119	0.002	NS
		none	Total Reef Area km2	-0.070	0.540	4.707	63.129	0.000	NS

Table 4. Single variable linear model results. (continued)

Table 4. Single variable linear model results. (continued)

Reef Type	Dep. Variable	Transformation	Ind. Variable	Adj. R-squared	p-value	Std.err.	AIC	Shapiro-p	Significance
Total	none	none	island.avg.SST	-0.107	0.725	4.787	63.465	0.000	NS
			lagoon.area.m	-0.121	0.863	4.817	63.590	0.001	NS
	log	log	pop.density	0.353	0.011	0.535	19.632	0.823	*
			pop.density.total	0.345	0.014	0.538	19.762	0.805	*
	log	log	Human Population	0.059	0.246	0.645	23.376	0.570	NS
			Total Reef Area km2	0.056	0.250	0.646	23.406	0.215	NS
	log	log	lagoon.area.m	0.024	0.301	0.657	23.743	0.176	NS
			island.10.year.avg.chla	0.011	0.325	0.661	23.877	0.867	NS
	log	log	latitude	-0.040	0.443	0.678	24.384	0.601	NS
			island.avg.SST	-0.120	0.860	0.704	25.124	0.148	NS
	none	none	pop.density	0.174	0.127	11.305	80.652	0.238	NS
			island.10.year.avg.chla	0.008	0.330	12.386	82.479	0.260	NS
	none	none	pop.density.total	-0.010	0.369	12.501	82.663	0.063	NS
			Total Reef Area km2	-0.030	0.415	12.620	82.853	0.069	NS
	none	none	Human Population	-0.055	0.486	12.772	83.092	0.082	NS
			latitude	-0.087	0.613	12.969	83.399	0.110	NS
	none	none	lagoon.area.m	-0.118	0.827	13.149	83.675	0.009	NS
			island.avg.SST	-0.124	0.950	13.188	83.733	0.017	NS



In contrast, stronger relationships existed between several measures of human presence and fish biomass within most trophic levels (Table 4). Human density metrics (humans per lagoon area, total reef area, and patch reef area) were consistently the top explanatory variables for most models (Figure 1, Table 4). As shown by the slopes in Table 5, sharks were the most sensitive group to changes in human population, followed by tertiary consumers, planktivores, total biomass, and finally secondary consumers. Only the biomass of the herbivore guild was not explained by human density measures.

Across inner reefs, large bodied groupers, snappers, unicornfish, parrotfish were the most sensitive functional fish groups to gradients in human presence (Table 6). When these larger bodied groups disappeared, the fish community became dominated by smaller-bodied, faster growing functional groups like small-bodied parrotfish, acanthurids, rudderfish, goatfish, and wrasses (Figure 2A). More specifically, the species of greatest conservation concern from these analyses were: *Plectropomus laevis*, *Lutjanus bohar*, *Macolor macularis*, *Macolor niger*, and *Variola louti* (Figure 2B). Meanwhile the species that dominated the biomass of inner reefs with high human presence were *Chlorurus bleekeri*, *Cheilinus fasciatus*, and *Ctenochaetus striatus*. Outer reefs followed a similar pattern with large-bodied unicornfish, snapper, and reef-pelagics declining in community biomass contributions, while small-bodied acanthurids, parrotfish, and rudderfish all increased. The most vulnerable species across the outer reefs were *Naso hexacanthus*, *Macolor macularis*, *Plectropomus laevis*, and *Macolor niger* (Table 7). The species whose biomass significantly increased in proportion included *Kyphosus cinerascens*, *Naso lituratus*, *Ctenochaetus striatus*, and *Chlorurus spilurus* (formerly *C. sordidus*).

Figure 1. Linear models of how fish biomass changes in respect to human population density per lagoon area.

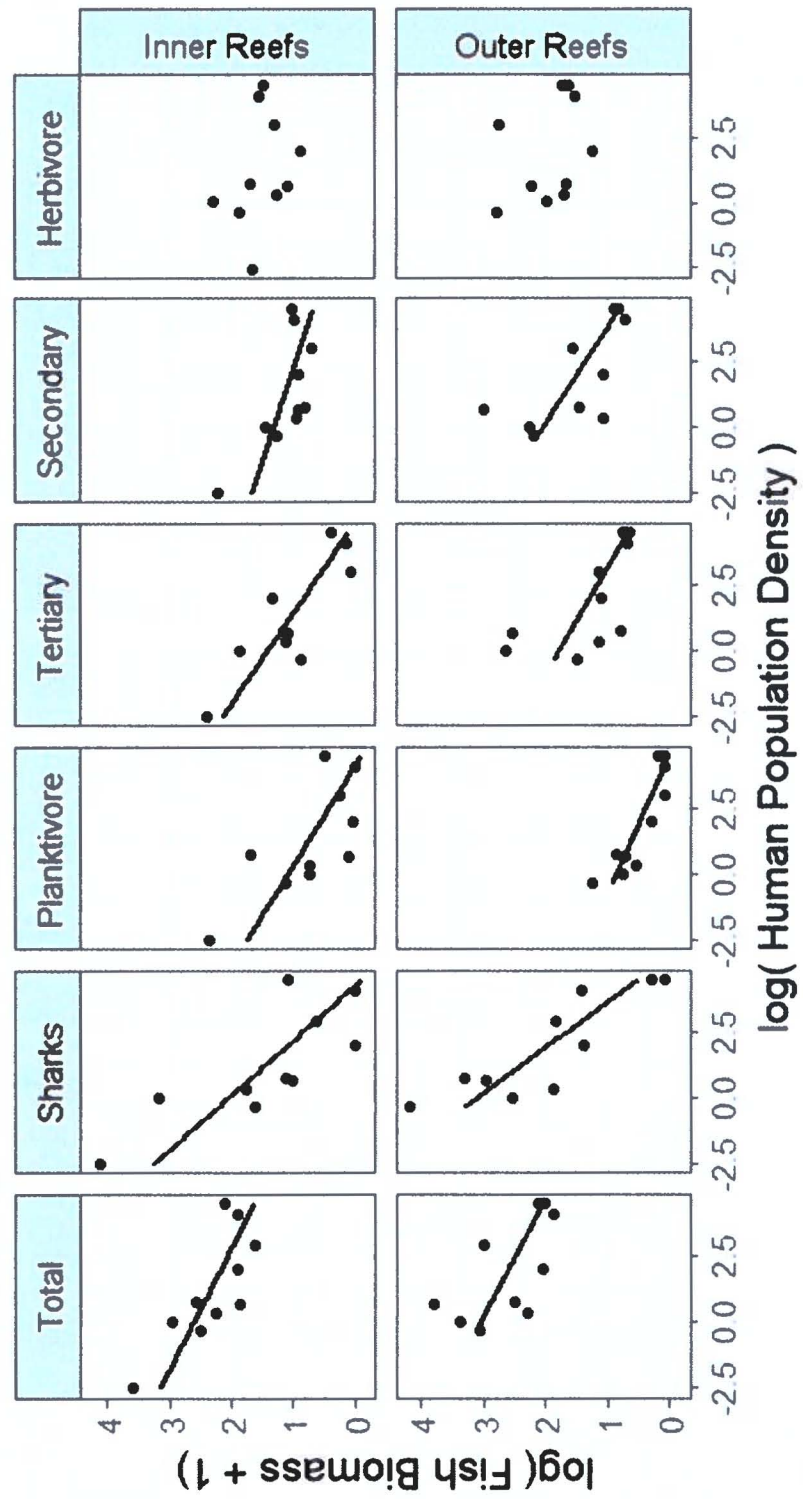




Table 5. Results from linear models of how fish biomass changes in respect to human population density per lagoon area.

<b>Biomass Grouping</b>	<b>Reef Type</b>	<b>Slope</b>	<b>Adj. R-squared</b>	<b>P value</b>	<b>Significance</b>	<b>Stability</b>
<b>Total</b>	Inner	-0.215	0.560	0.008	**	
	Outer	-0.223	0.353	0.041	*	
<b>Shark</b>	Inner	-0.477	0.573	0.007	**	
	Outer	-0.581	0.718	0.001	**	
<b>Tertiary</b>	Inner	-0.289	0.691	0.002	**	
	Outer	-0.342	0.461	0.018	*	
<b>Secondary</b>	Inner	-0.140	0.410	0.027	*	~
	Outer	-0.274	0.422	0.025	*	
<b>Planktivore</b>	Inner	-0.262	0.489	0.015	*	~
	Outer	-0.185	0.747	0.001	**	
<b>Herbivore</b>	Inner	-0.133	0.248	0.081	NS	
	Outer	-0.088	0.002	0.342	NS	

Table 6. Functional group changes in proportional contribution to overall biomass with increasing human density.

Reef Type	Functional Groups	Slope of Model	R2	P-value
Inner	Large-bodied grouper	-0.459	0.525	0.011
	Large-bodied snapper	-0.445	0.421	0.025
	Naso other	-0.347	0.325	0.050
	Large-bodied parrotfish	-0.295	0.332	0.047
	Small-bodied acanthurid	0.253	0.403	0.029
	Rudderfish	0.257	0.423	0.025
	Small-bodied parrotfish	0.291	0.336	0.046
	Goatfish	0.349	0.694	0.002
	Wrasse	0.386	0.633	0.004
Outer	Naso other	-0.432	0.718	0.001
	Large-bodied snapper	-0.316	0.597	0.003
	Large-bodied reef-pelagic	-0.290	0.480	0.011
	Small-bodied acanthurid	0.308	0.564	0.005
	Small-bodied parrotfish	0.316	0.656	0.002
	Naso lituratus	0.316	0.548	0.006
	Ruddertfish	0.357	0.744	0.000

Figure 2. Change in proportional contribution to total community biomass in (A) functional groups and (B) species with increasing human population density. X-axis denotes the slope of the regression for each.

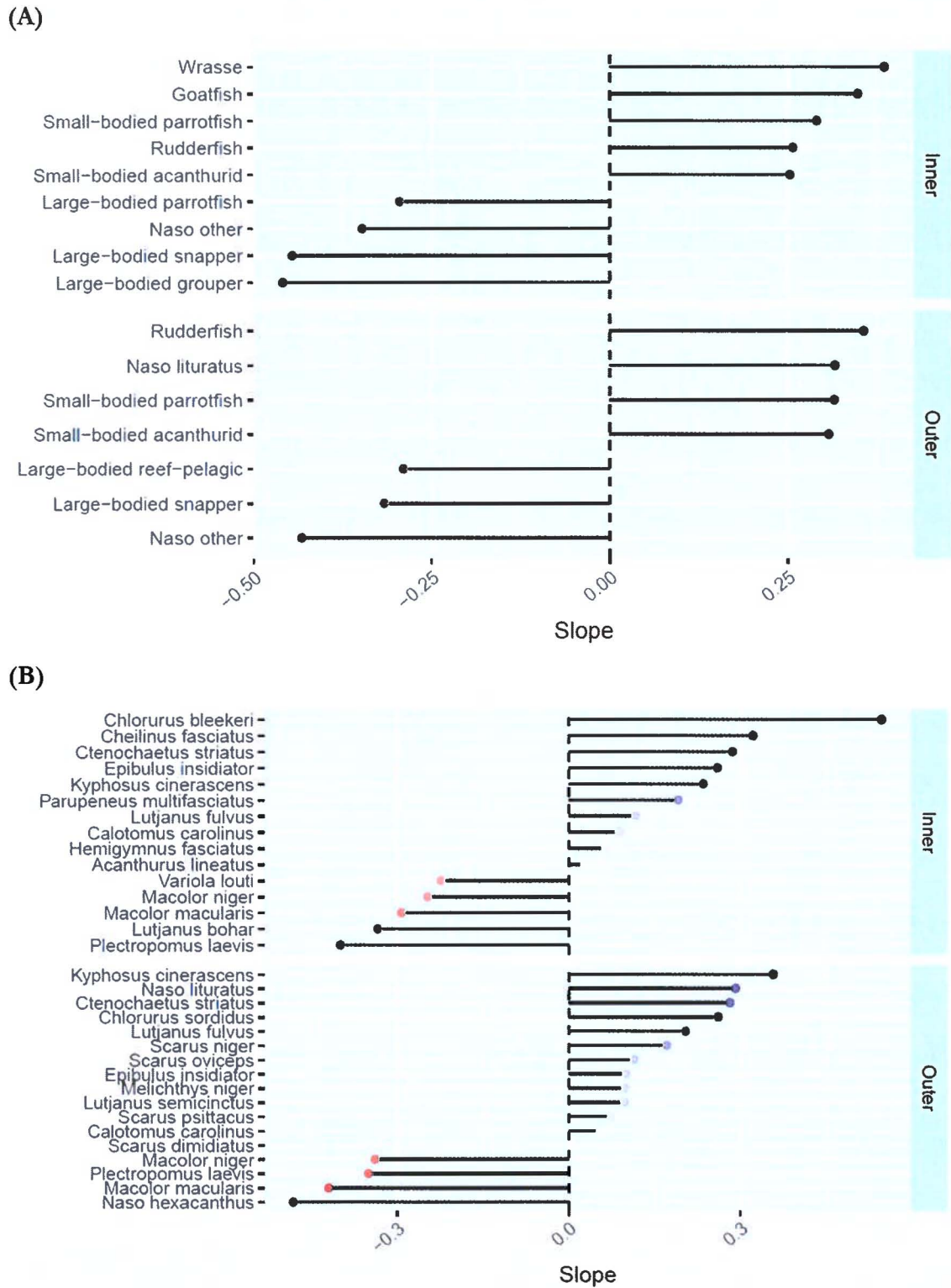


Table 7. Species level changes in proportional contribution to overall biomass with increasing human density.

Reef Type	Species	Slope of Model	R2	P-value
Inner	<i>Plectropomus lacvis</i>	-0.398	0.414	0.027
	<i>Lutjanus bohar</i>	-0.333	0.357	0.040
	<i>Macolor macularis</i>	-0.292	0.481	0.016
	<i>Macolor niger</i>	-0.246	0.456	0.019
	<i>Variola louti</i>	-0.223	0.526	0.011
	<i>Acanthurus lineatus</i>	0.028	0.344	0.041
	<i>Hemigymnus fasciatus</i>	0.064	0.513	0.012
	<i>Calotomus carolinus</i>	0.088	0.772	0.001
	<i>Lutjanus fulvus</i>	0.116	0.556	0.008
	<i>Parupeneus multifasciatus</i>	0.192	0.350	0.042
	<i>Kyphosus cinerascens</i>	0.235	0.345	0.043
	<i>Epibulus insidiator</i>	0.260	0.398	0.030
	<i>Ctenochaetus striatus</i>	0.286	0.345	0.041
	<i>Cheilinus fasciatus</i>	0.322	0.561	0.008
Outer	<i>Chlorurus bleckeri</i>	0.547	0.470	0.017
	<i>Naso hexacanthus</i>	-0.481	0.365	0.038
	<i>Macolor macularis</i>	-0.419	0.687	0.002
	<i>Plectropomus lacvis</i>	-0.349	0.552	0.008
	<i>Macolor niger</i>	-0.338	0.448	0.020
	<i>Scarus dimidiatus</i>	0.002	0.440	0.022
	<i>Calotomus carolinus</i>	0.055	0.476	0.016
	<i>Scarus psittacus</i>	0.074	0.659	0.003
	<i>Lutjanus semicinctus</i>	0.097	0.511	0.012
	<i>Melichthys niger</i>	0.099	0.403	0.029
	<i>Epibulus insidiator</i>	0.100	0.473	0.017
	<i>Scarus oviceps</i>	0.115	0.620	0.001
	<i>Scarus niger</i>	0.172	0.657	0.003
	<i>Lutjanus fulvus</i>	0.205	0.682	0.002
	<i>Chlorurus sordidus</i>	0.261	0.490	0.014
	<i>Ctenochaetus striatus</i>	0.282	0.515	0.012
<i>Naso lituratus</i>	0.292	0.432	0.023	
<i>Kyphosus cinerascens</i>	0.356	0.730	0.001	

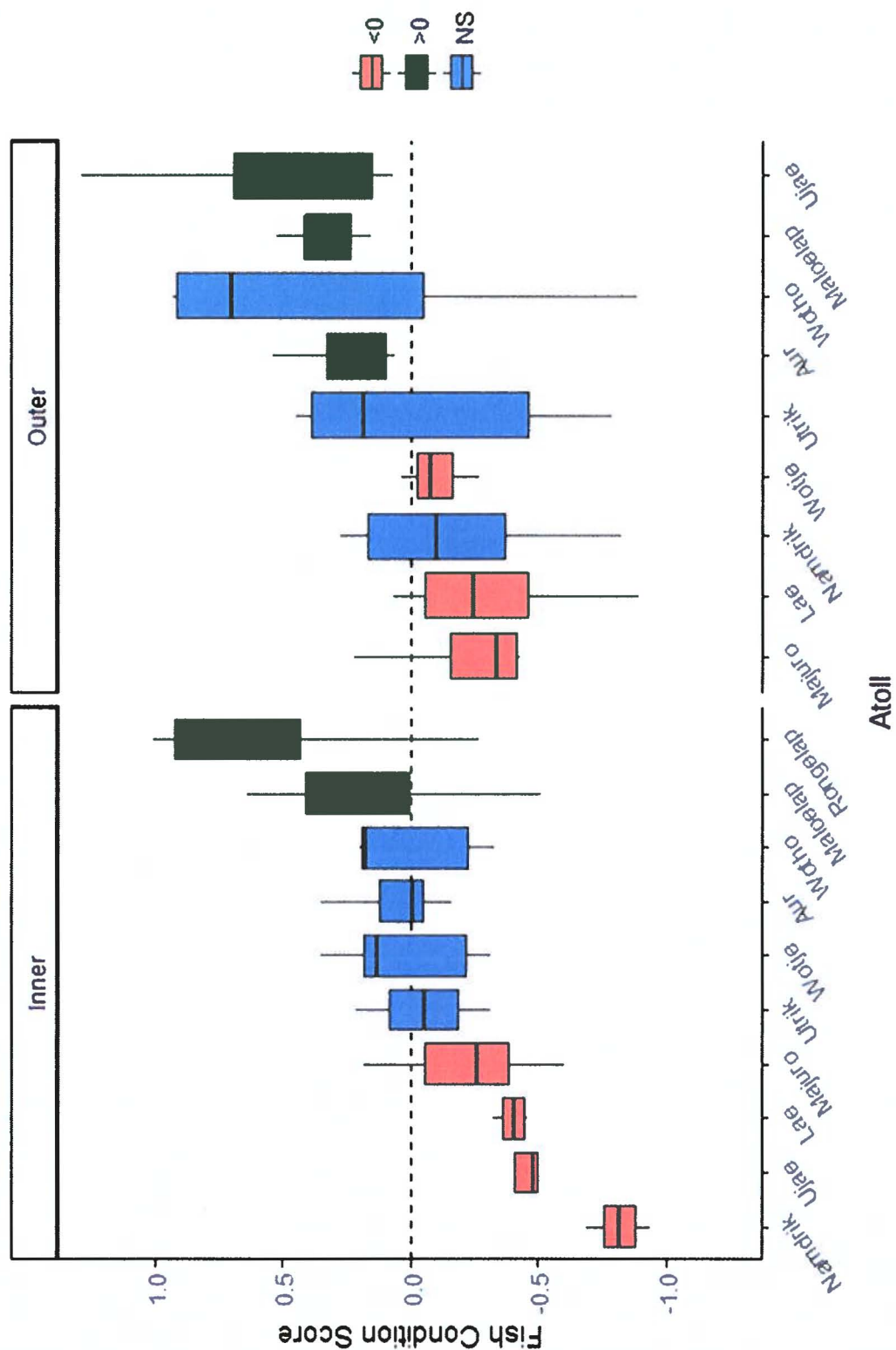
Within each reef type, we used the fish condition scores to confirm that inter-atoll differences we observed were not being unjustly biased by biomass. We found that across all inner reefs, the sites on Namdrik, Ujae, Lae, and Majuro were below average (Figure 3, one-tailed t-test,  $p= 0.02, 0.0002, 0.0000, \& 0.0005$ , respectively). Meanwhile, inner reef sites on Rongelap and Maloelap scored better than average (Figure 3, one-tailed t-test,  $p= 0.003 \& 0.03$ , respectively). For the outer reef sites, the condition scores of Majuro and Lae were again significantly substandard, as were those on Wotje (Figure 3, one-tailed t-test,  $p= 0.01, 0.03, \& 0.04$ , respectively). Finally, the outer reef sites on Aur, Maloelap, and Ujae received fish condition scores significantly better than the other atolls (Figure 3, one-tailed t-test,  $p= 0.02, 0.001, \& 0.0007$ , respectively).

### ***Intra-Atoll Models***

After finding the amount anthropogenic factors influence reef fish communities between islands, we aimed to investigate if there was also human induced variations within atolls. Although we previously found that population density accounts for more variation between islands than any of our other variables, we wanted to include all of the natural and unexplained variation in our local models. It was for this reason we chose to include island as a random factor in our mixed-effects model instead of population density. We found that for the fixed slope model, distance from the human population improved the fish condition score ( $\chi^2=15.3, p=0.00009^{***}$ ) by  $0.89 \pm 0.22$  across an atoll. The random slope model found an even more pronounced relationship, with distance increasing the condition of a site  $1.04 \pm 0.25$  ( $\chi^2=10, p=0.0016^{**}$ ). This relationship was also not a linear one as expected. The influence of a human population decreased exponentially with distance.



Figure 3. Distribution of calculated fish condition scores for each atoll. Atoll color corresponds to how it compares to other atolls, based on the results of a one-tailed t-test (green= above average, red = below average, blue= non-significant).



## **Discussion**

The present study revealed that human presence was the strongest factor driving reef fish assemblages across 10 atolls and 1 island in the Republic of the Marshall Islands. Several natural factors that were expected to serve as covariates and predict some of the fish assemblage attributes had weaker than expected effects sizes or were not apparent. Previous studies have reported that chlorophyll- $\alpha$ , temperature, island size, and other natural factors examined here had comparatively stronger effects on fish biomass across the Pacific (MacNeil et al. 2009; Williams et al. 2015; Heenan et al. 2016). Tropical piscivores have been found to thrive on large islands and atolls (MacNeil et al. 2009; Williams et al. 2015), especially at higher latitudes (Ferreira et al. 2004). Island size serves as a proxy for one or more underlying mechanisms, such as habitat space and potentially bottom-up enrichment, while latitude is a proxy for a collection of environmental variables, including temperature and chlorophyll- $\alpha$ , which vary with distance from the equator. The present trends between large piscivores and latitude are undoubtedly due to a combination of factors that may include higher primary productivity and lower metabolic requirements at higher latitudes (Hillebrand 2004; Floeter et al. 2005; Fisher et al. 2010; Williams et al. 2015). Tertiary consumer biomass on inner reefs was also positively related to total reef area, highlighting the importance of habitat space in a limited environment like a lagoon. Similarly, planktivore biomass had a positive relationship with atoll size, which agrees with findings from other studies (MacNeil et al. 2009; Williams et al. 2015). Planktivores are thought to benefit from larger lagoons due to a hypothesized increase in primary productivity, and greater habitat availability in their preferred back reef habitat (MacNeil et al. 2009; Friedlander et al. 2010). However, our offshore measure of oceanic chlorophyll- $\alpha$  was not significantly related to planktivore or tertiary consumer biomass which is contradictory to previous studies (Williams et al. 2015). This difference was likely due

to the geographic scales of the present study (within the Marshall Islands) and other investigations across many Pacific islands with greatly differing environmental settings. Regardless, natural factors serve to establish the biological capacity of any given reef system, but the combination of human factors can obstruct researchers from detecting natural processes. This was evidenced by moderate fish biomass on Majuro despite having a considerably larger human population than all other atolls. The size of Majuro coupled with the centralized human population may help buffer reefs far from the population center.

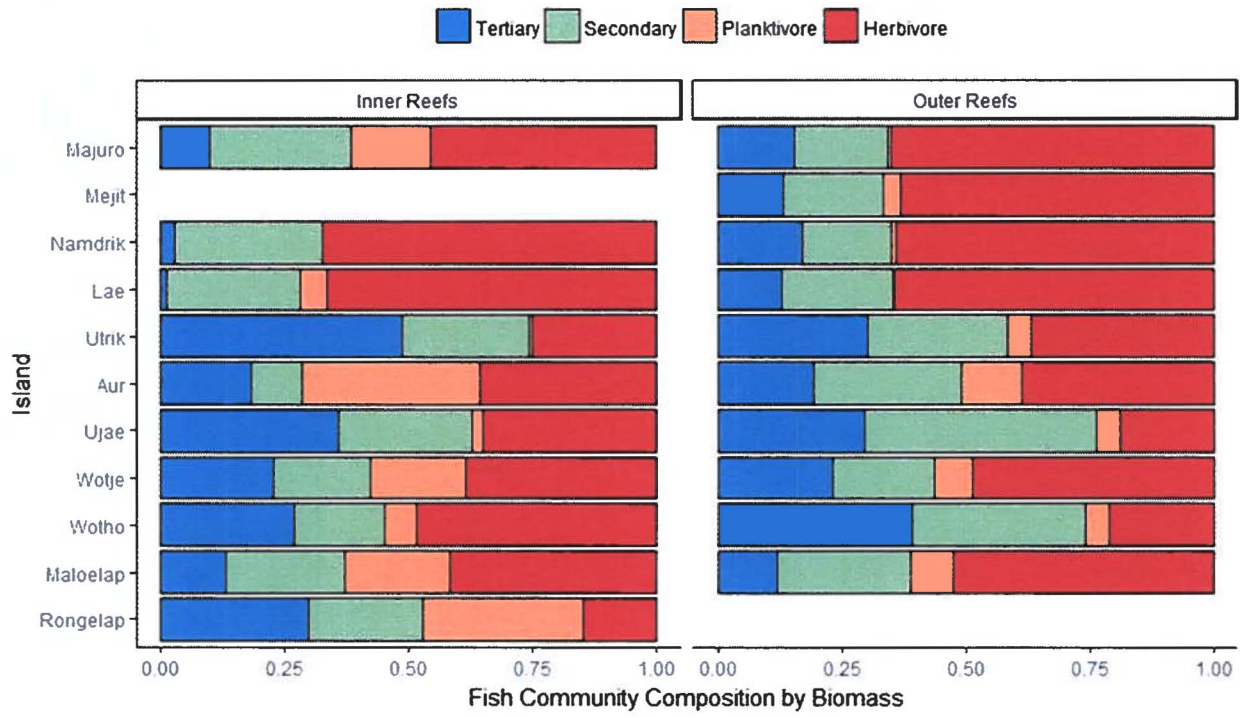
Moving on from natural predictors, we found human density to be the leading explanatory variable for fish biomass at the inter-atoll scale. Sharks were the most sensitive and variable group in our study. In some instances the average biomass of sharks encountered surpassed that of all other fish combined (Table 3, Figure 4). There is evidence to suggest that this is a common scenario when estimating shark and other top predator abundances on remote reefs (Friedlander and DeMartini 2002). However, results like these are potentially misleading due to the large range size of sharks, difficulty in accurately estimating size of large fast-moving fish, and inherent differences in behavior depending on the frequency of interactions the sharks have had with humans, and more specifically scuba divers (Ward-Paige et al. 2010; McCauley et al. 2012). After sharks, large-bodied piscivores and planktivores were the most sensitive groups to human presence (Figure 2A, Table 6), also consistent with previous studies (Friedlander and DeMartini 2002). This may be due to (i) their susceptibility, and (ii) preferential fishing pressure that targets the largest fish with the least effort (i.e., maximize catch-per-unit-effort). Our study found that although tertiary consumers as a whole declined in biomass with human presence (Figure 1), the proportional contribution to overall biomass on outer reefs remained relatively consistent across islands with the exception of Majuro, the most populated island (Figure 5).

Figure 4. Average fish biomass recorded per SPC for each island and reef type.





Figure 5. Proportional contribution of each trophic guild to total fish community biomass.





Yet, the structure within this guild changed considerably. Species like *Plectropomus laevis*, *Lutjanus bohar*, and *Macolor spp.* constituted a substantial amount of this biomass across the less populated atolls. These species did not disappear entirely on other islands, but smaller snappers like *Lutjanus fulvus* began to replace those sensitive species (Table 7, Figure 6). Secondary consumers followed a similar pattern with fast growing generalist species proving to be resilient to human factors. As larger piscivores disappear, small wrasse and goatfish species made up a larger proportion of the secondary consumer biomass (Figure 7). Although total herbivore biomass did not change with human population, the herbivore guild did account for the majority of the biomass on impacted reefs (Figure 8). Naturally, large parrotfish are the predominate herbivore species in terms of biomass on remote RMI atolls, while on populous atolls the composition of the community shifted to small and cosmopolitan species like *Ctenochaetus striatus*, *Kyphosus cinerascens*, and *Chlorurus bleekeri* (Fig 2B, Table 7)(Houk and Musburger 2013). Shifts like these have ecological consequences because larger individuals provide a disproportional amount of ecosystem services such as scraping and bioerosion that an equal biomass of smaller species cannot compensate for (Bellwood et al. 2003; Lokrantz et al. 2008; Birkeland 2017). Last, the sensitivity of planktivores to human presence was primarily driven by *Naso hexacanthus*, a large-bodied species that is susceptible to harvesting because they commonly form large schools and forage pelagically on outer reef slopes and in lagoonal waters adjacent to reefs without refuge (Table 6, Table 7, and Figure 9).

In order to fully investigate the differences between islands, we used our site level fish condition scores to appreciate patterns that might not be found using biomass alone. A preliminary analysis of these scores revealed that sites on our most populous atoll, Majuro, were consistently substandard. Across outer reefs, Majuro scored worse than all other atolls. For inner reefs Majuro was significantly below average, however it did outperform Namdrik,

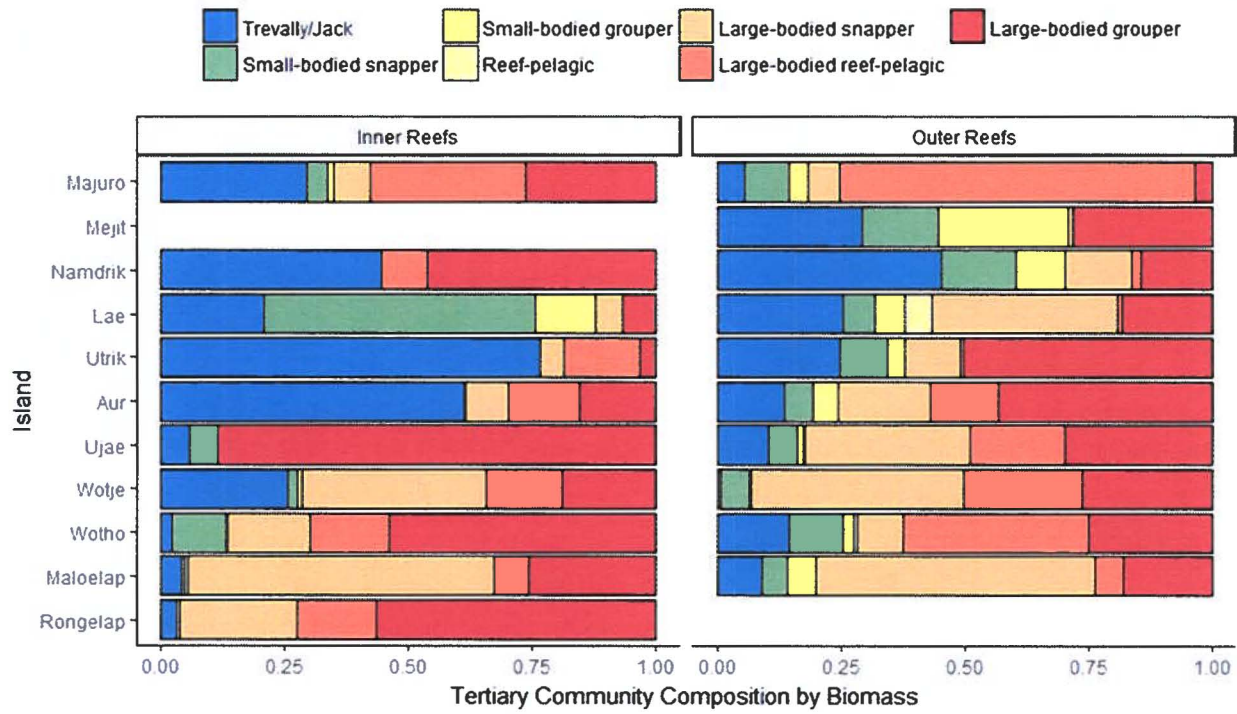


Figure 6. Proportional contribution of functional groups to total tertiary consumer biomass.

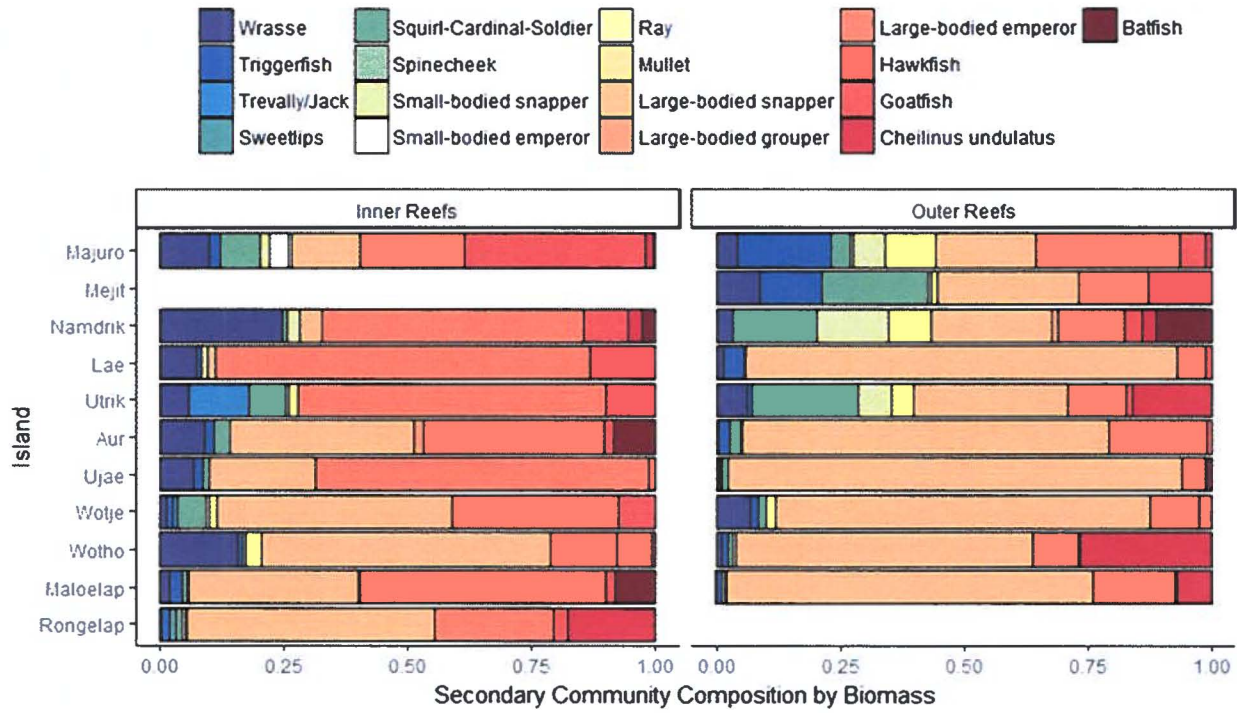


Figure 7. Proportional contribution of functional groups to total secondary consumer biomass.

Figure 8. Proportional contribution of functional groups to total herbivore biomass.

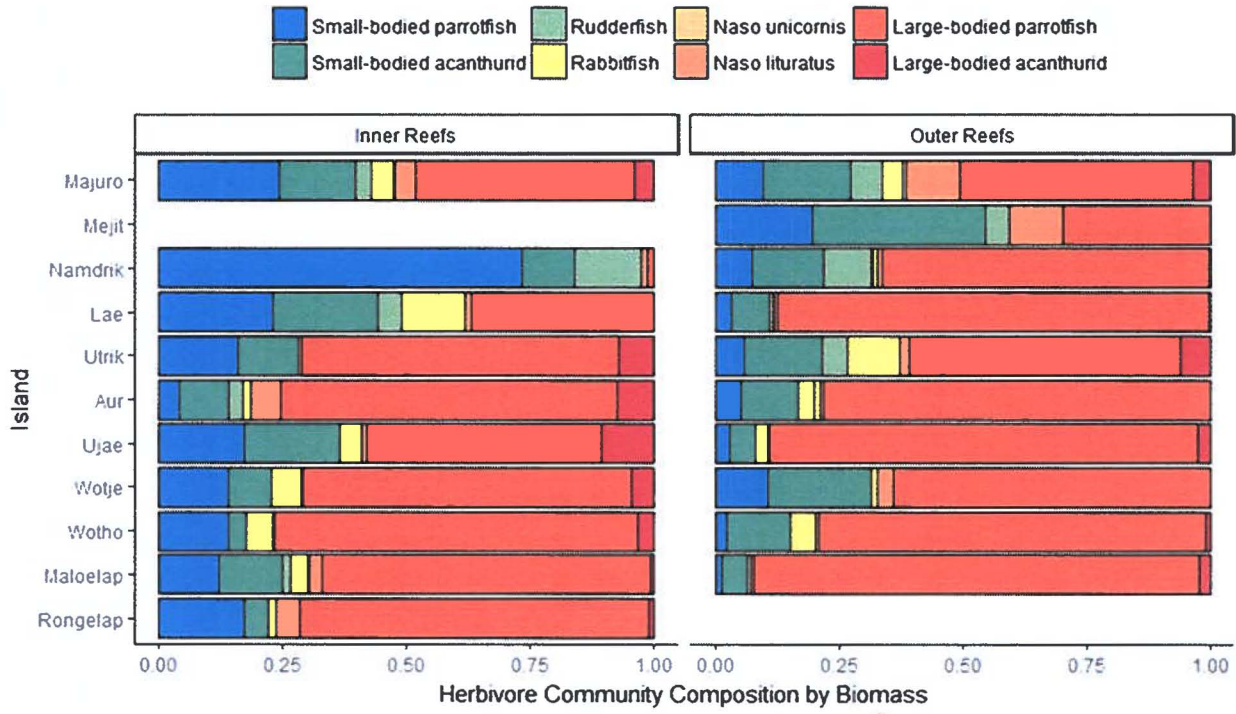
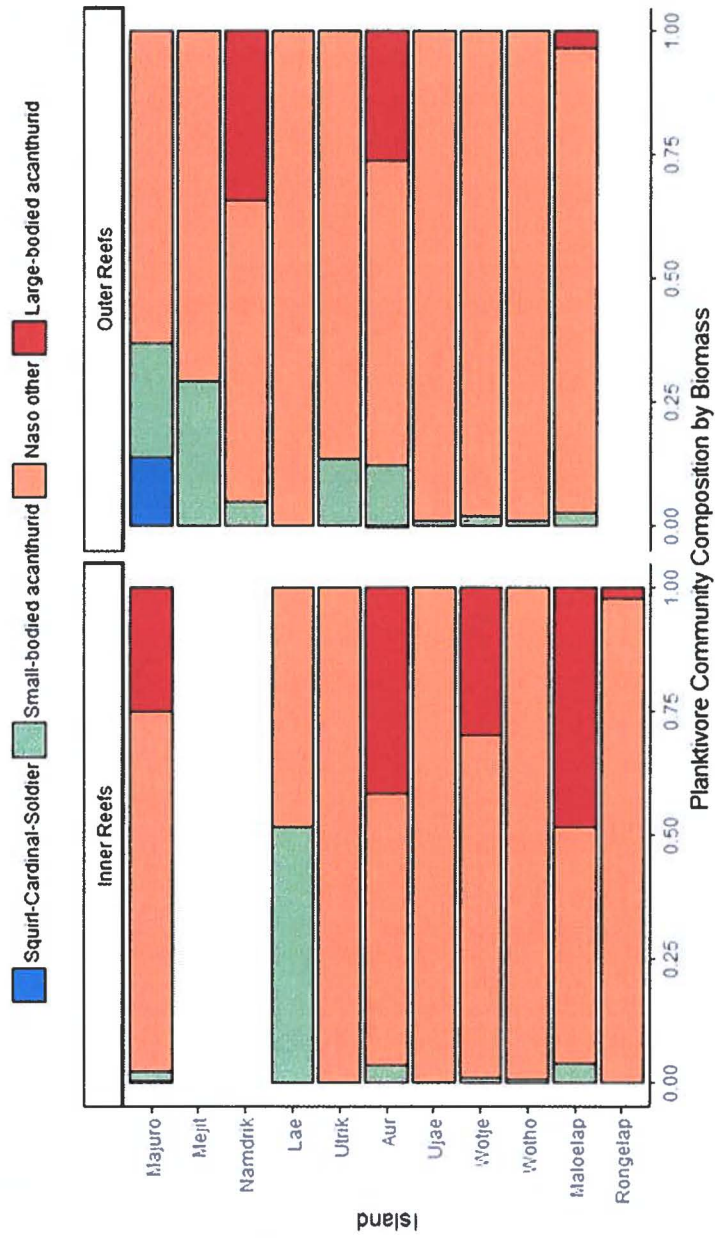




Figure 9. Proportional contribution of functional groups to total planktivore biomass.



Lae, and Ujae, all of whom have smaller lagoons and fewer patch reefs. Unsurprisingly, Rongelap was superior to all other atolls on inner reefs, followed by Maloelap. Notably, Rongelap and Maloelap were also the two largest atolls in our study. Across outer reefs, our second smallest atoll, Lae, was only marginally better than Majuro. Wotje also scored significantly below average, however with its large lagoon and moderate human population its possible this result is due to its unusual disturbance history as a Japanese naval base. There were three atolls with outer reefs that scored above average; Aur, Maloelap, and Ujae. All three atolls have extremely low human densities with less than, or equal to, two people per square kilometer of lagoon.

Finally, we reduced the scale of our analyses in order to identify anthropogenic spatial trends, or human footprints, within atolls. Our mixed effects models showed that multiple atolls have human footprints, however, the strength of this relationship differs between atolls. From this model we can observe that this pattern can be observed on both inner and outer reefs. The influence of humans appears to decrease exponentially with distance from the population centers, suggesting that smaller atolls are at greater risk for overharvesting.

As inconvenient as it may be, our results show that even at low densities, humans have drastically altered the trophic structure of reef fish assemblages across the Marshall Islands. There is currently a growing artisanal fishery that sells fish harvested from outer atolls at a government market on Majuro and our inter-atoll analyses offered some guidance for best management practices. The present results identified a suite of larger-bodied species that were disproportionately impacted and should be prioritized for species-based studies and management. Possible management actions could include implementing size limits or quotas based upon species-specific knowledge to ensure these identified population maintain a functional and ecological presence that supports the goods-and-services offered to outer island

residents. Additionally, our intra-atoll analysis revealed that the majority of current human impacts are localized near populated areas and careful spatial management may be the best way to dilute the added pressures of commercial harvesting. Although this study did contain data from 11 different islands, the Republic of the Marshall Islands has an additional 19 atolls and 4 islands for which we do not yet have biological data. Because data collection of this nature requires a considerable amount of time and resources, it is not likely it will be completed anytime soon. However, there is environmental and anthropogenic data available for the entire country. The models developed in this study give us the ability to predict fish assemblage traits for these atolls missing data, arming managers with the ability to make educated decisions and begin conservation measures sooner rather than later.

In conclusion, we have provided evidence that across the Republic of the Marshall Islands humans are the primary driver of reef fish community biomass, assemblage structure, and condition at both the regional and local scale. Within these communities, certain species and functional groups are especially sensitive to human factors. Consequently, important ecosystem functions, like herbivory, are being impaired. Although further research will be required, this study supplies local resource managers with the knowledge to make decisions that will protect these reef fish populations for the benefit of the ecosystem and the people that depend on it.

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