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Reef Fish Biodiversity in the Florida Keys National Marine Sanctuary

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Reef Fish Biodiversity in the Florida Keys National Marine Sanctuary

by

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A thesis submitted in partial fulfillment
of the requirements for the degree of
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Marine Science
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College of Marine Science
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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The biological diversity of reef-fish in the Florida Keys National Marine Sanctuary (FKNMS) from 1999 – 2016 was evaluated in terms of abundance, biomass, species richness, evenness, Shannon diversity, Simpson diversity, and functional diversity, using observations collected by multiple agencies and institutions under the Reef Visual Census (RVC) program. To compare the different diversity indices species richness, Shannon diversity, Simpson diversity, and functional diversity were converted into effective number of species. I examined the seven indices by no-take marine zones, in seven benthic habitat strata, and across the three-distinct geographic subregions in the Florida Keys domain (Upper, Middle, and Lower Keys). The objective was to describe changes in reef fish community responses through time and space in the Florida Keys, and to determine whether patterns in reef fish diversity indices were attributable to levels of protection, benthic habitat strata, or geographic subregion. The goal was to develop a framework for reef fish biodiversity assessments that can inform management and policy in the FKNMS, and support updates to the periodic Condition Reports generated by the Sanctuary.

Diversity indices (with the exception of evenness) were significantly higher in no-take marine zones compared to areas open to fishing. All indices were significantly different by strata type. High Relief Reef habitats had the highest abundance, biomass, richness, Simpson diversity, Shannon diversity, and functional diversity, but had moderate evenness values. The biodiversity metrics for the Upper Keys and Lower Keys were not significantly different, but both of these areas were significantly different from the Middle Keys for all indices except species richness, which did not vary by subregion. Generalized additive models revealed that the principal driver across indices was habitat structure (strata and depth). Time (year), space (latitude, longitude), and no-take marine zones (0, unprotected and 1, protected) explained roughly similar proportions of deviance across all indices.

Simpson diversity, Shannon diversity, and functional diversity showed similar trends in no-take marine zones, strata, and subregion through time. The Florida Keys is characterized as having relatively low functional diversity due to a few common traits shared by many individuals and many rare traits shared by a few individuals. This suggests that the Florida Keys reef fish are less vulnerable to functional loss due to high functional redundancy among species. However, functionally rare traits, those possessed by few individuals, are vulnerable to functional loss and will have a larger impact on ecosystem functioning than species that share similar traits. Low functional diversity also suggests lower adaptability to environmental perturbations. Given the minimal robustness of traits, the ecosystem is less likely to possess functions that can withstand disturbances.

The impacts of two types of perturbations were examined in a qualitative manner: hurricanes and cold-temperature events. Disturbance by hurricanes in 2004 and 2005 and the extreme cold event of January 2010 had a high impact on reef fish community composition. Between 2004 and 2006, following two consecutive years of hurricanes, abundance of reef fish declined 31%, biomass declined 53%, species richness declined 18%, Simpson diversity declined 12%, Shannon diversity declined 14%, and functional diversity declined 8%. Following a year without hurricanes in 2007 abundance of reef fish increased 11%, biomass increased 13%, richness increased 14%, Simpson and Shannon diversity increased 10%, and functional diversity increased 6%. After the January 2010 extreme cold event, reef fish abundance and biomass also declined

17%, richness declined 10%, Simpson diversity and Shannon diversity declined 5% and 6%, and functional diversity declined 2%. All matrices increased the following year, where abundance increased 13%, biomass increased 31%, richness increased 13%, Simpson diversity increased 7%, Shannon diversity increased 10%, and functional diversity increased 8%.

Based on my findings and literature review, to better preserve biodiversity and enhance ecosystem functioning, I recommend prioritizing conservation efforts in source habitats (e.g., High Relief Reefs) and habitats with varying complexity by implementing corridor reserves that facilitate the natural migration of organisms between different habitat types. I also recommend prioritizing preservation of species that possess functionally rare traits with few individuals (e.g., cleaner species) by preserving areas with greater functional diversity (e.g., Higher Relief Reefs and Forereef Deep Linear Reefs).

1

Introduction

1. Background

Biodiversity as defined by the United Nations Convention on Biological Diversity is the variability among living organisms, including diversity within species, between species, and of ecosystems (Norse, 1986; Congress, 1987; Glowka et al., 1994). Biodiversity is an essential indicator of ecosystem structure, stability, resilience, and functioning (Bengtsson, 1997; Magurran, 1988; Sala & Knowlton, 2006). Greater biological diversity within and across a broad range of trophic levels is considered to facilitate biogeochemical and biological processes and increased ecosystem resistance to disturbance, species invasion, and disease (McNaughton, 1977; Schulze & Mooney, 1994). Over time, a plethora of diversity measures and indices have been developed to try to quantify biodiversity and ecosystem resilience, but no single metric manages to encapsulate all the elements of biological and habitat diversity.

An alternative approach to conceptualize biodiversity is by composition, structure, and function of organisms in a particular region (Franklin et al., 1981; Duelli & Obrist, 2003). Composition is the array and relative abundance of species; structure describes the spatial arrangement and habitat complexity; and function incorporates species traits that influence ecological processes such as energy flow and nutrient cycling. Noss (1990) nests these attributes into a hierarchy: genetic, population-species, community-ecosystem, and regional landscape. The hierarchy concept emphasizes that biodiversity should be measured at multiple levels of organization and multiple spatial and temporal scales.

The consensus among ecologists indicates monitoring biodiversity requires a multifaceted approach. The components of biodiversity highlighted in the thesis are species richness, species evenness, species diversity, and functional diversity. Each measure has its benefits and limitations and is interconnected to the different components of biodiversity (Figure 1). A summary of the various indices used in this study of the Florida Keys reef fishes is presented below.

2. Species richness

Species richness, the number of species in a habitat sampled, is the most fundamental and traditional measure of biodiversity. Species richness does not include abundance values, and thus it gives rare species the same weight as dominant species. Species richness provides a snapshot of a biome's diversity. It has been used to identify hotspots of life and regions with high degrees of endemism for conservation (Fleishman et al., 2006). Traditional biodiversity indices assume and imply that each species plays a de facto functional role in a habitat or ecosystem (Bengtsson, 1998; Cadotte et al., 2011). Extensive evidence shows there is indeed a positive relationship between species richness and complexity of ecosystem function (Tilman et al., 1997; Schwartz et al., 2000; Hooper et al., 2005; Cardinale et al., 2006; Duffy et al., 2017). However, to better target policy and management decisions for ecosystem resilience and sustainable use of marine resources, it is also necessary to better understand how individual species and species assemblages are changing in composition, and how these species contribute to particular ecosystem functions. In many cases, there is redundancy in the function that different fish species provide (Micheli et al., 2005; Chabanet et al., 2010; Guillemot et al., 2011; Micheli et al., 2014). Identifying these cases may be useful for maintaining ecosystem functions as particular species and assemblages decline, or if they are replaced by others with similar functional roles.

Species richness also is limited in that it does not track species rarity, which is an important characteristic of a community. Species richness fails to capture changes in community composition by not accounting for changes in species abundances (Chao et al., 2014). Thus, in addition to understanding a community's taxonomic diversity, it is important to understand the species assemblage and the functional role of individual species (Duncan et al., 2015).

3. Species evenness

In order to provide an accurate reflection of the community dynamics in a habitat, biodiversity measures should incorporate both species richness and relative abundance or density (Peet, 1974; Magurran, 2013). Accounting for the number of individuals in different populations reflects the community's evenness (how similar species are in abundances) and dominance (the most common species; Smith & Wilson, 1996). Evenness is high when the all species have equal abundances and evenness is low when a community has many rare species.

Complementary to richness, species evenness is the proportion of individuals across species. If a community is perfectly even, each species has the same abundance. The degree of evenness can help us understand the processes that shape a community's structure and composition. Smith & Wilson (1996) developed a list of 14 criteria that an evenness measure should meet. For example, an evenness index must be independent of species richness (Heip, 1974). However, Jost (2010) shows it is impossible for evenness and richness to be mathematically independent of one another. He argues that evenness should be depicted relative to the number of species in a community.

The relative logarithmic evenness can be measured by dividing the log form of Simpson by the number of species (Jost, 2010):

$$relative\ logarithmic\ evenness = \frac{\ln(Simpson\ diversity)}{\ln S}$$

Relative logarithmic evenness is analogous to Pielou's evenness measure (Pielou, 1966). Evenness ranges from 0 (only a single species present) to 1 (all species with the same abundance). The more similar species abundances are, the greater the evenness of the community.

4. Species diversity

Species diversity is defined for this work as a measure of heterogeneity that incorporates both richness and evenness (Good, 1953). The Simpson diversity index (also referred to as the Gini-Simpson index) is one of the more popular diversity indices (Jost, 2006; Magurran, 2013; Chao et al., 2014a). It measures the probability that two individuals randomly selected from a sample will belong to the same species (Simpson, 1949):

$$Simpson\ diversity\ (D) = \left(\sum_{i}^{s} p_i^2\right)$$

Where D is Simpson diversity, S is the number of species (richness) and p_i is the proportion of individuals in the ith species (Jost, 2006). However, the Simpson diversity index is usually expressed as the reciprocal (1/D) or complement (1-D) so that it ranges from 0-1, where 1 is more diverse.

Simpson diversity is preferred over other diversity indices because it provides a measure of dominance, by emphasizing the most abundant species and is not sensitive to rare species (Jost, 2006). Species diversity indices that incorporate abundance, like Simpson's index, outperform species richness at discriminating between communities (Morris et al., 2014).

Another common measure of species diversity is Shannon diversity (also known as the Shannon-Wiener index or Shannon-Weaver index). Similar to Simpson diversity, the Shannon index incorporates both species richness and relative abundance (Shannon & Weaver, 1949). However, while Simpson diversity disproportionately favors the most common species (i.e., the species with higher populations), Shannon diversity does not disproportionately favor either rare or common species (Keylock, 2005; Jost, 2007). The Shannon diversity index is a measure of entropy (Hill, 1973); it is the uncertainty in the species identity of a sample. It is calculated as:

$$Shannon\ diversity\ (H') = \left(-\sum_{i=1}^{S} p_i \ \ln p_i \right)$$

Where $H^{'}$ is Shannon diversity, S is the number of species (richness) and p_i is the proportion of individuals in the ith species (Jost, 2006).

Despite its popularity as a benchmark for measuring biodiversity, the Shannon index has received a lot of criticism (May, 1975; Magurran, 1988; Lande, 1996). The index assumes the species are randomly sampled from an infinitely large population, and that all the species in the population are represented in the sample (Pielou, 1975). Although species may not be detected in a study because of the sampling method or seasonal effects or diel activity patterns or because they are rare. The index is also sensitive to sample size. Usually the index falls between 1.5 and 3.5 (Margalef, 1972). In order to receive an index of 5.0 or greater, given typical a log normal patterns of species abundance, it would require a sample with 1,000,000 species (May, 1975). This is rarely accomplished in any survey. Given Shannon diversity's strong effect on sample size, the index can be difficult to interpret between different sample sizes.

Yet the Shannon index is still often preferred over Simpson diversity because it doesn't favor rare or common species but weighs all species by their frequencies (Jost, 2006). The Shannon index is also the only diversity index that can measure independent alpha and beta from multiple unequal-sized communities (Jost, 2007), where alpha diversity is the mean diversity within an assemblage/site and beta diversity is the compositional heterogeneity and/or dissimilarity between sites/assemblages (Tuomisto, 2010).

Measures of species richness, evenness, and diversity are all powerful tools for measuring biodiversity. However, the utility of the indices is limited in terms of providing information on functional diversity, as each species is considered distinct even if two or more species have similar functions.

5. Functional diversity

Functional diversity measures the dissimilarity among species based on morphological and behavioral traits. For example, species can be grouped by trophic group or partitioning of resources (e.g., habitat preferences). It is therefore used as an indicator of ecosystem functioning. Traditionally, terrestrial ecologists have applied functional diversity to morphological traits of plants as a predictor of nutrient cycling and productivity (Hooper et al., 2005). In the last decade, marine ecologists have implemented the trait-based approach to better characterize the ecosystem stability and functioning (Halpern & Floeter, 2008; Guillemont et al., 2011; Stuart-Smith et al., 2013; Bates et al., 2014; Mouuillot et al., 2014; Coleman et al., 2015; Duffy et al., 2016; Plass-Johnson et al., 2016)

Functional diversity indices, for example, can reflect subtle changes resulting from the implementation of marine zones, while traditional biodiversity indices seem to be less sensitive (Babcock et al., 2010). Coleman et al. (2015) detected changes in individual trait values within four years of the implementation of new enforcement measures in a marine reserve, whereas traditional species diversity indices detected little or no response. Species traits also provide a means to evaluate ecosystem vulnerability to functional loss and disturbances (Guillemot et al., 2011; Mouillot et al., 2014; Wiedmann et al., 2014). When several species share similar functional traits, it provides a level of functional redundancy or “functional insurance" against the loss of ecosystem functioning (Yachi & Loreau, 1999; Bellwood et al., 2003; Guillemot et al., 2011; Mouillot et al., 2013a). If one species were to be lost, another species that performs similar functions can compensate for it so that the integrity of the ecosystem would, in principle, not be compromised to the extent to which it would if such redundancy was not present (Purvis et al., 2000; Petchey et al., 2007).

Functional diversity has been calculated using Rao’s Quadratic entropy. Functional diversity is then the mean functional dissimilarity between two randomly selected individuals within a community weighted by their relative abundances. It is calculated as:

$$Functional\ diversity\ (Rao's\ Q) = \left(\sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} p_i p_j \right)$$

where S is the number of species (richness), p_i is the relative abundance of species i, p_j is the relative abundance of species j, and d_{ij} is the functional distance between species i and j ($d_{ij} = d_{ji}$

and $d_{ii} = 0$; Figure A1). Functional distance is the difference between the i-th and j-th species, and is calculated using a distance function and ranges between zero and one (Gower, 1971; Legendre & Legendre 1998; Podani, 2000). If the functional distance between all species is one (e.g., $d_{ij} = 1$ for all $i \neq j$) then all species are functionally equivalent and functional diversity reduces to the complement of Simpson diversity (Rao, 1982; Botta-Dukat, 2005).

Functional diversity is influenced by species diversity (Simpson diversity), the univariate trait distribution, and the covariance between traits (unless all species have the same abundance in which case the covariance is zero; Botta-Dukat, 2005). It is unique in that functional diversity may decrease if species richness increases. Introduction of new species into a community increases species diversity (e.g., Simpson diversity and Shannon diversity), but it may decrease functional diversity if the new species decreases the average dissimilarity among species (Botta-Dukat, 2005).

Ecosystems with high functional diversity are characterized as having low redundancy between species and traits. These communities tend to result from strong inter-specific competition or environmental heterogeneity (Mouillot et al., 2007; Wiedmann et al., 2014). Communities with high functional diversity also tend to have a greater adaptability to disturbances due to a large number of different traits, but are also more vulnerable to functional loss since since there is less redundancy.

In contrast, ecosystems with low functional diversity, are characterized as having high functional redundancy, where many species share similar functional traits. Communities with high functional redundancy are often a result of environmental (e.g., abiotic stressors). For example, the species may be required to have similar functional traits to the survive in the environment (e.g., temperature, physical disturbances). Communities with high functional redundancy also implies lower vulnerability to functional loss. However, it also implies lower adaptability to some types of disturbance.

Functional diversity and the designation of functional groups have a degree of arbitrariness. There is no defined or standard way to assign functional traits. In reality, no species are perfectly functionally identical, and each species can be regarded as having a unique function. Costello et al. (2015), for example, prioritized ten traits for the inclusion of the open access database World Register of Marine Species (WoRMS). These traits included taxonomic classification, environment, geography, depth, substratum, mobility, skeleton, diet, body size, and reproduction. The traits I selected were based on criteria of applicability across taxa, data availability, and potential usage. Unfortunately, a limiting factor for trait-based studies is the lack of traits available for a lot of species in large databases (e.g., FishBase, BIOTIC). Applicability of trait-based studies would benefit from further literature review and studies on species traits.

6. Diversity as "effective number of species"

Indices based on proportional abundances of species help capture the evenness of a community. However, the diversity indices in their current form are not intuitive, and can lead to misinterpretation because they do not follow the doubling property (aka replication principal; Jost et al., 2010). Meaning if we have two equally distinct communities (e.g., equal number of individuals and equal number of species), with no overlap in species, each with a diversity of X that when pooled together the diversity becomes 2X. For example, given a community with four equally common species of reef fish, such that the species richness is four and Simpson diversity is 0.75, and another community with four different, but equally common species, also with a species richness of four and Simpson diversity of 0.75, when combined you would expect species richness and Simpson diversity to double (Figure 2). However, the combined community results in a Simpson diversity of 0.875 and does not follow the doubling property. The same concept applies for Shannon diversity.

Some biologists are not concerned about this since they use the indices to derive statistical significance and not changes in magnitude. However, the argument remains that diversity indices should behave more intuitively by satisfying the doubling property and this can be established by converting the indices into an "effective number of species", also referred to as a Hill number (Hill, 1973; Ellison, 2010; Jost, 2006).

The effective number of species is the number of equally common species needed to produce the observed value of a diversity index (MacArthur, 1965; Jost, 2006; Jost et al., 2010). The indices converted to effective numbers behave more intuitively by following the doubling property. Hill numbers can be applied to multiple diversity indices including Simpson, Shannon, and functional diversity. This provides a unified framework for computing biodiversity (Table 1). Species richness already obeys the replication principal and is in and of itself in units of effective number of species. Simpson diversity and Rao's Q are converted by subtracting these indices from unity and taking the reciprocal, and Shannon diversity is converted by taking its natural exponential (MacArthur 1965; Jost 2006). In a community with equally common species (completely even) the species diversity indices (e.g., Simpson diversity, Shannon diversity) would be equal to the number of species (species richness). All "true" diversity indices must be equal to or less than species richness. The conversion also allows for the diversity indices to be in the same units of effective number of species (Jost, 2006; Chao et al., 2014a).

CHAPTER ONE:
PATTERNS AND DRIVERS OF DEMERSAL REEF FISH COMMUNITY IN THE FLORIDA KEYS NATIONAL MARINE SANCTUARY FROM 1999 – 2016

1. Introduction

Biodiversity is essential to maintaining ecosystem functions and services critical for human life. The realization that coastal and marine living resources are under increasing pressures from humans, climate change, and invasive species (e.g., Jackson et al., 2001) has led to an increased attention to the preservation, conservation, and restoration of biodiversity on the global agenda (Pimm et al., 1995; Sala & Knowlton, 2006; Cheung et al., 2009; Fautin et al., 2010; Barnosky et al., 2011; Lafferty & Eckerberg, 2013; Secretariat, 2013). The Group on Earth Observation's Biodiversity Observation Network (GEO BON), for example, developed a series of Essential Biodiversity Variables to help organize efforts to study and monitor biodiversity change (Pereira et al., 2013; Paganini et al., 2016; Proneca et al., 2016; Turak et al., 2016). The United Nations developed a series of Sustainable Development Goals, which include the conservation and sustainable use of ocean spaces and marine resources through biodiversity monitoring (UN, 2015). Furthermore, the Convention on Biological Diversity developed a list of Aichi Biodiversity Targets to improve the status of biodiversity and promote sustainable use (CBD, 2013). As part of the global initiative, the Marine Biodiversity Observation Network (MBON), a theme within GEO BON, seeks to develop a community of practice to monitor changes in biodiversity and ecosystem function (Duffy et al., 2013; Muller-Karger et al., 2014).

My thesis complements the MBON objectives by assessing the status and trends of reef-fish abundance, biomass, and biodiversity within the Florida Keys National Marine Sanctuary

(FKNMS). Here, I characterize the spatial and temporal patterns in reef-fish abundance, biomass, evenness, richness, Simpson diversity, Shannon diversity, and functional diversity over 17 years (1999-2016) in the FKNMS.

There is a known relationship between the number of species present and ecosystem functioning (Tilman et al., 1997; Cardinale et al., 2006). However, an increase in species richness does not always match a monotonic increase of ecosystem functioning. Species do not contribute equally to the various ecosystem processes. Keystone species, foundation species, and ecosystem engineers may be considered more ecologically important than other species because of their traits or characteristics that influence ecosystem functions (Bengtsson, 1998). Species richness also doesn't incorporate measures of species relative abundance (population size), weighing rare species with small populations equally to common species, i.e. those with high population sizes. Evenness indices and species diversity indices, like Gini-Simpson and Shannon entropy, are more informative measures of a community's diversity by incorporating the number of individuals.

To better understand the variability in ecosystem functioning requires measuring changes in species richness, evenness, and diversity, and changes in the diversity and composition of traits. Functional diversity incorporates the relative abundance of species as well as their traits as an indicator of ecosystem functioning (Mouillot et al., 2013; Wiedmann et al., 2014; Duncan et al., 2015; Duffy et al., 2016; Plass-Johnson et al, 2016).

Reef fish communities in the FKNMS have been routinely surveyed since the late 1970's (Bohnsack & Meester, 1998; Bohnsack et al., 1999). Prior to that, reef fish assessments focused on single species of economic importance (Bohnsack & Meester, 1998). Since the turn of the 21st century, regional and federal resource management agencies have shifted toward implementing ecosystem-based management approaches to conserve and manage the sustainable use of marine resources (Bohnsack & Bannerot, 1986; Cook et al., 2014). Part of this effort included designing and carrying out multispecies assessments and developing ecosystem models that take into account biological interactions and environmental parameters (Ault et al., 2005; Keller & Causey, 2005; Kelble et al., 2013; Nuttle & Fletcher, 2013). Reef fish community observations have since been evaluated in terms of richness, abundance, density, biomass, and population and community size structure to better understand species assemblages, composition, and spatial distributions throughout the Florida Keys (Jeffrey et al., 2001; Kramer & Heck, 2007; Bartholomew et al., 2008; Ault et al., 2013). However, our understanding of changes in species diversity and functional diversity of reef fish communities in the FKNMS has remained limited.

This study was guided by the Florida Keys National Marine Sanctuary (FKNMS) Condition Report question: What are the status and trends of biodiversity and how is it changing? (ONMS, 2011). Specifically, we sought to analyze and compare changes in seven community variables: 1) abundance, 2) biomass, 3) species evenness, 4) species richness, 5) Simpson diversity, 6) Shannon diversity, and 7) functional diversity. These indices were examined as "response variables" to temporal, spatial, habitat structure, and no-take marine zones from 1999 – 2016 throughout the Florida Keys domain. The observations were evaluated for different levels of protection, and were also segmented across seven distinct habitat strata, and three geographic subregions.

The ultimate objective of this research is to better inform management and policy with practical tools to evaluate the integrity of coral reef fish and the level of resilience of these communities in the face of growing pressures from environmental change and human uses of resources. The hypotheses that guided the study were as follows:

1) Biodiversity is greater inside no-take marine zones than outside these zones. Marine Protected Areas that are closed to all fishing and extraction uses have a span of benefits including enhancing marine ecosystem biodiversity (Bohnsack and Ault 1996, Bohnsack et al., 2004).

2) The indices are positively correlated to strata, where more complex habitats have greater diversity. Species richness and abundance are known to increase with habitat complexity providing reef fish with shelter and foraging grounds (Luckhurst & Luckhurst, 1978; Gratwicke & Speight, 2005).

3) The indices differ by subregion, where the Upper Keys and Lower Keys have greater diversity than the Middle Keys. The rationale is that the Upper Keys and Lower Keys shield the reef tract from more extreme seasonal changes that occur in Florida Bay relative to the Atlantic Ocean near the Keys. The Upper and Lower Keys therefore have more abundant and diverse coral reefs known to inhabit more reef fish.

2. Methods

2.1 Study Site

The FKNMS encompasses 2,896 square nautical miles from Miami to the Dry Tortugas (Figure 3). The Sanctuary includes a shallow (<10m) and narrow (7-10 km) reef tract (Lee & Williams, 1999). The sanctuary was designated by the United States Congress in 1990 and expanded in 1999 to conserve, protect, and enhance marine biodiversity, ecological integrity, and the cultural legacy of the nation’s only shallow water continental barrier reef and is the third largest barrier reef in the world (Kruczynski and Fletcher, 2012). The study area consists of the Florida Keys domain from Key Largo to Marquesas Key (Upper, Middle, and Lower Keys). The Dry

Tortugas region was omitted because of limited data and differences in habitat strata relative to the rest of the Keys.

The Florida Keys domain is composed of 23 no-take marine zones established in 1997. The no-take zones include 18 Sanctuary Preservations Areas (SPA), four Special Use/Research Only Areas (SU/RO; each on average 0.85 km^2), and one larger Ecological Reserve (ER; 18.7 km^2; US DOC 1996; Kruczynski & Fletcher, 2012). Collectively, the zones account for less than 1% of the surface area of the sanctuary (NOAA, 2007; Keller & Wilmot, 2008). I treated all the no-take marine zones as equal (0, unprotected and 1, protected) in the analysis and did not differentiate between reserve size and location.

The Florida Keys are inhabited by a diverse marine fauna and flora that includes species common to the tropical Caribbean region, subtropical waters of the Gulf of Mexico, and the East Coast of North America (Kruczynski & Fletcher, 2012). Habitats include mangroves, seagrass beds, patch reefs, bank reefs, and other hard bottom and sand habitats (ONMS, 2011). The coral reef ecosystem is characterized by cross-shelf reef strata determined by reef structures and habitat characteristics, and spatial distribution of low to high variance of reef fish density (Smith et al., 2011; Harford et al., 2016). The three primary types of reef structures found in the Florida Keys are linear reefs, patch reefs, and spur and groove reefs (Shinn et al., 1989). Linear reefs are oriented parallel to the shoreline, patch reefs are isolated coral boulders formed on the shelf, and spur and groove reefs have shallow ridges (spurs) separated by deep channels (grooves) that are oriented perpendicular to the shoreline (Walker et al., 2008).

Geographic variables and environmental conditions divide the Florida Keys reef tract into four geographical subregions: Upper Keys, Middle Keys, Lower Keys, and Dry Tortugas (Figure 3; Ginsburg & Shinn, 1995; FMRI, 1998). The Upper Keys, defined as the area from Key Largo to Upper Matecumbe Key, is the largest region and has the largest land mass. This land barrier separates Florida Bay and the Gulf of Mexico from the reef tract, which is located on the east side of the Keys, and from Atlantic Ocean waters. The Upper Keys have the greatest abundance of patch reefs, followed by the Lower Keys and Dry Tortugas (FMRI, 1998). The Middle Keys, from Upper Matecumbe Key to Pigeon Key, have several wide channels that allow large volumes of water to be exchanged between Florida Bay, and the Florida Straits in the Atlantic Ocean (Jaap et al., 2008). The Middle Keys reef tract has the lowest abundance of reefs likely due to extreme changes in temperature, salinity, nutrients, and turbidity associated with waters from Florida Bay (FMRI, 1998). This variability impedes coral growth (Ginsburg and Shinn, 1964; Jaap et al., 2008). The Lower Keys, from Pigeon Key to Marquesas Key, has the widest land mass and several narrow channels. Similar to the Upper Keys, the land mass shields the reef tract from the seasonal variations in shallower areas of the eastern Gulf of Mexico and Florida Bay. Such shielding has allowed for spur and groove reef formations in the Lower and Upper Keys (Jaap 1984).

2.2 Reef Fish Surveys

Reef fish community data used in this study were collected as part of the multi-agency Reef Visual Census (RVC; Ault et al., 2002; Brandt et al., 2009; Brandt et al., 2010; Smith et al., 2011). Fish communities were visually surveyed by trained SCUBA-divers annually in the mainland Florida Keys from 1999 to 2012, and then every other year (biennially) from 2012 to 2016. Most sampling (90%) occurred between May and October. The survey applied a habitat-based, two-stage randomly stratified survey design to sample reef fish communities along the Florida Keys reef tract. In its current form, the Florida Keys domain is partitioned into 7 cross-shelf habitat strata (Figure 3). The strata include Forereef Deep Linear Reef (FDLR; 18 – 33 m), Forereef Medium

Linear Reef (FMLR; 6 -18 m), Forereef Shallow Linear Reef (FSLR; <6 m), High Relief Reef (HRRF; >2m vertical relief), Inshore Patch Reef (INPR), Midchannel Patch Reef (MCPR), and Offshore Patch Reef (OFPR; Brandt et al., 2009). The strata were defined by environmental characteristics such as bottom depth, reef morphology, and topography, because they were expected to be drivers of variance of fish density (Luckhurst & Luckhurst, 1978; Gratwicke & Speight, 2005; Smith et al., 2011). The majority of no-take marine zones occur within the High Relief Reef spur and groove reefs and no protected areas occur in the stratum Forereef Deep Linear Reef.

The first stage of the survey design consists of a primary sampling unit (PSU). The PSU is defined as a 200 m x 200 m map grid (40,000 km^2). A secondary sampling unit (SSU) is defined as a 15 m (177 m^2) diameter circular plot (Figure 3). Increased habitat mapping of the coral reef tract has allowed the survey method to implement a 100 m x 100 m map grid (20,000 km^2) in 2014 and 2016. Each PSU was randomly selected by stratum. At each SSU two divers used a stationary point count method, listing all species observed in the first five minutes, followed by recording the abundances and fork length. The species data and environmental characteristics recorded at each SSU are averaged to produce the PSU-level variables.

The number of PSUs sampled varied among years and strata (Table 2). Sampling typically focused on hard-bottom reef habitats located between 1 and 30 m depth. A greater proportion of sites was sampled in higher complexity habitats because these are known to have higher fish densities (Smith et al., 2011). The increased sampling effort here is intended to characterize real variability in populations and uncertainty in the methods. The survey is designed to optimize the observation of conspicuous and diurnally active reef fish, specifically economically and ecologically important reef fish species (Bohnsack and Bannerot, 1986). Crevice-dwelling and cryptic species are not as effectively sampled. See Brandt et al. (2009) for more information on the RVC sampling method.

2.3 Calculation of indices

Reef fish abundance and biomass for every sampling event between 1999 and 2016 were obtained from NOAA's National Marine Fisheries Service Southeast Fisheries Science Center. The data were extracted using the functions GetPSUAbundance and GetPSUBiomass in the rvc package (Ganz, 2015). The abundance is defined as count per SSU extrapolated for an entire PSU. The estimated abundance does not take into consideration detectability and therefore likely yields an underestimation of abundance. Because the effort does not vary across years, ignoring the level of detectability should not be a problem, as the bias is consistent across time (Buckland et al., 2011). Biomass was computed from abundance per PSU and species growth parameters in g/mm (NOAA, n.d.). Growth parameters were available for 308 (97%) species; the remaining species were omitted from the biomass calculations.

To detect variability in diversity through time and space (habitat and region), indices were computed for each year and primary sampling unit. We omitted any taxa that were not identified to the species level (7% of the dataset). This allowed the computation of diversity indices based on 64 families with a total of 316 species (Table A1; Table A2). PSU's with zero or one species present were removed from the analysis (0.04%) to enable diversity calculations. In total 5,238 sampling events across all years were used to calculate indices.

Species richness was calculated as the number of species detected at a given station. The evenness index was calculated as per Jost (2010) and is equivalent to Pielou's evenness. Evenness can be between zero (one species present) and one (all species with equal abundances). Species diversity was calculated as the complement of Simpson (1-D) and Shannon diversity in units of effective number of species. Where Simpson diversity is the probability that two individuals randomly selected from a sample belong to different species. Simpson diversity is a measure of dominance, as it emphasizes the more abundant species (Simpson, 1949). Shannon diversity incorporates both species richness and abundance. The Shannon index weighs all species equally (Shannon & Weaver, 1949; Magurran, 2013). Species richness, Simpson diversity, and Shannon diversity were computed with species abundances using functions specnumber and diversity in the VEGAN package (Oksanen et al., 2017) and were converted into units of effective number of species following Jost (2006) conversions.

A species-trait matrix was developed using eight traits for the 316 species detected along the FKNMS reef tract. The eight functional traits selected have been used in previous studies to analyze temperate and tropical reef fish functional diversity and are known to influence their functional roles (Bates et al., 2013; Stuart-Smith et al., 2013; Coleman et al., 2015; Duffy et al., 2016; Plass-Johnson et al., 2016). Functional traits influence fish assemblage through the life history of each species (average maximum length), trophic position (trophic group, trophic breadth), behavior (water column position, diel activity pattern, gregariousness), and habitat associations (preferred substrate, habitat complexity; Table 3). Traits influence ecosystem processes through resource partitioning and competition. The species-trait matrix was obtained from Stuart-Smith et al. (2013) for 200 reef fish species. The traits for all remaining species were obtained from Fishbase, literature search, and expert opinion (Humann & DeLoach, 1989; Froese & Pauly, 2016).

Functional distances were derived following Lefcheck et al. (2014). Because the traits included both continuous and categorical values, Gower distances (Gower, 1971) were calculated using the Podani (1999) correction for ordered traits (using gowdis in the FD package; Laliberté et al., 2014). I employed hierarchical cluster analysis on the dissimilarities (Petchey & Gaston, 2002) and then converted the distances to an ultrametric dendrogram, using the function cl_ultrametric in the clue package (Hornik, 2017). Because the dendrogram is sensitive to the clustering algorithms, I used multiple algorithms as suggested by Mouchet et al. (2008) to determine the algorithm that best preserved the non-ultrametric distances (Mérigot et al., 2010). Finally, I extracted the pairwise distances from the unweighted arithmetic average clustering functional dendrogram that best preserved the original distances using cl_dissimilarity in the clue package and scaled the maximum value so that all values were between 0 and 1 (Devictor et al., 2010). The complete functional dendrogram is presented in Figure A1. Functional diversity was subsequently calculated using Rao's quadratic entropy formula in units of effective number of species. This is a measure of pairwise functional differences between species weighted by their relative abundances (Botta-Dukat, 2005).

To explore the contributions of the eight traits to functional diversity in the Florida Keys, I removed each of the traits from the full matrix and recomputed Rao's Q eight times. I then compared the functional diversity estimates to the functional diversity calculated from the full trait-matrix using linear regression. The traits with higher contribution to the full functional diversity, when dropped, resulted in low R^2 values (Table A3).

2.4 Statistical Analysis

To visualize the spatial trends in the fish community I mapped each index from 1999-2016 using a kriging interpolation technique with ArcGIS (Figure 5; ESRI, 2014). This approach has been applied in other studies to assess the spatial distribution of diversity (Devictor et al., 2010; Lefcheck et al., 2014b). To examine the differences between protected and unprotected areas, I plotted the mean (+/- Standard Error or SE) of each index by level of protection across years (Figure 6). To examine the differences among strata across years, I plotted the mean (+/- SE) of each index for each stratum across years (Figure 7). To examine the differences among subregions across years, I combined data across strata and plotted the mean (+/- SE) of each index by subregion across years (Figure 8).

To examine spatial and temporal trends in the reef fish indices I first checked the indices for normality and homoscedasticity to determine whether to use parametric or non-parametric statistical procedures. The abundance and biomass transformed data did not meet assumptions of normal distribution, and had unequal variances. The transformed diversity matrices had normal distributions but unequal variances, so I proceeded with non-parametric tests.

I performed non-parametric Kruskal-Wallis analysis of variance (ANOA) on Ranks to test significance of each index against level of protection, strata, and geographic subregion (Kruskal and Wallis, 1952). Where significance was detected ($p = <0.01$), I proceeded with post-hoc analysis using Dunn's test for multiple comparisons, to determine which variables differ from each other (Dunn, 1964). Dunn test allows for unequal number of groups (Zar, 2010) and was calculated with function dunnTest in the FSA package (Ogle, 2017). I also performed generalized additive models (GAMs) to determine the drivers of the different indices (Wood, 2006; Zuur et al., 2009).

I evaluated four main components that have been found to influence temperate and tropical reef fish composition: temporal (year), spatial (latitude and longitude), habitat structure (strata type and depth), and NTMR (whether the sampling area was in an unprotected area or protected, characterized as a 0 or 1; Luckhurst & Luckhurst, 1978; Bohnsack and Ault, 1996; Bohnsack et al., 2004; Gratwicke & Speight, 2005; Bohnsack et al., 2009). The explanatory variables included categorized factors that were modeled parametrically to determine their mean effect sizes and continuous covariates that were modeled using non-parametric smoothing functions. The full GAM was defined as:

$$y_i = a + \alpha_1(Year) + \ \alpha_2(NTMR) + \ \alpha_2(Strata) + \ g_1(depth) + \ g_1(Lat, Long)\ x\ (Year) + \varepsilon_i$$

where y_i is the response variable (the index) for sample i, $\alpha's$ are the estimated mean effects for each year, strata, and no-take marine zones, and g's are the nonparametric smoothing functions for the continuous covariates depth, and latitude and longitude. Following Lefcheck et al. (2014) I incorporated a smoother to account for potential interactions between space and time (i.e., separate latitude smoothers for each year). Thin plate regression spines were applied to all continuous covariates. The intercept, a, scales the model prediction back to the level of the response variable because each smooth estimate (g) is constrained to average to zero over the entire dataset. The ε is the residual error at PSU i, and is assumed to be independent and identically distributed with a mean of zero and common variance.

The full model was fitted to richness using Poisson distribution and a log link. Evenness was arcsine-square root transformed. All other indices were log-transformed to better meet the assumptions of normality. To assess the explanatory power of each variable following Lefcheck et al. (2014), I calculated partial deviances by sequentially removing each predictor from the full model for all possible permutations. I then averaged the deviances for all models for which the predictor variable appeared and calculated the standard error. Essentially, the partial deviances are the proportion of total explained deviances of the model explained by each predictor time, space, environment, and management. This approach is analogous to variance partitioning in linear regression models (Legendre & Legendre, 1998).

All analyses were performed in R (R core team, 2017). Maps were developed in ArcGIS (ESRI, 2014).

3. Results

3.1 Patterns in indices by protection level across years

Across all years, the indices (except evenness) were consistently higher inside no-take marine zones than in unprotected areas (Figure 6). Marine protected areas had on average 22% more individuals, 50% more biomass, 10% more species, 6% greater Simpson diversity, 7% greater Shannon diversity, and 4% greater functional diversity. There was no significant difference between evenness inside and outside no-take marine zones (Table A4).

I detected similar trends in indices in reserves and fished areas over short periods during the timeframe examined. For example, abundance declined 31%, biomass declined 53%, richness declined 18%, Simpson diversity declined 11%, Shannon diversity declined 14%, and functional diversity declined 8% between 2004 and 2006. The indices than increased the following a year, where abundance increased 11%, biomass increased 31%, richness increased 14%, Simpson diversity and Shannon diversity increased 10% and functional diversity increased 6%.

I also detected marked declines in 2010, when abundance and biomass declined 17%, richness declined 10%, Simpson diversity and Shannon diversity declined 5% and 6%, and functional diversity declined 2%. The following year abundance increased 13%, biomass increased 31%, richness increased 13%, Simpson diversity increased 7%, Shannon diversity increased 10%, and functional diversity increased 8%.

3.2 Patterns in indices by strata across years

3.2.1 Abundance

All indices were significantly different by strata type (Table A5). Across all samples and years, I found mean abundance to be greatest in the following habitat strata: Forereef Deep Linear Reef (peaks in 2005 – 2012) and High Relief Reef (peaks in 1999-2001, 2014, and 2016; Figure 7). Mean abundance peaked in 2001 in stratum High Relief Reef with 915 individuals. Mean abundance was lowest in Inshore Patch Reef (minimal in 2000-2001, 2003-2005, 2007-2008, and 2014), Midchannel Patch Reef (minimal in 1999, 2002, 2006, and 2011-2012) and Forereef Shallow Linear Reef (minimal in 2009-2010 and 2016).

Mean abundance was large in Inshore Patch Reef in 2002, Offshore Patch Reef in 2003, and Midchannel Patch Reef in 2004 compared to other years because of schools of fish detected in each of the strata at one of the sample sites. At a single PSU in Inshore Patch Reef in 2002, divers detected a school of 10,000 Reef Silverside (Hypoatherina harringtonensis). In Offshore Patch Reef in 2003, divers detected a school of 5,000 Round Scad (Decapterus punctatus). In Midchannel Patch Reef in 2004, divers detected a school of 5,000 Reef Silverside. The schools caused the PSU's mean abundances to be 26-39 times greater than the mean abundance for the given year and for strata without such observations. Removing the above PSU's the mean abundances are respectively 269, 222, and 188 species.

Dunn’s test of multiple comparisons also revealed there was no significant difference in abundance between: Forereef Deep Linear Reef and High Relief Reef, Inshore Patch Reef and Midchannel Patch Reef, Forereef Shallow Linear Reef and Midchannel Patch Reef, and Forereef Shallow Linear Reef and Offshore Patch Reef (Table A7).

3.2.2 Biomass

Mean biomass was greatest in High Relief Reef for 14 years and peaked in 2001 with 58 kilograms per 40,000 km^2. In 2009 and 2010, High Relief Reef had the second greatest mean biomass behind Inshore Patch Reef. Mean biomass was most often lowest in Forereef Shallow Linear Reef (minimal in 2002, 2006-2010, 2012, and 2014) and Inshore Patch Reef (minimal in 2000-2001 and 2004-2005; Figure 7). Dunn’s test of multiple comparisons revealed biomass in Inshore Patch Reef and Midchannel Patch Reef, Inshore Patch Reef and Forereef Medium Linear Reef, Inshore Patch Reef and Offshore Patch Reef, and Forereef Medium Linear Reef and Midchannel Patch Reef were not significantly different (Table A8).

3.2.3 Evenness

Mean evenness was commonly greatest in Offshore Patch Reef with an average of 0.59 (peaks in 1999-2003, 2005, 2010, 2014, and 2016) and lowest in Forereef Deep Linear Reef with an average of 0.48 (minimal in 2001-2016; Figure 7). Here, 1 is maximally even and 0 is maximally uneven (one species present). For all strata across all sampling years, the mean evenness did not vary much among strata and ranged from 0.45 to 0.67 for all strata, except for Forereef Deep Linear Reef, which ranged from 0.34 to 0.54. Dunn’s test of multiple comparisons also revealed evenness was not significantly different in six of the 21 strata permutations (Table A9).

3.2.4 Richness

Across all sampling years I found mean richness to be greatest in strata High Relief Reef, except 2008 where Forereef Deep Linear Reef was greatest followed by High Relief Reef. Mean richness peaked in 2016 in High Relief Reef with an average of 54 species detected and a maximum of 73 species detected at a single PSU. Mean richness was smallest in Inshore Patch Reef (minimal in 1999-2005, 2007, 2010, 2012, 2014, and 2016) and Forereef Shallow Linear Reef (minimal in 2006, 2008-2009, and 2011; Figure 7). Richness was significantly different for all strata types except Forereef Medium Linear Reef and Offshore Patch Reef (Table A10).

3.2.5 Simpson diversity and Shannon diversity

Simpson and Shannon diversity, which incorporated both richness and evenness, showed largely identical patterns through time (Figures 7). Mean Simpson and Shannon diversity were greatest in Offshore Patch Reef and High Relief Reef environments and lowest in Inshore Patch Reef and Forereef Deep Linear Reef. On average, Simpson diversity and Shannon diversity were 1.5 times greater in High Relief Reef and Offshore Patch Reef than in Inshore Patch Reef. However, Inshore Patch Reef increased between 2005 and 2007 and then decreased between 2007 and 2010. Species richness was on average across years and strata 5 times greater than Simpson diversity and 3 times greater than Shannon diversity. Given a perfectly even community Simpson diversity and Shannon diversity would be equal to species richness.

Simpson diversity was not significantly different in Forereef Medium Linear Reef and Forereef Shallow Linear Reef, High Relief Reef and Offshore Patch Reef, and Forereef Deep Linear Reef and Inshore Patch Reef (Table A11). Shannon diversity was not significantly different in Forereef Medium Linear Reef and Midchannel Patch Reef, and Forereef Deep Linear Reef and Forereef Shallow Linear Reef (Table A12).

3.2.6 Functional diversity

Functional diversity, which incorporated species richness, evenness, and functional traits, was on average greatest in High Relief Reef (peaks in 2000-2002, 2004, 2006, 2010-2012, 2014, and 2016) followed by Forereef Deep Linear Reef (peaks in 2003, 2005, and 2008-2009) and Offshore Patch Reef (with peaks in 1999 and 2007), and lowest in Forereef Shallow Linear Reef (minimal in 2000-2011, 2014, and 2016), Forereef Medium Linear Reef (minimal in 1999 and 2004), and Inshore Patch Reef (minimal in 2012; Figure 7). The Dunn's test revealed functional diversity was not significantly different between High Relief Reef and Forereef Deep Linear Reef, Forereef Medium Linear Reef and Inshore Patch Reef, and Midchannel Patch Reef and Offshore Patch Reef (Table A13).

Overall, functional diversity, across strata, was one third of Simpson diversity. If all species were completely distinct (no functional redundancy) then functional diversity would be equivalent to Simpson diversity. Of the eight traits trophic group, diel activity pattern, and preferred substrate contributed the most to functional diversity, and preferred habitat complexity and gregariousness contributed the least to functional diversity (Table A3).

3.3 Patterns in indices by subregion

Dunn's test for multiple comparison revealed species abundance, evenness, Simpson diversity, Shannon diversity, and functional diversity were not significantly different between the Upper and Lower Keys, but the Upper and Lower Keys were significantly higher from the Middle Keys (Table A14 and A16-A19). Species richness was not significantly different between all three subregions (Table A15) and species biomass was significantly different between all three subregions (Table A15).

To better visualize the differences between subregions I examined the Upper Keys, Middle Keys, and Lower Keys across years combined with strata (Figure 8). With all strata combined, I detected slightly (7%-12%) greater biodiversity indices in the Upper Keys and Lower Keys than the Middle Keys.

3.4 Potential drivers of observed patterns in indices

Using the generalized additive models, habitat structure (strata and depth) accounted for the largest proportion of the total explained deviance for all the community response variables (10% of abundance, 14% of biomass, 9% of evenness, 20% of richness, 9% of Simpson diversity, 9% of Shannon diversity and 14% of functional diversity; Figure 9). Time (year of survey) accounted for the smallest proportion of the total explained deviance for all the community response variables (2% of abundance, 2% of biomass. 1% of evenness, 2% of richness, 1% of Simpson diversity, and 1% of Shannon diversity). Functional diversity was an exception, for which the smallest proportion was explained by space (latitude and longitude) at 1.2% compared to time at 1.4%. Space, no-take zones (0, unprotected and 1, protected), and time were similar in magnitude for biomass, evenness, Simpson, Shannon, and functional diversity indicating that these variables influence each of the indices more or less equally. However, space explained a larger proportion of the deviance in abundance, approximately 10%.

4. Discussion

4.1 No-take marine zones and habitat characteristics

The 23 no-take marine zones make up a small portion of the Florida Keys surface area (<1%). Yet reef fish abundance, biomass, richness, Simpson, Shannon, and functional diversity were significantly greater in no-take marine zones compared to the rest of the Sanctuary. This finding supported my first hypothesis. The Florida Keys reserves are known to increase density and size of exploited fish within the no-take boundaries (Bohnsack, 1997; Ault et al., 2006; Bohnsack et al., 2009; Harford et al., 2016). However, whether an area was fully protected or not only accounted for 1-3% of the total explained deviance for all indices. Variability in the results may be attributed to reserve size and placement.

Of the 23 no-take marine zones in the Florida Keys study area 18 are sanctuary preservation areas, primarily implemented to prevent user conflicts in heavily used areas. The sanctuary preservation areas allow non-consumptive activities like SCUBA diving and snorkeling. These areas are small and are not believed to provide greater ecosystem protection than open areas (NOAA, 2017). The four special use/research only areas (Looe Key, Eastern Sambo, Tennessee Reef and Conch Reef) are also small, but were designed for research and education, and to help restore degraded living resources. These sites are designated no-take and no-entry without a research permit (NOAA, 2011). The Western Sambo Ecological Reserve is nine square nautical miles and was established to protect biodiversity and encompass large, contiguous, diverse habitats to protect and enhance spawning, nurseries, and permanent-residence areas for fish and other marine life. Since they are all "no-take," reserves I treated them equally and did not address the potential differences in biodiversity between the different types and sizes of marine reserves.

However, there is conflicting evidence in landscape ecology as to whether it is better to have one large or several small no-take marine reserves (Roberts and Hawkins, 1997; Edgar and Barret, 1999; Halpern, 2003). The size and placement of reserves are influenced by species movements. Exploited reef fish with large home ranges may benefit from larger marine reserves (Edgar and Barrett, 1999) whereas site-attached sedentary adult reef fish may benefit from smaller reserves (Friedlander, 2001).

Bartholomew et al. (2008) evaluated changes in exploited fish density in the Florida Keys between the different sizes of marine reserves and to nearby reference reefs located outside of the reserves. The study indicated marine reserves exhibited greater fish density for exploitable fish than nearby nonprotected sites, but that the size of the marine reserve was not the main factor influencing fish recovery. Bartholomew et al. (2008) suggested the reserves which boundaries corresponded to natural reef habitat boundaries may have larger recovery rates than the reserves in which the boundaries intersected reef habitats. Future studies should examine if there is a relationship between reserve size and reef fish biodiversity in the Florida Keys to better inform managers when designing marine reserves.

The Florida Keys marine reserves may also not have been the main predictor of diversity because of spillover effects or larval export. Areas open to fishing often benefit from no-take marine zones as species emigrate from reserves to the surrounding open fishing grounds (Roberts et al., 2001; Gell and Roberts, 2003; Sale et al., 2005). The no-take marine reserves are also minimally enforced (Davis and Moretti, 2005). The Sanctuary relies heavily on voluntary compliance with the reserves regulations.

The marine reserves may also have exhibited significantly greater abundance, biomass and diversity because of their placement relative to the underlying habitat. Upon further investigation, of the 1,393 sampling events in no-take zones, a third were in stratum High Relief Reef (Table A20), which are characterized as complex habitats with a vertical relief of at least two meters. My results indicate abundance, biomass, and diversity indices are significantly greater in the stratum High Relief Reef. The GAM also indicated habitat structure (strata and depth) was the largest contributor of all the community response variables. These findings supported my hypothesis that reef fish abundance, biomass, and diversity indices are greater in more complex and rugose habitats.

The average number of fish species and individuals in the study area are known to be dependent on habitat complexity (Bohnsack and Bannerot, 1986). Studies in the region detected greater densities of herbivorous fishes (Paddack et al., 2006) as well as Yellowtail snapper (Ocyurus chrysurus), Gray Snapper (Lutjanus griesus), and Black Grouper (Mycteroperca bonaci) in high relief habitats (Bohnsack et al., 2009). Reef fish often prefer more complex habitats because they provide refuge sites as well as foraging grounds (Luckhurst and Luckhurst, 1978; Ohman and Rajasuriya, 1998). Of the 316-species detected in the Reef Visual Census survey, I classified 192 species in the species-trait matrix as preferring medium or high habitat complexity.

Although, not all reef fish preferentially select high relief reefs. For instance, Harford et al. (2016) study determined occurrence probability of Red Grouper (Epinephelus morio) in the Keys was higher in nearshore patch reef habitats than in offshore forereef habitats. My results also indicated habitat strata with varying degrees of complexity can have high species composition and diversity values. Next to High Relief Reef habitats, evenness, Simpson diversity, and Shannon diversity were on average across all years greatest in Offshore Patch Reefs environments. Species abundance, richness, and functional diversity were on average across all years greatest in Forereef Deep Linear Reefs following the stratum High Relief Reef. This has strong management implications. Using traditional species diversity indices, a manager may prioritize conservation in High Relief Reef and Offshore Patch Reef habitats and place little emphasis on Forereef Deep Linear Reef habitats. However, integrating functional traits suggests preserving High Relief Reef and Forereef Deep Linear Reef will result in greater functional diversity and therefore greater ecosystem processing and stability. Future studies should incorporate components of functional diversity when selecting areas for marine protection as well as consider comparing species composition and biodiversity by habitat characteristics.

Although I compared the indices among the different strata which are determined by different habitat characteristics, I did not directly compare components of habitat complexity within or between stratum that may influence reef fish abundance, biomass, and diversity. Habitat complexity varies by substrate rugosity, vertical relief, variety of refuge hole sizes and percent live coral (Gratwicke and Speight, 2005). Future studies should especially consider comparing indices in reference to live coral cover where there have been conflicting results.

Some studies indicate there is a positive relationship between species richness and live coral cover (Bell and Galzin, 1984; Lewis 1997) whereas others do not (Luckhurst and Luckhurst, 1978; Roberts and Ormond, 1987). Percent coral cover has been declining in the Florida Keys since 1980s (Jaap et al., 1988; Shinn, 1989; Hughes, 1994; Miller et al., 2002). Deterioration of the coral reefs are due to a combination of diseases (Aronson and Precht, 2001), hurricanes (Gardner et al, 2003), nutrient loading (Ginsburg and Shinn 1994; Leichter et al., 2003), herbivore reduction (Carpenter, 1990; Jackson et al., 2001; Pandolfi et al., 2003) and climate change (Walther et al., 2002; Hughes et al., 2003). The Florida Keys coral reef ecosystem has undergone a phase-shift from coral-dominated to macroalgal-dominate communities (Dustan 1977; Hughes 1994; Garner et al., 2005; Maliao et al., 2008). To better inform management how to select sites for preservation in the face of a changing ecosystem, we need to better understand how reef fish composition and diversity changes between sites with different degrees of complexity, including percent live coral cover.

My results further supports that the reef fish composition and diversity may be more heavily influenced by habitat type (i.e., strata) than by the hydrography or connections to Florida Bay in each of the subregions in which the same type of habitat is located. When comparing indices by subregion across years, the Upper Keys and Lower Keys were significantly greater in abundance, evenness, Simpson diversity, Shannon diversity, and functional diversity than the Middle Keys. The regional variation in reef structure is influenced by the Florida Bay. The Upper Keys has the most abundant and diverse reefs, followed by the Lower Keys, in which the few narrow channels connecting to the Bay may impede coral growth and coral diversity, followed by the Middle Keys which has several wide channels connecting to the Bay that limits coral growth, complexity, and diversity. It is likely that reef fish abundances, and therefore species diversity indices, are limited by availability of habitat structures in the Middle Keys for shelter and foraging. The importance of habitat characteristics in controlling reef fish composition and diversity indicates the need to investigate the relationship between habitat complexity within and between strata types and subregions to diversity indices.

Other processes that may be influencing reef fish species composition and diversity in the Florida Keys is proximity of coral reef habitats to other reef habitats as well as seagrass beds and mangroves. Although many Caribbean reef fish in their adult stage are known to be sedentary and display high reef residency and site fidelity (Chapman and Kramer, 2000; Gell and Roberts, 2003;

Lindholm et al., 2005; Tamburello and Cote, 2015), many of the exploited reef fish are also known to immigrate between reef habitats (Hixon and Carr, 1997; Harford et al., 2016). The low diversity habitats, such as Inshore Patch Reefs and Forereef Shallow linear reefs, may also serve as sources to the high diversity habitats, such as High Relief Reefs and Forereef Deep Linear Reefs, that may be ecological sinks. Source-sink population theory is based on the concept that source habits have greater birth rates than death rates, but exhibit no net population growth overtime, whereas sink habitats have greater death rates than birth rates, but exhibit net population growth overtime due to immigration of individuals from the source habitats (Pulliam, 1988). Crowder et al. (2000) emphasizes the importance of understanding source-sink populations to better select no-take marine reserves when there are greater socioeconomic concerns at play, like the establishment of the FKNMS. Crowder et al. argues that because of social pressures, especially from local fisherman, the FKNMS management plan settled for several smaller reserves placed relatively haphazardly throughout the Keys. He believes that if there were greater scientific evidence supporting the reasons behind the placement of the reserves, like source-sink habits, than there may have been more public support for the sanctuary and the no-take marine reserves.

Lastly, high densities of juvenile reef fish are found in seagrass beds and mangroves, which function as nursery grounds (Lay et al., 1999; Nagelkerken et al., 2000; Nagelkerken et al., 2001; Mumby et al., 2003; Dorensbosh et al., 2007). Many of these reef fish exhibit ontogenetic habitat shifts, utilizing different habitats between juveniles and adults (Lindeman et al., 1998). The distance of the coral reefs habitats from the nursery grounds as well as to other nearby reef sites that serve as sources likely influences species richness, species diversity, and functional diversity. Based on the results of this study as well as results of other studies described above, managers should preserve a variety of habitats to enhance species composition and diversity, specifically the connected corridors that facilitate the natural migration of species.

The biological and physical components of the marine ecosystem work in unison to develop the complexity and heterogeneity of coral reef ecosystems. To maintain biodiversity and ecosystem functioning it is important to monitor and preserve a representative number of the habitats within an ecosystem (Crowder and Norse, 2008). Originally, Wilson and Willis (1975) proposed protecting corridors based on the equilibrium theory of island geography. It has since been extended to the metapopulation paradigm (Levins, 1970). The corridor concept employs the underlying connectivity matrix between species and habitats to select areas for preservation (Crowder et al., 2000; Siitonen et al., 2002; Mumby, 2006). Thus, it may maximize biodiversity, by not only preserving source habitats and aggregation sites, but also habitats which species utilize throughout the ecosystem (Ong et al., 2002).

4.2 Species diversity and functional diversity

This study also determined the Florida Keys coral reef ecosystem can be characterized as having low Simpson and Shannon diversity in comparison to species richness. Across all years by level of protection, strata, and subregion Simpson and Shannon diversity were significantly lower than species richness. This may be attributed to the Florida Keys coral reef ecosystem being dominated by a few species with large populations and many rare species. Of the 316 species detected 293 species accounted for less than 1% of the total abundance data across years. Low species diversity is also often a result of intense competition (Levins, 1968; Huston, 1979). When species compete for resources, one species may out compete the others there by decreasing species evenness and eventually number of species resulting in a community with low species diversity.

The combined species diversity and functional diversity (incorporating all level of protections, strata, and subregion) also appeared to remain relatively constant overtime (Figure 12). This may be because the species are in a state of fluctuating competitive equilibrium (reduction and exclusion of some species). Huston (1979) hypothesis that species diversity may be stable when a dynamic balance is established between rate of competition displacement and the frequency of population reduction. Although natural ecosystems rarely exhibit competitive equilibrium because of changes in the physical environment, recruitment, predation, and anthropogenic pressures, ecosystems can still result in a stable diversity. Huston (1979) explains this by comparing the rates of competitive displacement. If one species is dominant and if all other competing species populations are increasing at a very low rate than the rate of competitive displacement for that community would be low and allow for longer periods of coexistence among competitors and therefore maintaining diversity levels.

Another reason Simpson diversity, Shannon diversity, and functional diversity appeared to be relatively stable through time may be because the coral reef ecosystem was significantly degraded prior to the start of the survey. Overfishing has been evident in the Florida Keys since the late 1970's (Ault et al., 1998; Ault et al., 2001) coupled with degrading coral reef habitats (Gardner et al., 2003; Palandro et al., 2012). The Florida Keys were considered an "ecosystem-at-risk," by the National Oceanic and Atmospheric Administration (NMFS, 1996). Long-term monitoring of reef fish populations and habitat assessments is critical to assess temporal trends in biodiversity and to better determine if the status of biodiversity is within its natural range of variation (Fischer et al., 2010).

The Florida Keys ecosystem can also be characterized as having low functional diversity in comparison to Simpson diversity. If all species were functionally distinct (no traits in common) than functional diversity would be equal to Simpson diversity. However, Simpson diversity was on average three times greater than functional diversity across all years by level of protection, strata, and subregion. This may be due to the Florida Keys being dominated by a few species with large population sizes and similar functional traits, and many species with small population sizes and dissimilar functional traits (Table A1, Figure A2).

For example, Redband Parrotfish (Sparisoma aurofrenatum), Striped Parrotfish (Scarus iseri), Doctorfish (Acanthurus chirurgus), Blue Tang (Acanthurus coeruleus), and Ocean Surgeon (Acanthurus bahianus) are functionally similar with an average functional dissimilarity of 0.25 (where 0 the species are not dissimilar and 1 the species are completely dissimilar) and accounted for 11% of species abundance data across all years. Additionally, Sergeant Major (Abudefduf saxatilis), Creole wrasse (Clepticus parrae), and Brown Chromis (Chromis multilineata) make up 5% of total species abundance data across years and had an average functional dissimilarity of 0.24.

Ecosystems with low functional diversity, like the Florida Keys, are characterized as "underdispersed", or having high functional redundancy between species and traits (Wiedmann et al., 2014; Mouillot et al., 2007). The redundancy hypothesis states that the loss of a species may not necessarily have negative impacts on ecosystem functioning because it may be compensated by other species with similar functional roles (Lawton & Brown 1993, Ehrlich & Walker 1998). The high functional redundancy observed indicates that the Florida Keys coral reef ecosystem may be relatively insensitive to species loss. Species redundancy provides a level of functional insurance and is an important component that contributes to ecosystem resilience.

Complementary to functional redundancy is functional rarity, or the extent to which species are functionally distinct and taxonomically scarce. Violle et al. (2017) identifies functionally rare species as ecological outliers. There is contrasting evidence on the importance of rare species for ecosystem functioning. Efforts to better conserve biodiversity and ecosystem functions should focus on protecting functionally rare species (few individuals that possess rare traits), that are more vulnerable to being loss by preserving their habitats (e.g., High Relief Reefs and Forereef Deep Linear Reef). For instance, Sharknose Goby (Elacatinus evelynae) and Neon Goby (Elacatinus oceanops) were the only species in the species-trait matrix that were classified as cleaners and accounted for less than 1% of the abundance data. These fish are ecologically important on reefs for removing ectoparasites off higher carnivorous fish (Arnal and Cote, 1998; Cheney and Cote, 2001; Grutter and Lester, 2002; Sikkel et al., 2004; Cheney and Cote, 2005).

Additionally, functional diversity and functional redundancy has a level of inherited antagonism. Low functional diversity ecosystems, like the Florida Keys, has many species with functionally redundant traits providing a level of functional insurance, but the ecosystems are also less likely to possess functions that can withstand a disturbance. The greater the functional diversity, the more complex, productive, and resilient the ecosystem will be to disturbances (e.g., climate change; Cadotte et al., 2012; Cadotte, 2013; Monaco and Prouzet, 2015) In other words, a new species in an ecosystem may either increase the functional redundancy and therefore functional insurance, or a new function is created and therefore may enhance the resiliency of the ecosystem to withstand a disturbance (Manaco and Prouzet, 2015).

In contrast to the observed high functional redundancy observed in the FKNMS, Micheli et al. (2014) observed low functional redundancy for a suite of Caribbean tropical and temperate reef fish. His study analyzed functional groups based on three functional traits including diet, maximum length, and habitat use (all of these were part of the trait-based matrix used in my study). Micheli et al. (2014) found that a few functional groups contained the majority of species, and that a large fraction of the functional groups contained 1-2 species of reef fish. According to the Mouillot et al. (2014) definition of functional diversity, Micheli et al. (2014) results show that the Caribbean coral reef ecosystem is functionally over-redundant, with the overall level of redundancy is disproportionately distributed into a few functional groups or entities. The differences between my results and those of Micheli et al. (2014) for the Caribbean may be attributed to the fact that I incorporated eight functional traits.

The relationship between species diversity and functional diversity is largely based on the functional classification scheme. If you assign too many functional traits to the point where each species is functionally unique than the relationship between functional diversity and species diversity will be linear with a slope of one. In contrast, if you assign too few functional traits to the point where each species is functionally redundant than the relationship between species diversity and functional diversity would quickly result in a flat asymptote (Guillemot et al., 2011). Thus, all scenarios between species diversity and functional diversity is a result of the functional classification scheme. The ambiguity of selecting traits is a major limitation for trait-based approach studies and is why it is essential to select traits that have important implications for ecosystem functioning.

The majority of reef fish functional diversity studies to date included components of fish diets and fish length (Halpern and Floeter, 2008; Guillemont et al, 2011; Stuart-Smith et al, 2013; Wiedman et al, 2014; Bates et al, 2014; Coleman et al, 2015; Costello et al, 2015; Plass-Johnson et al, 2016; Duffy et al, 2016). Dietary groups or trophic groups are a key component of ecological interactions and is a proxy for susceptibility to predation (Sale, 1997; Holmlund and Hammer, 1999; Kulbicki et al., 2005; Bellwood et al., 2006). Trophic groups generally consist of piscivores, carnivores, herbivore, omnivores and planktivores. These groups can further be broken down by specific groups. For example, herbivores can further be classified as scrapers, browsers, and grazers (Cheal et al., 2012). Size largely defines the predator-prey interactions and determines the energy required for metabolism (Costa, 2009; Fisher et al., 2010). Species size also influences population abundances, geographic distributions, and life history adaptations (Schaffer and Elson, 1975; Leggett and Carscadded, 1978, Blackburn and Gaston, 1994; Hildrew et al., 2007)

Other important fish traits include water column position, schooling behavior (e.g., level of gregariousness), and diel activity patterns (Stuart-Smith et al., 2013; Mouillot et al., 2014; Bates et al., 2014; Coleman et al., 2015; Duffy et al., 2016). Water column position is an indicator of energy flow from benthic to pelagic areas (Schuhmacher and Zibrowius, 1985). School behavior or gregariousness influences how nutrients are transferred within an ecosystem (Robertson et al., 1976; Meyer and Schultz, 1985). The diel activity patterns reflect competition for resources since diurnal species and nocturnal species do not feed on the same prey (Fox and Bellwood, 2011).

Furthermore, the differences between my results and those of Micheli et al. (2014) for the Caribbean reef fish functional diversity may be attributed to the methods of how functional diversity was calculated. Micheli et al. (2014) compared species in functional groups whereas I looked at overall dissimilarities between species. Assigning species to functional groups implies there is no functional overlap between groups. Intuitively a functional group of mid-water herbivores and another functional group consisting only of benthic herbivores has some level of functional similarity, however when computing functional diversity based on groups or entities you risk overestimating how functionally dissimilar the species are. I encourage future studies to first calculate the overall functional dissimilarity between species based on their selected traits and then incorporate species abundances using Rao's Q to get a more accurate reflection of the ecosystems functional diversity and redundancy.

4.3 Disturbances

All indices decreased by level of protection and by strata type in 2005 and 2006 and increased in 2007. The decrease in diversity index values may be due to a total of seven tropical cyclones directly impacting the region in 2004 and 2005, with index values increasing following a year without hurricane disturbances (Table 5; Figure 11; Unisys, 2017). Because sampling occurred primarily between May and August, prior to the hurricane events of 2004 and 2005, the effects on the reef fish population is not reflected until the following sampling years (2005 and 2006).

Tropical cyclones, characterized by their wind intensity as hurricanes, tropical storms, and tropical depressions (McAdie et al., 2009) cause reef fish mortality and affect behavior and distribution (Robins 1957; Bohnsack et al., 2009). Reef fish mortality can be associated with fish strandings from storm surges or suffocation due to high suspended matter load in the water column (Conner et al., 1989; Tabb and Jones, 1962). Changes in reef fish behavior and distribution can be associated with changes in atmospheric pressures (Heupel et al., 2003), or changes in water quality and habitat availability (Kaufman, 1983; Patterson et al., 2001; Walsh, 1983; Watterson et al., 1998). Due to high turbidity and storm surge, hurricanes can cause fish to become disoriented and displaced. Fish may be redistributed to other sites (Patterson et al., 2001). This results in more homogenous reef fish populations and may explain why I detected an increase in Simpson, Shannon, and functional diversity on Inshore Patch Reefs and Midchannel Patch Reefs in 2006 and 2007 and a decrease in High Relief Reef habitats following two consecutive years of intense hurricanes. These trends in reef fish composition after the 2004 and 2005 hurricanes were also detected in the region by Ault et al. (2013), Smith et al. (2011), and Bohnsack et al. (2009).

Additionally, the record breaking cold temperatures (<16 °C), spanning 13 days in January 2010, caused significant mortality in corals (Lirman et al., 2011; Kemp et al., 2011; Colella et al., 2012) and many reef fish (Boucek & Rehage, 2014; Adams et al., 2012). Percent coral mortality was 20 times higher than normal following the 2010 cold event (Lirman et al., 2013). Adams et al. (2012) reported common snook abundance in 2010 was 75.6% below 2008 levels and 41.8% below 2009 levels. Boucek and Rehage (2014) applied a trait-based approach using temperature and salinity lethal limits to characterize the functional traits of the reef fish community, and found the 2010 cold front virtually eliminated the tropical species (large-bodied snook, mojarra species, and stripped mullet) but had little effect on the temperate fishes, which could withstand the abnormally cold waters. To better determine reef fish resilience to environmental changes including temperature, salinity, and nutrients, future studies should investigate reef fish environmental maximum and minimum limits to the functional traits.

Lastly, introduction of the invasive Indo Pacific lionfish (Pterois volitans and Pterois miles) are impacting reef fish populations and richness in the Florida Keys (REF). Lionfish were first released off the southeast coast of Florida in the mid 1980's (Albins and Hixon, 2013; Green and Côté, 2009; Schofield, 2010). Lionfish were first sighted in the FKNMS Reef Visual Survey near Key Largo in January 2009 (Table A), with abundances and frequency of occurrence increasing three to six-fold throughout the sanctuary by 2011 (Ruttenberg et al., 2012; Schofield, 2010).

At present there are frequent sightings of abundant lionfish throughout the western Atlantic, Caribbean, and Gulf of Mexico (Albins & Hixon, 2008; Morris & Akins, 2009). Lionfish densities continue to increase rapidly and the species is considered a threat to native coral reef fish communities (Albins, 2013; Côté & Maljković, 2010; Green et al., 2012a). However, this study did not detect a noticeable difference in any of the biodiversity indices between before and after invasive lionfish detection in 2009. This is possibly a result of the design of the Reef Visual Census method. The survey applies a stationary point count, which is not optimal for detecting small and cryptic species, like gobbies and blennies, which account for a large portion of lionfish diet (Morris & Akins, 2009). Lionfish are known to primarily prey on solitary, small, and shallow-bodied reef fish (Green et al., 2012b; Arias-Gonzalez et al., 2011; Morris & Akins, 2009).

Studies that have found significant negative effects of lionfish on coral reef fish communities throughout the Caribbean used roving visual census techniques, which also target cryptic prey fish less than 10cm in total length (Côté & Maljković, 2010; Green et al., 2012b; Munoz et al., 2011). The FKNMS has also implemented control measures to mitigate regional lionfish impacts, including allowing removal of lionfish from no-take marine zones, targeted removals, lionfish derbies, and public education (Johnston et al., 2015). The FKNMS management controls may have reduced the types of impacts documented in other areas of the Caribbean and may explain in part why there are no significant differences in indices after the lionfish invasion.

SUMMARY

Abundance, biomass, evenness, richness, and Simpson, Shannon, and functional diversity of reef fish of the Florida Keys were used to assess community response through space and time over 17 years in the FKNMS. The study revealed habitat type was the greatest driver in determining patterns in diversity. High Relief Reef habitats have the greatest abundance, biomass, richness, species diversity, and functional diversity, but have moderate evenness values. The study also detected abundance, biomass, and diversity indices (except evenness) were significantly greater inside no-take marine zones than areas open to fishing. This may be attributed to the underlying habitat since a majority of marine zones are in High Relief Reef habitats that harbor a greater diversity of reef fish. However, the no take marine zones only explained a small proportion of total percent deviance in all the indices, this may be a result of the reserve sizes and placement, spillover effect, larval export, and minimum enforcement.

The data also revealed no significant differences in the indices between the Upper Keys and Lower Keys. The study documented slightly greater abundance and diversity in the Upper Keys and Lower Keys verses the Middle Keys. This can be attributed to similar habitat types as a result of the fewer tidal passages and exchange of the nutrient rich Florida Bay.

The coral reef ecosystem of the Florida Keys is also characterized as having low functional diversity due to few dominant species with similar functional traits and many rare species with dissimilar functional traits. Low functional diversity and high trait redundancy indicates the coral reef ecosystem is more susceptible to environmental changes like pollution, nitrification, turbidity, temperature, and salinity, but is less susceptible to functional loss due to high functional redundancy. I encourage future research to include species traits that influence ecosystem functioning to shed further light on marine ecosystem functioning and processes. Particularly, future trait-based studies should include reef fish environmental range limits to better determine which reef fish are most vulnerable to climate events and human perturbations.

The thesis results may aid in setting priorities for conservation and management. In efforts to increase functional diversity, I recommend managers prioritize protection for species that possess unique traits (e.g cleaning species) by protecting areas of greater functional diversity (e.g., High Relief Reef and Forereef Deep Linear Reef). To promote biodiversity and ecosystem functioning in the Florida Keys I believe the key is to develop reserves that correspond to source habitats as well as encompass a diverse number of habitats within the region that adhere to reef fish ontogenetic shifts by implementing reserve corridors.

This study also highlighted the impacts on reef fish composition of intense hurricanes in 2004 and 2005 as well as an extreme cold event in 2010. To further gauge the coral reef ecosystem integrity and resilience, in addition to monitoring functional diversity, future studies should monitor changes in trophic structure, keystone species and foundation species. Studying functional groups and individual species that regulate essential ecosystem functions can better inform conservation biologist and managers on ecosystem process and stability.

TABLES AND FIGURES

Table 1. Conversion of common indices to true diversities (Jost, 2006).

Index x:	Diversity in terms of x:	Diversity in terms of p_i:
Species richness x $\equiv \sum_{i=1}^{S} p_i^0$	x	$\sum_{i=1}^{S} p_i^0$
$Shannon\ entropy \equiv -\sum_{i=1}^{S} p_i \ln p_i$	exp(x)	$\exp\left(-\sum_{i=1}^{S} p_i \ln p_i\right)$
Gini Simpson x $\equiv 1 - \sum_{i=1}^{S} p_i^2$	1/(1-x)	$\frac{1}{\sum_{i=1}^{S} p_i^2}$

Table 2. Reef Visual Census by number of Primary Sampling Units per year and stratum in the Florida Keys domain. Strata not sampled in a given year are denoted by '-'.

YEAR	FDLR	FMLR	FSLR	HRRF	INPR	MCPR	OFPR	Total
1999	-	71	14	39	8	21	8	161
2000	-	97	27	41	17	30	16	228
2001	14	86	44	79	12	54	15	304
2002	18	179	19	53	18	45	24	356
2003	13	70	32	59	15	33	15	237
2004	9	33	17	42	3	11	12	127
2005	25	81	32	47	8	43	20	256
2006	22	115	52	51	12	50	25	326
2007	24	124	37	48	10	56	18	317
2008	23	146	54	44	14	58	37	376
2009	48	201	60	57	23	73	54	516
2010	32	166	62	23	10	47	39	379
2011	73	146	62	32	14	40	35	402
2012	40	172	51	26	9	72	46	416
2014	35	134	67	40	17	87	52	432
2016	31	111	64	52	16	75	55	404

Table 3. Functional traits of reef fish used to characterize functional niche (from Stuart Smith et al., 2013).

Functional Trait	Category	Type	Units
Maximum length	Body size – resource partitioning	Numeric	Total length (cm), continuous
Trophic breadth	Trophic niche – resource partitioning	Numeric	Number of prey phyla consumed. Range from 1-8
Trophic group	Trophic niche – resource partitioning	Factor	Browsing herbivore, scraping herbivore, benthic invertivore, planktivore, higher carnivore
Water column position	Behavior – space and habitat partitioning	Factor	Benthic, demersal, site-attached pelagic, roaming pelagic
Gregariousness	Behavior – space and habitat partitioning	Ordered Factor	Index 1-3, representing singleton, paired to sometimes forming small schools, always schooling
Diel activity pattern	Behavior – resource partitioning, predator avoidance	Factor	Diurnal, Nocturnal
Preferred substrate	Habitat use – resource partitioning, predator avoidance	Factor	Hard substrate, soft substrate
Habitat Complexity	Habitat use – space and habitat partitioning	Factor	Typically associated with habitats characterized by low, medium, high structural complexity

Table 4. Disturbances between 1999 – 2016 in the Florida Keys. All hurricanes occurred within 100 nautical miles of the Florida Keys (Office for Coastal Management, 2017).

Year	Disturbance events between 1999 – 2016	Dates
1997		
1998	Hurricane Georges (Category 2) Hurricane Mitch (Category 2)	September 25th October 24th
1999	Data collected before Tropical Storm Harvey Data collected before Hurricane Irene (Category 1)	September 22nd October 15th
2000		
2001		
2002		
2003		
2004	Data collected before Hurricane Charley (Category 2) Data collected before Hurricane Frances (Category 2) Data collected before Tropical Storm Ivan	August 13th September 4th September 21st
2005	Data collected before Hurricane Dennis (Category 2) Data collected before Hurricane Katrine (Category 2) Data collected before Hurricane Rita (Category 2) Data collected before Hurricane Wilma (Category 3)	July 9th August 27th September 21th October 24th
2006	Data collected before and after Tropical Storm Ernesto	August 30th
2007		
2008	Data collected before and after Tropical Storm Fay	August 18th
2009	First invasive lionfish sighting	January 6th
2010	Data collected after extreme cold-water event Data collected before and after Tropical Storm Bonnie	January 12th July 23rd
2011		
2012	Data collected before and after Tropical Storm Isaac	August 27th
2013		
2014		
2015		
2016	Data collected before and after Tropical Storm Hermine	August 28th

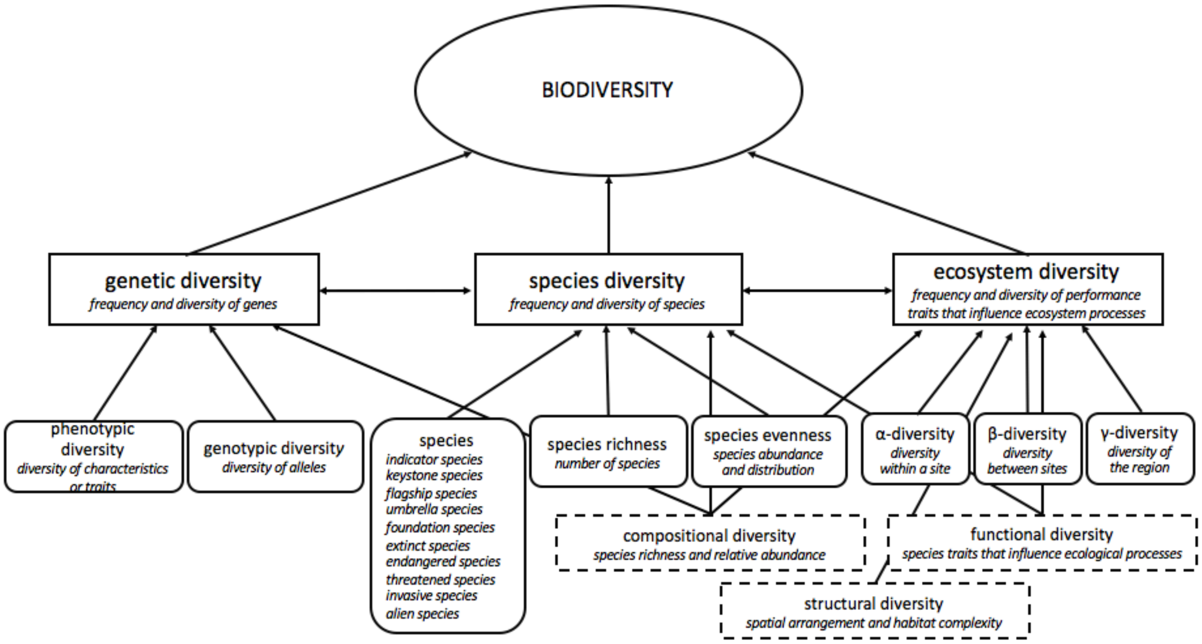


Figure 1. Biodiversity as a multifaceted conceptual framework. Rectangular boxes with a solid border are the "standard" components of biodiversity, the round-corner rectangles are related concepts, and the rectangles with a dashed border represent an alternative approach. In italics is a brief description of each component (Modified from Duelli et al., 2003).

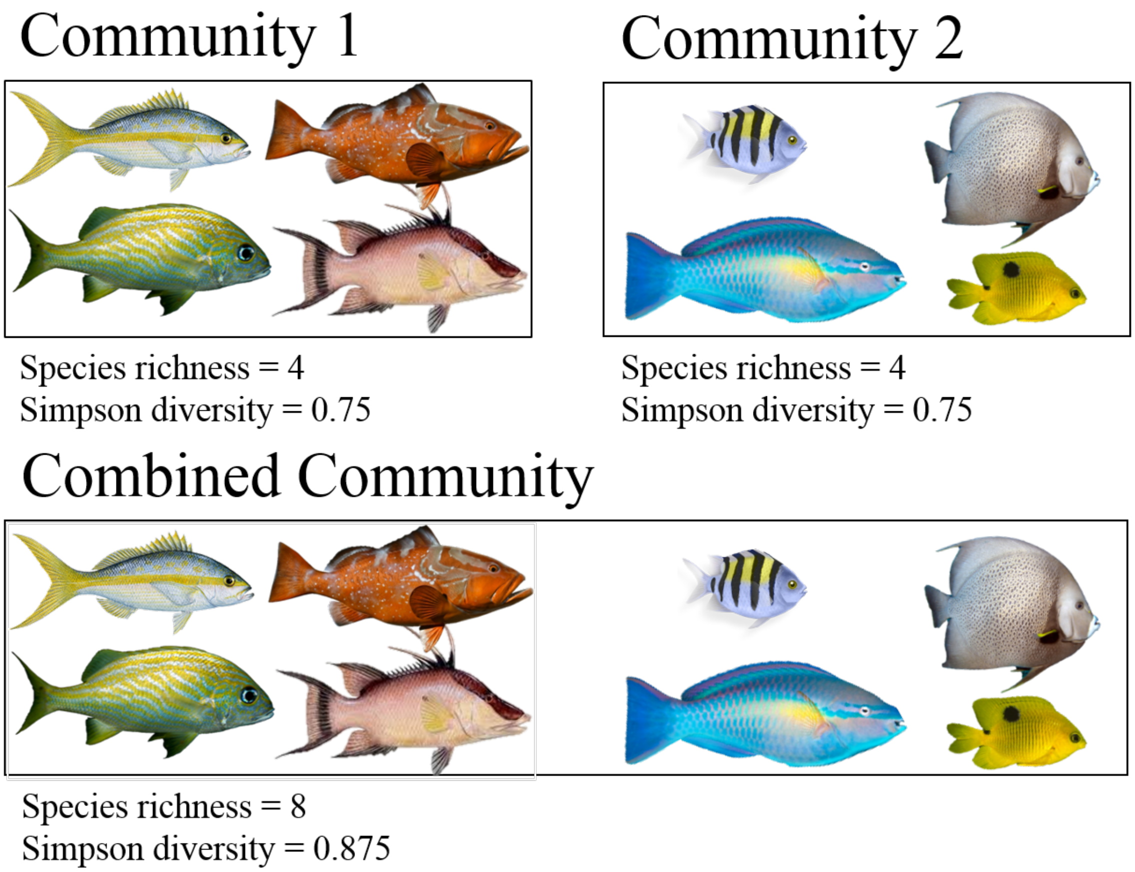


Figure 2. Example of two communities with the same number of species (but no overlap in species) and equally abundant species. When the two communities are combined species richness doubles following the doubling property, but Simpson diversity does not.

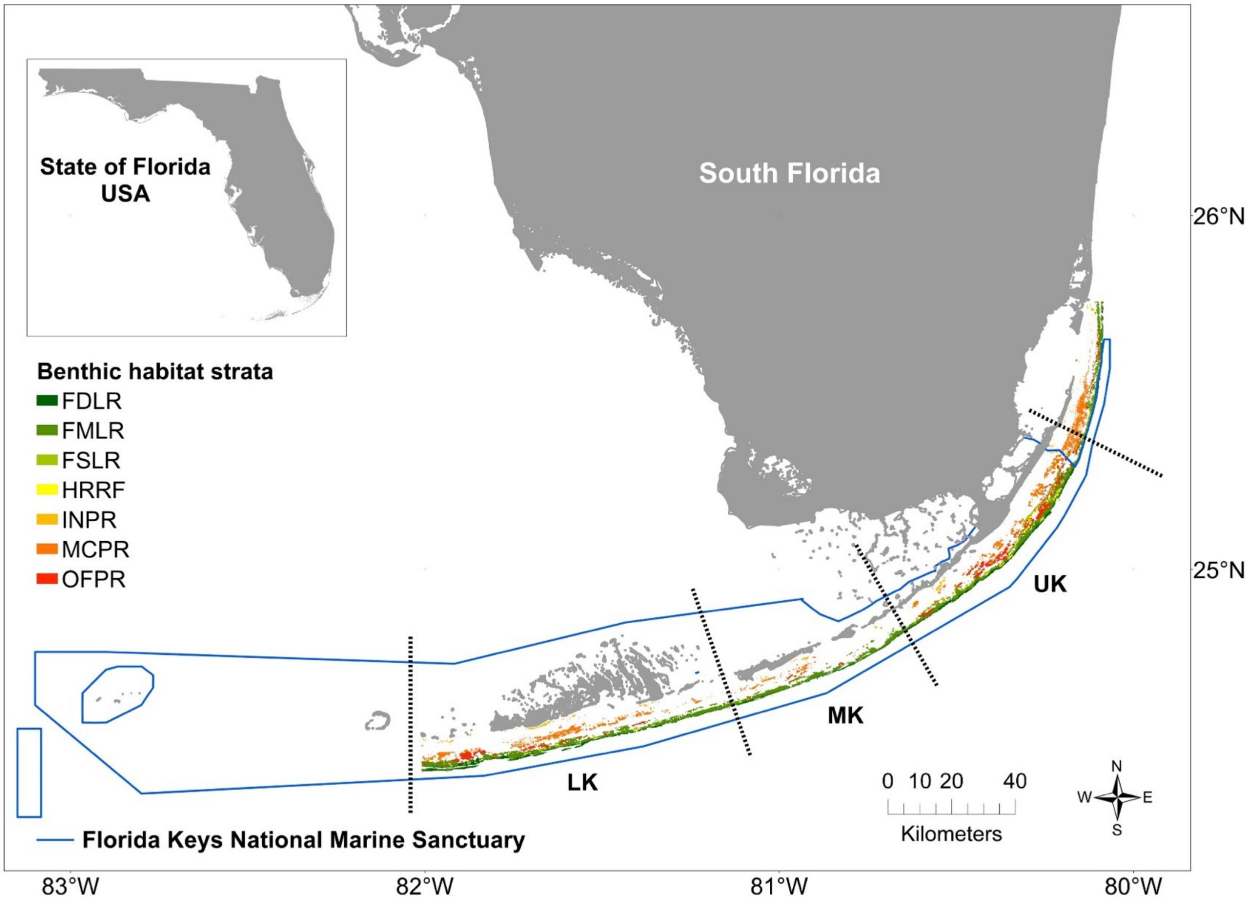


Figure 3. Map of the Florida Keys domain by geographic subregion (Upper Keys, Middle Keys, Lower Keys) and classified by habitat strata: Forereef Deep Linear Reef (FDLR), Forereef Medium Linear Reef (FMLR), Forereef Shallow Linear Reef (FSLR), High Relief Reef (HRRF), Inshore Patch Reef (INPR), Midchannel Patch Reef (MCPR) and Offshore Patch Reef (OFPR).

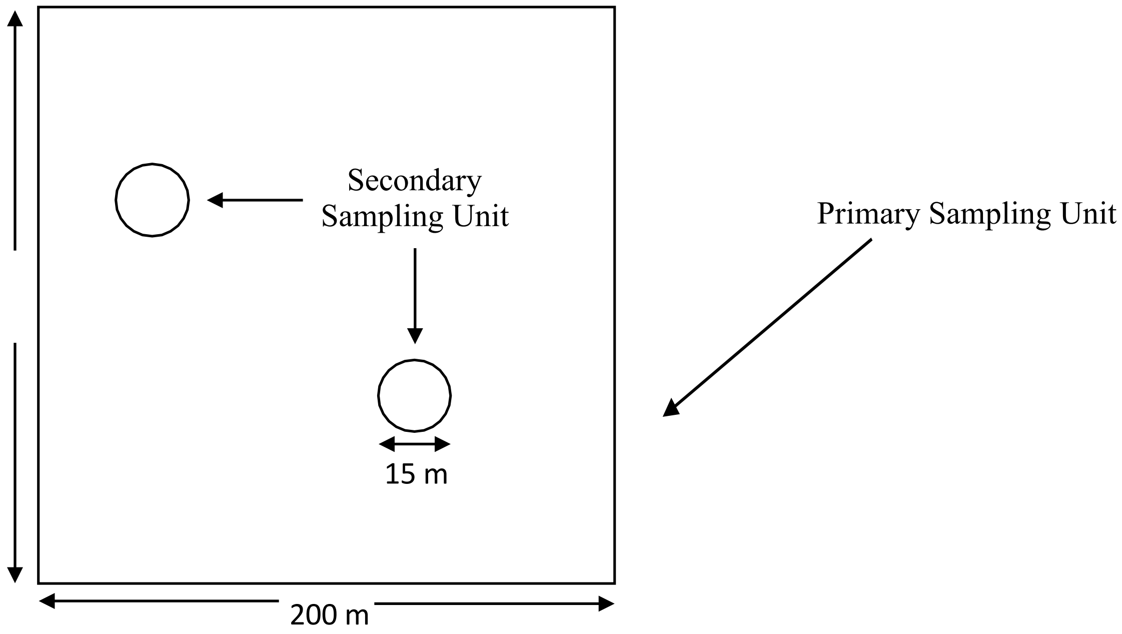
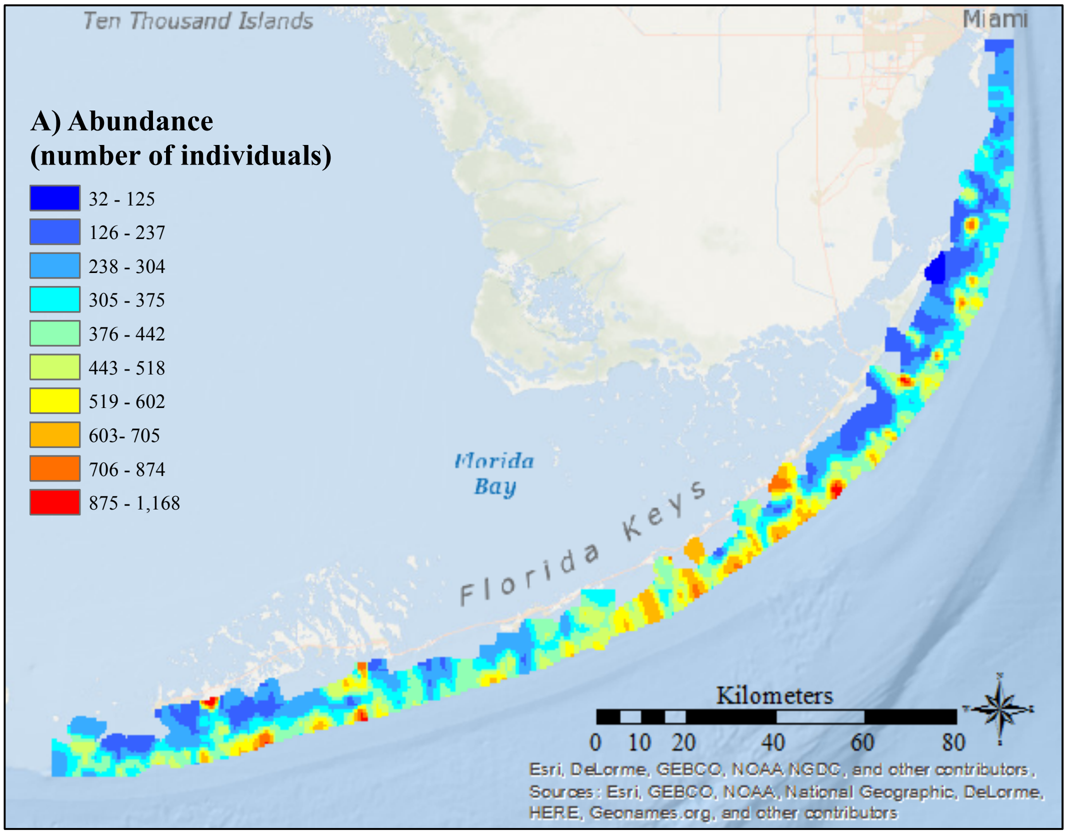
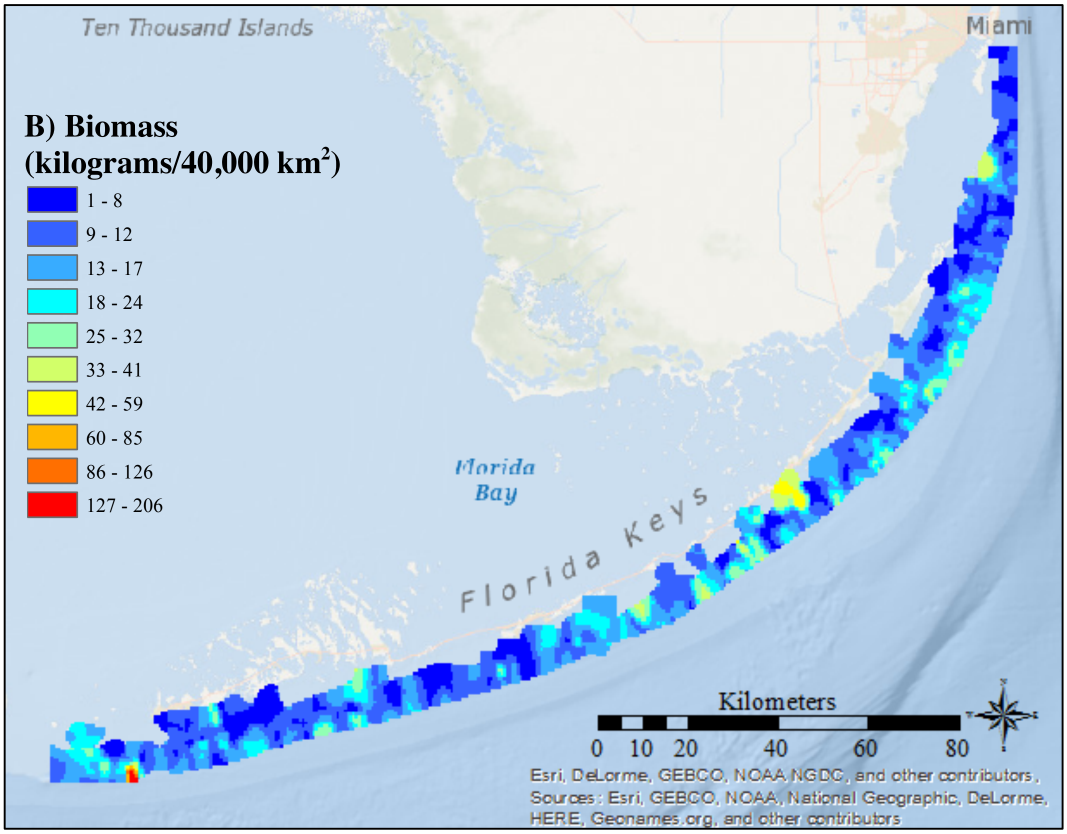
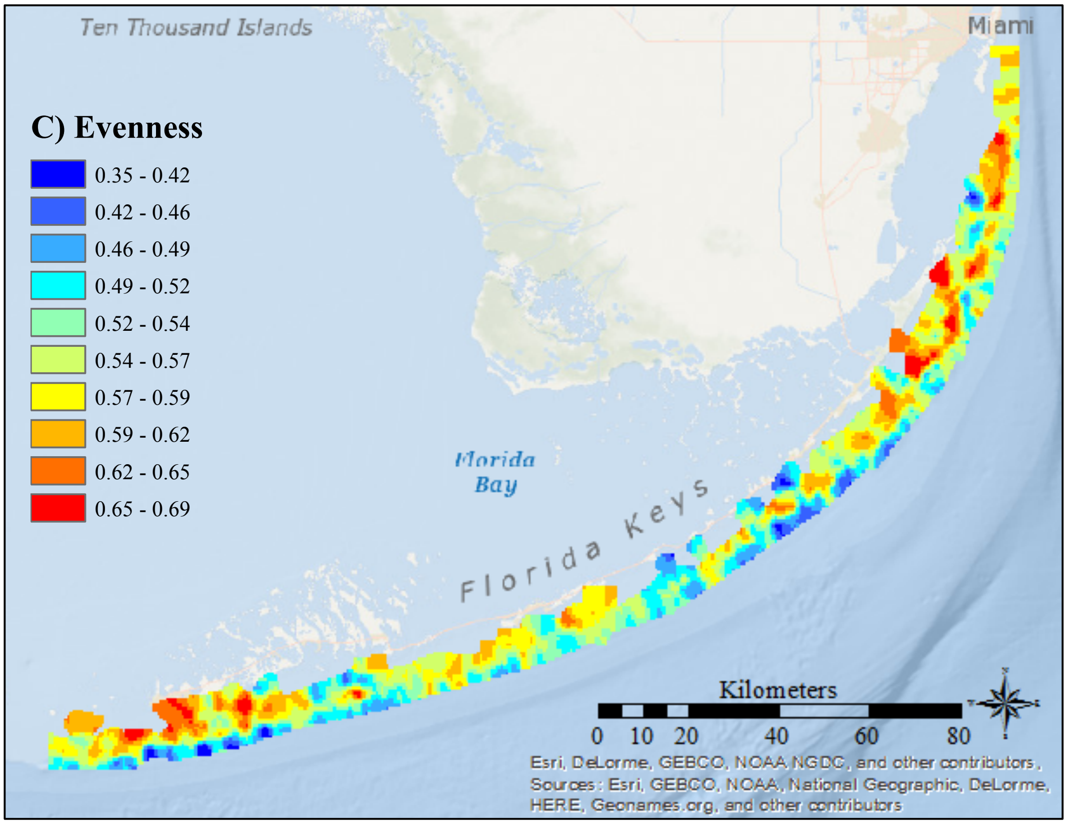


Figure 4. Spatial layout of the primary and secondary sampling units.


Ten Thousand Islands
Miami
A) Abundance
(number of individuals)
32 - 125
126 - 237
238 - 304
305 - 375
376 - 442
443 - 518
519 - 602
603- 705
706 - 874
875 - 1,168
Florida Bay
Florida Keys
Kilometers
0 10 20 40 60 80
Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors,
Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors


Ten Thousand Islands
Miami
B) Biomass
(kilograms/40,000 km²)
1 - 8
9 - 12
13 - 17
18 - 24
25 - 32
33 - 41
42 - 59
60 - 85
86 - 126
127 - 206
Florida Bay
Florida Keys
Kilometers
0 10 20 40 60 80
Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors,
Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors


Ten Thousand Islands
Miami
C) Evenness
0.35 - 0.42
0.42 - 0.46
0.46 - 0.49
0.49 - 0.52
0.52 - 0.54
0.54 - 0.57
0.57 - 0.59
0.59 - 0.62
0.62 - 0.65
0.65 - 0.69
Florida Bay
Florida Keys
Kilometers
0 10 20 40 60 80
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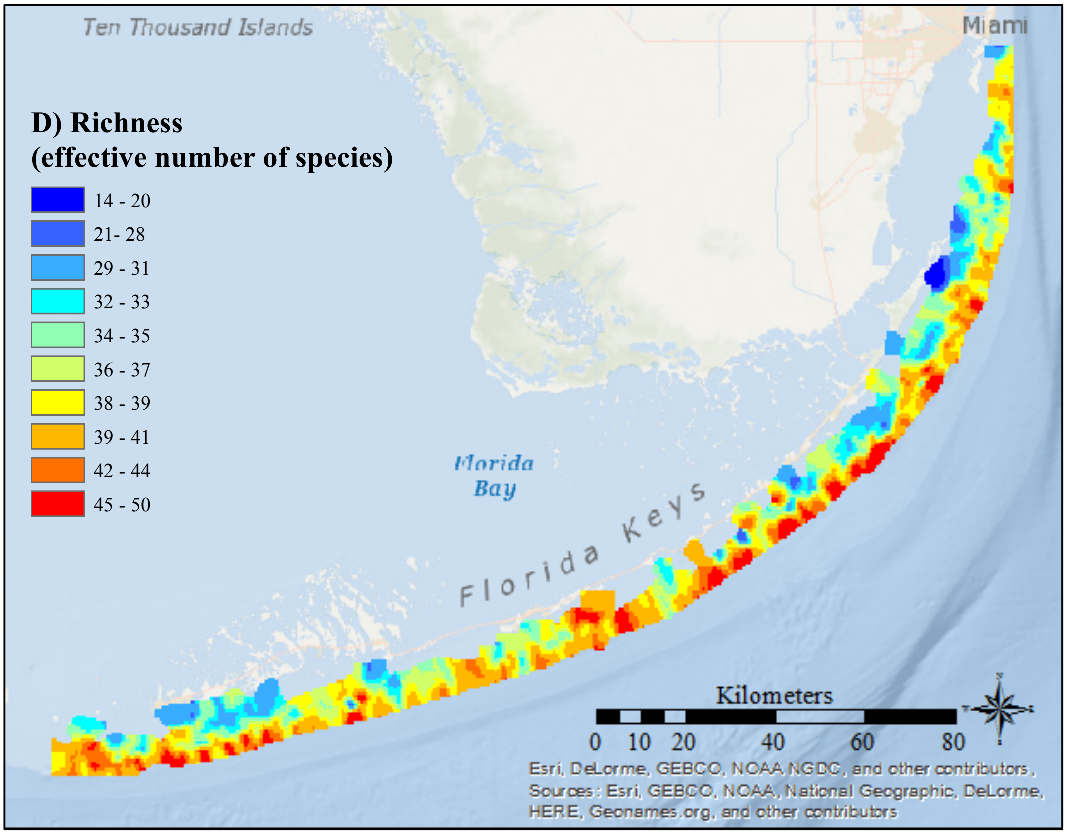
Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme,
HERE, Geonames.org, and other contributors


Ten Thousand Islands
Miami
D) Richness
(effective number of species)
14 - 20
21- 28
29 - 31
32 - 33
34 - 35
36 - 37
38 - 39
39 - 41
42 - 44
45 - 50
Florida Bay
Florida Keys
Kilometers
0 10 20 40 60 80
Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors,
Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme,
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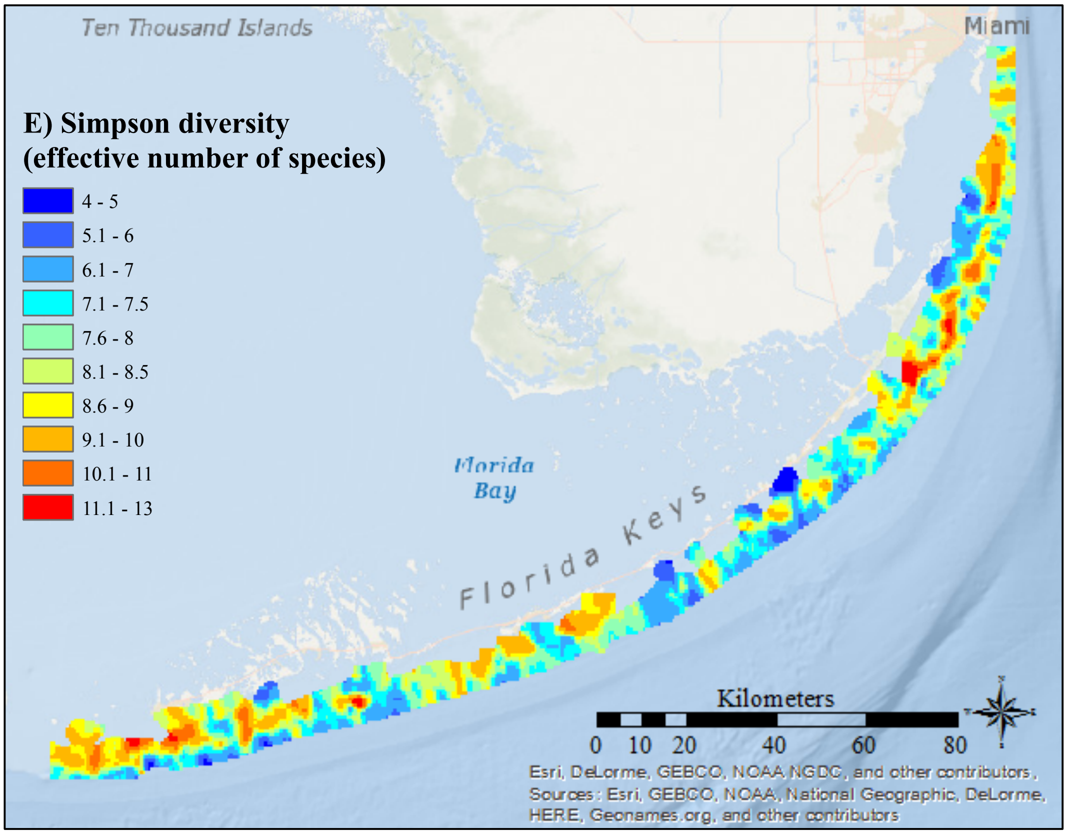
Ten Thousand Islands
Miami
E) Simpson diversity
(effective number of species)
4 - 5
5.1 - 6
6.1 - 7
7.1 - 7.5
7.6 - 8
8.1 - 8.5
8.6 - 9
9.1 - 10
10.1 - 11
11.1 - 13
Florida Bay
Florida Keys
Kilometers
0 10 20 40 60 80
Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors,
Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme,
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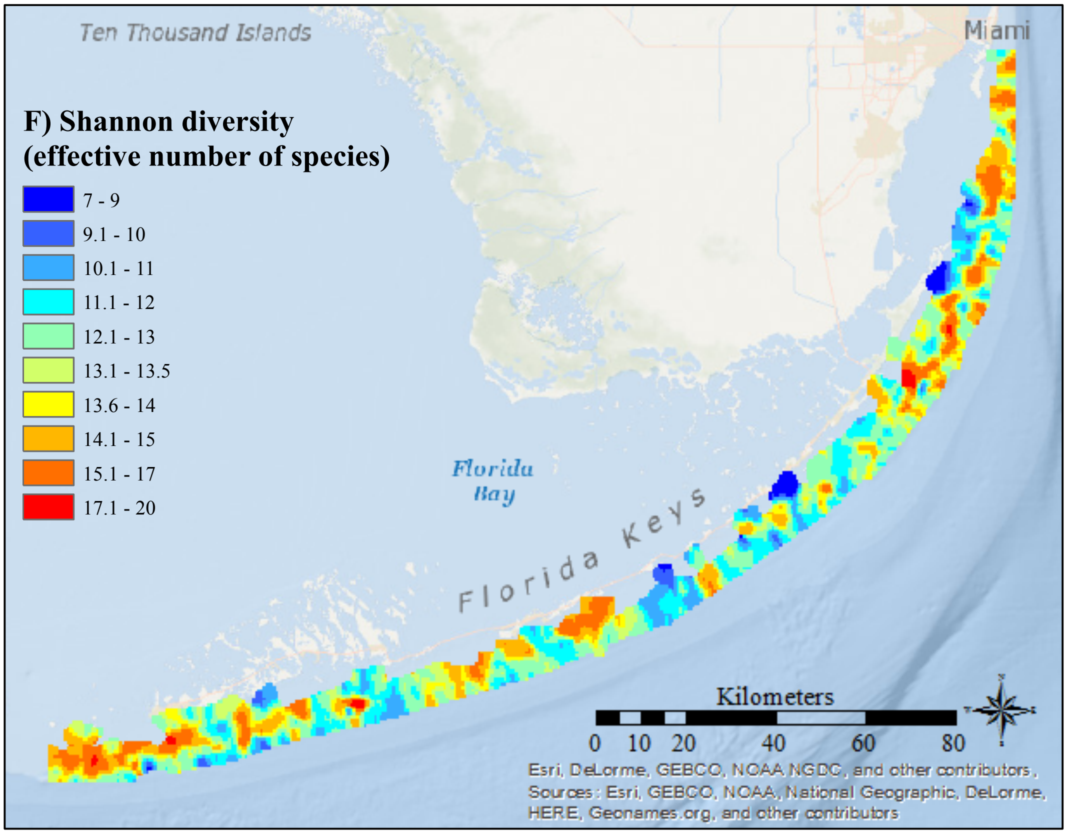
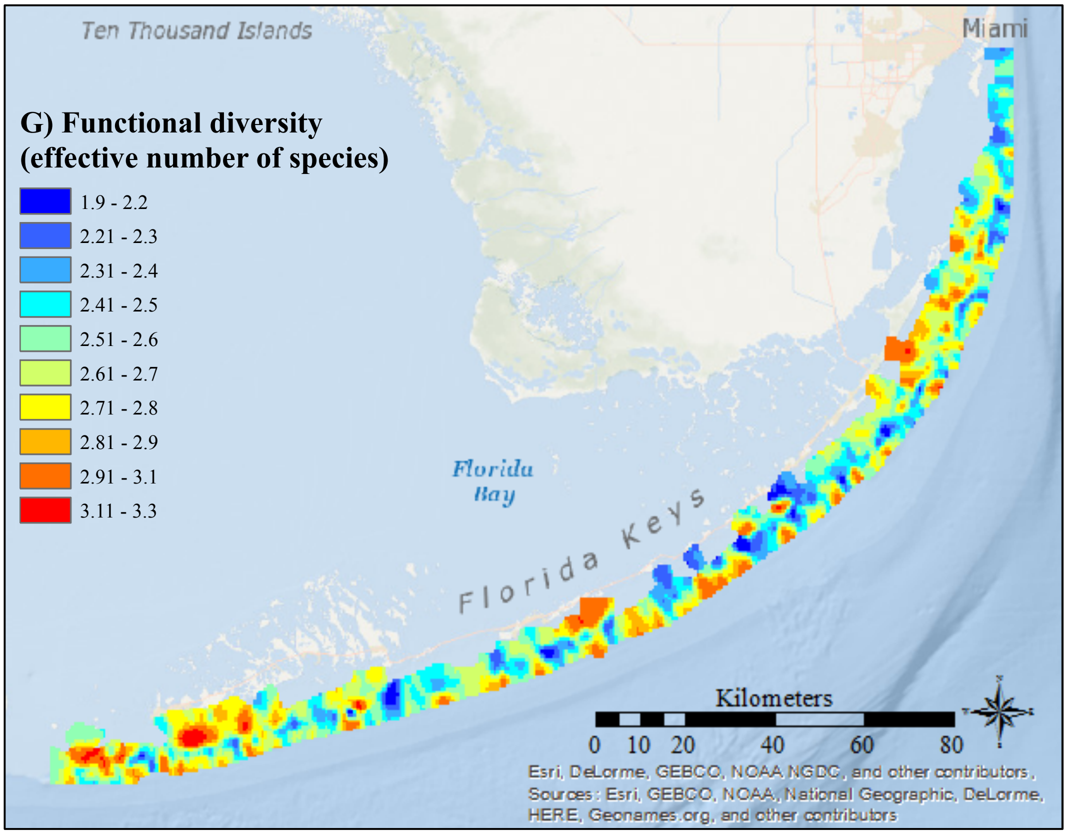

Ten Thousand Islands
Miami
F) Shannon diversity
(effective number of species)
7 - 9
9.1 - 10
10.1 - 11
11.1 - 12
12.1 - 13
13.1 - 13.5
13.6 - 14
14.1 - 15
15.1 - 17
17.1 - 20
Florida Bay
Florida Keys
Kilometers
0 10 20 40 60 80
Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors,
Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme,
HERE, Geonames.org, and other contributors



Esri, DeLorme, GEBCO, NOAA NGDC, and other contributors, Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors

Figure 5. Kriging interpolation of reef fish abundance, biomass, and each diversity index along the Florida reef tract using data from all years combined. Warm colors indicate high values of abundance, biomass, or diversity and cool colors indicate low values. The scale for panel A is abundance (number of individuals), panel B is kilograms per 40,000 km^2, panel C is units ranging from 0 (maximally uneven) to 1 (maximally even), and panels D-G are in units of effective number of species.

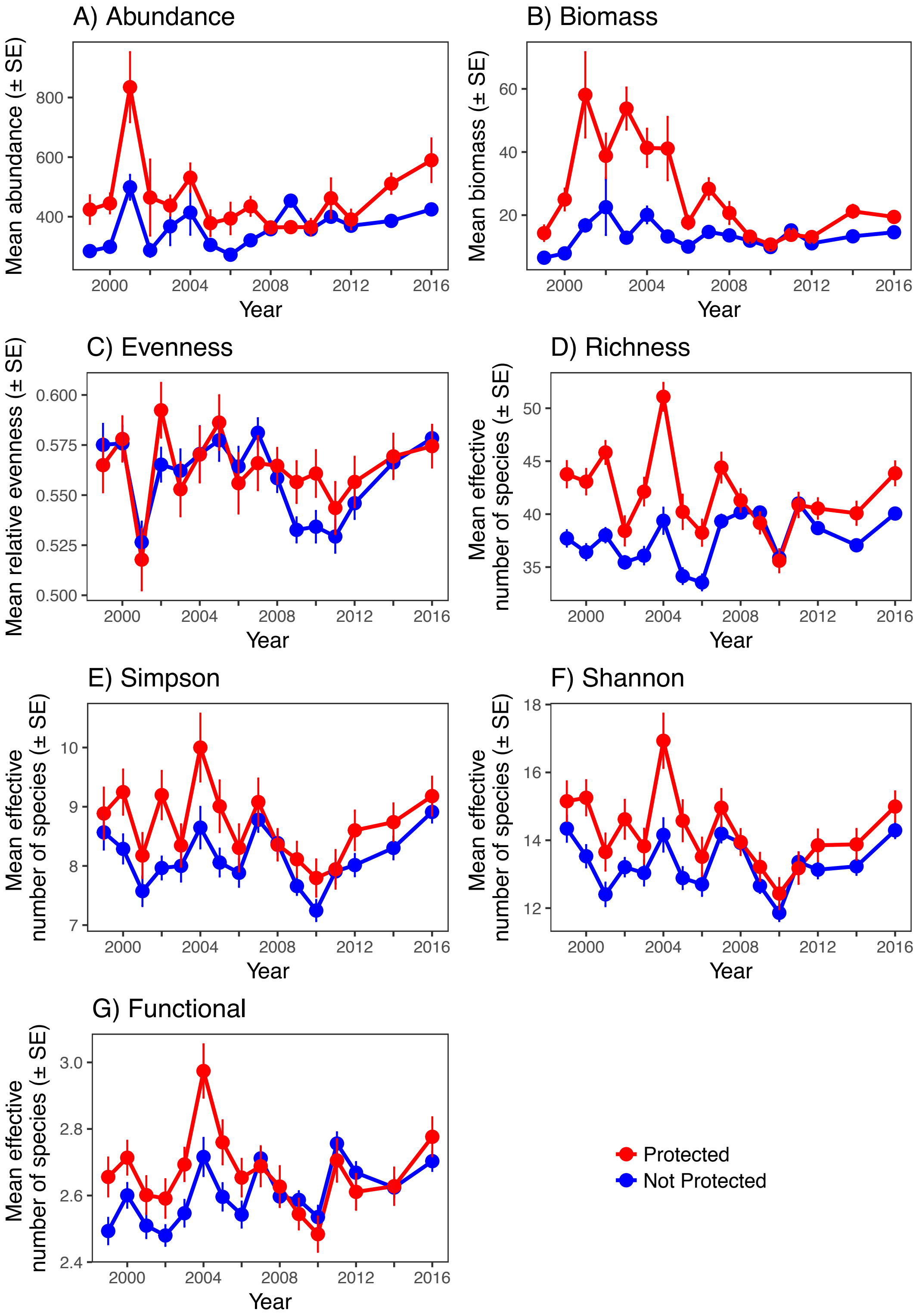


Figure 6. Plots of reef fish indices inside (protected) and outside (not protected) no take marine zones across years in the Florida Keys. The units for panel A are abundance (number of individuals), panel B is kilograms per 40,000 km^2, panel C is units ranging from 0 (maximally uneven) to 1 (maximally even), and panels D-G are in units of effective number of species.

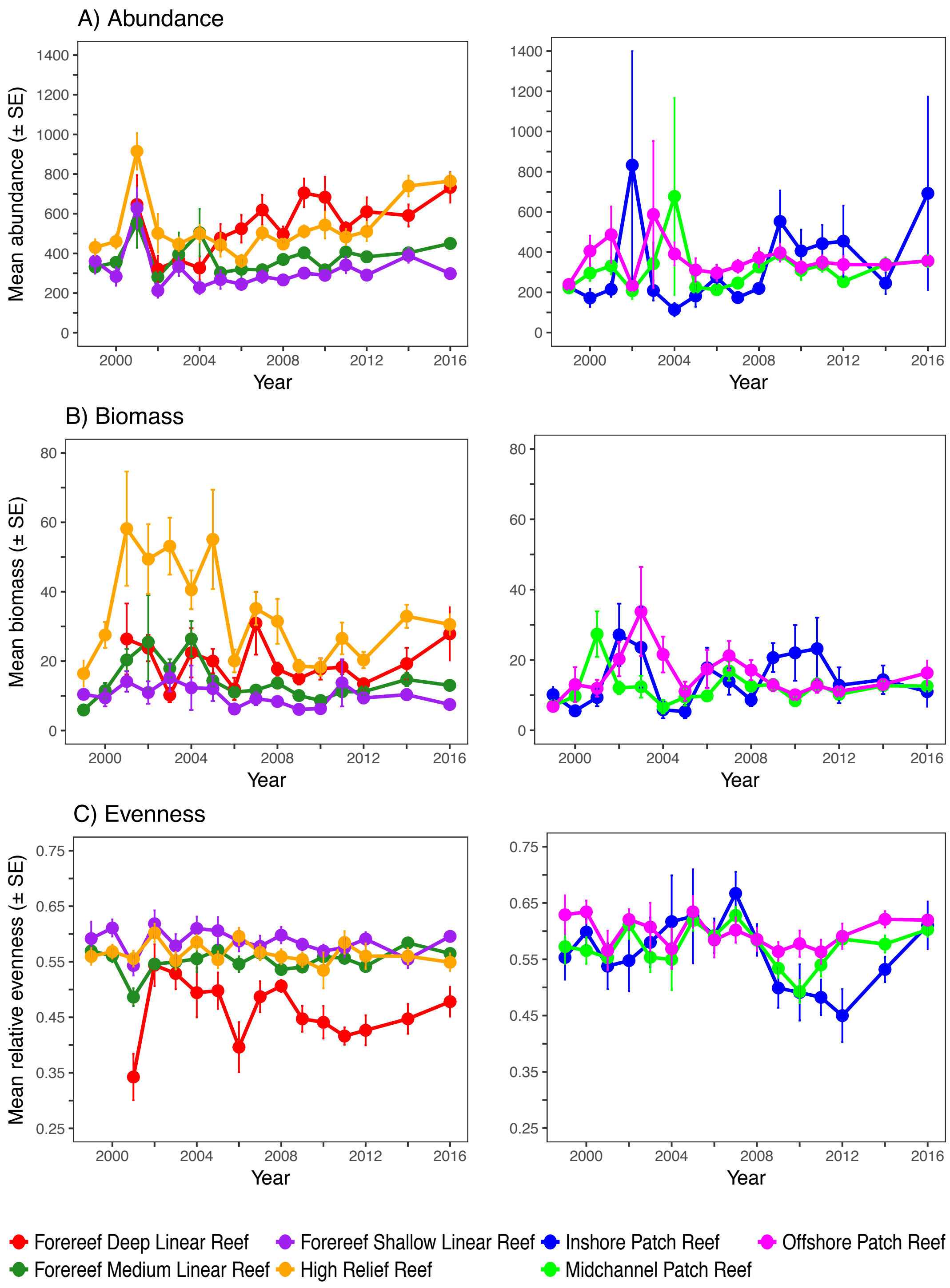


Figure 7. Plots of reef fish abundance, biomass, and evenness by strata and across years in the Florida Keys. The strata correspond to the partitioned habitat classes in the sampling design. The units for panel A are abundance (number of individuals), panel B is kilograms per 40,000 km^2, and panel C is units ranging from 0 (maximally uneven) to 1 (maximally even).

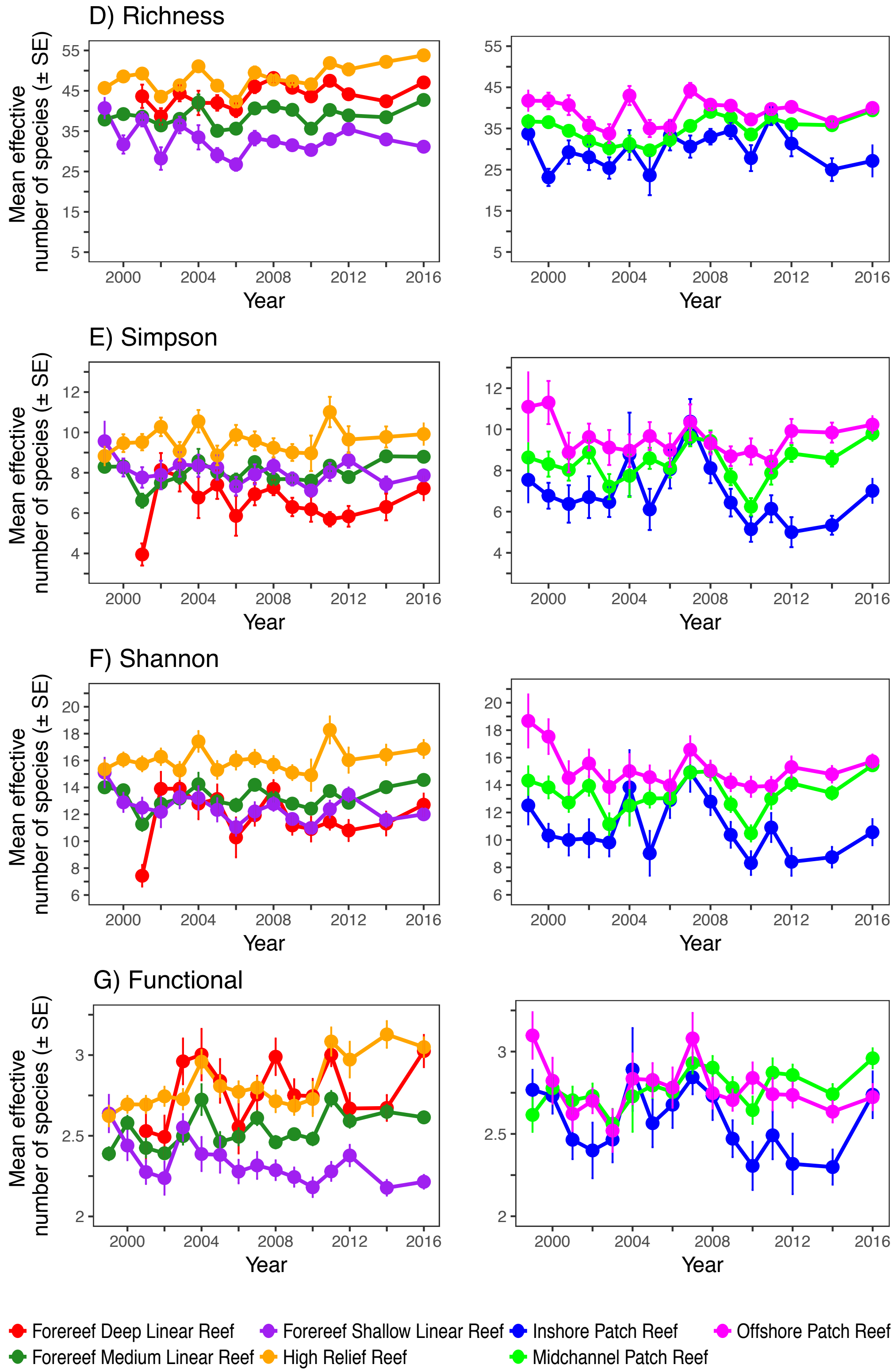


Figure 8. Plots of reef fish richness, Simpson diversity, Shannon diversity, and functional diversity by strata and across years in the Florida Keys. The strata correspond to the partitioned habitat classes in the sampling design. The units for panels D-G are in units of effective number of species.

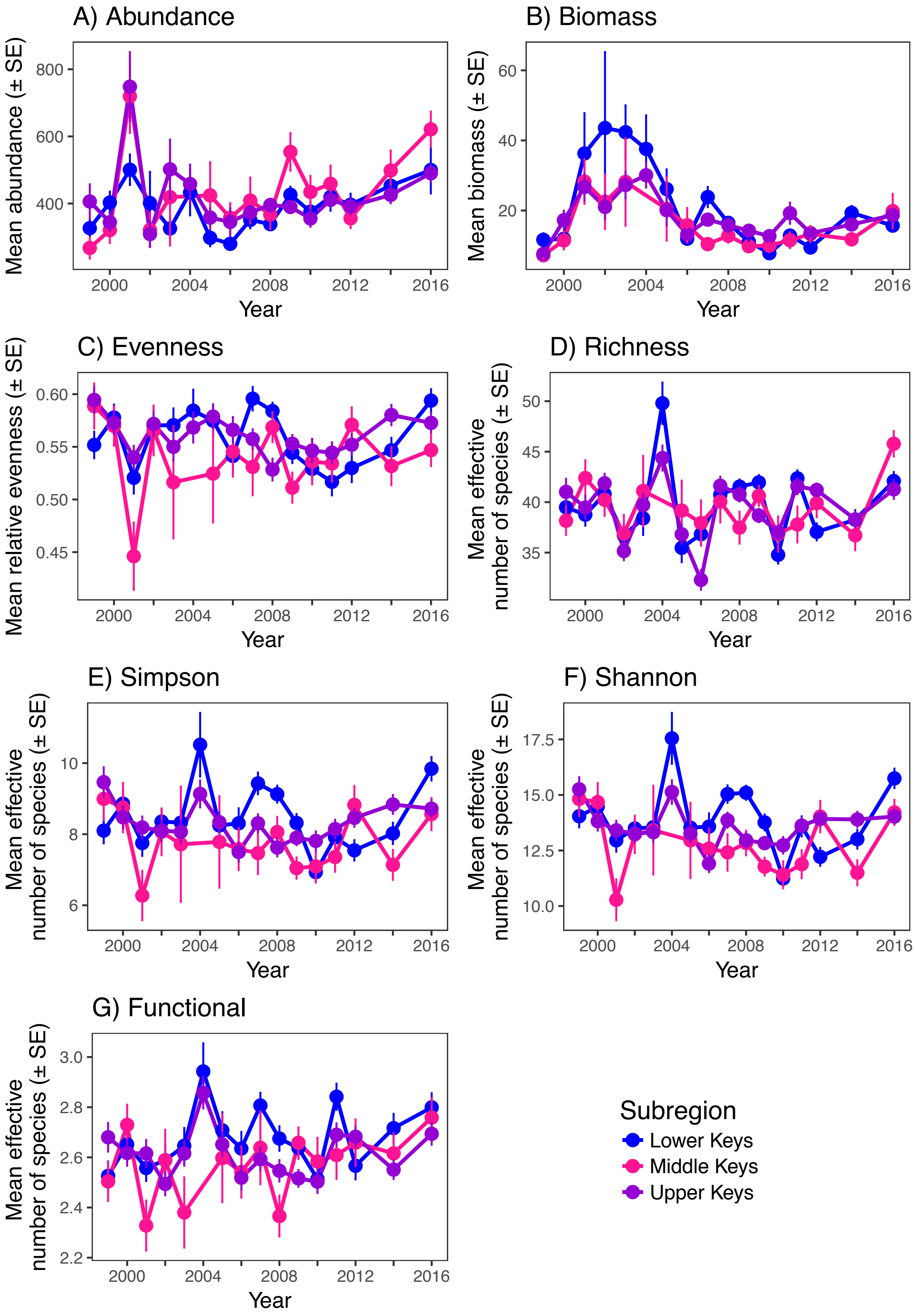


Figure 9. Plots of reef fish indices by subregion across years with strata combined. The units for panel A is abundance (number of individuals), panel B is kilograms per 40,000 km^2, panel C is units ranging from 0 (maximally uneven) to 1 (maximally even), and panels D-G are in units of effective number of species.

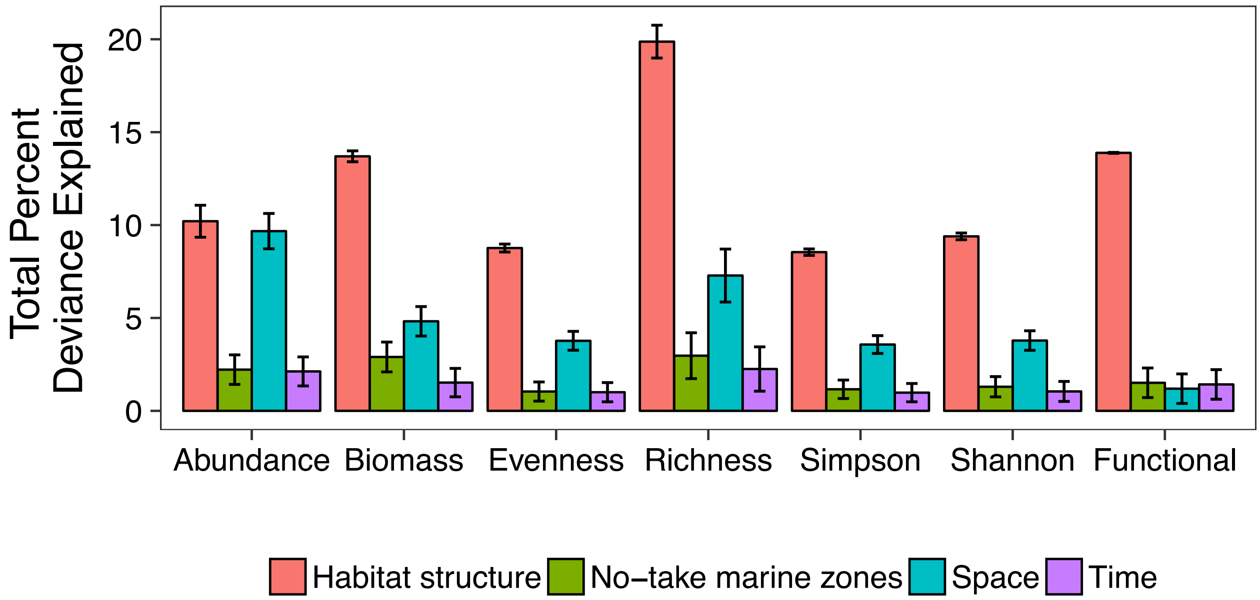


Figure 10. The partial contributions of habitat structure, no-take marine zones, space, and time to the total explained deviance from generalized additive models fit to abundance, biomass, evenness, richness, Simpson diversity, Shannon diversity, and functional diversity. Space was smoothed by latitude and longitude by year and environment was smoothed by depth. Units are in percentage of total explained deviance, and error bars denote ± SE on partial deviance estimates.

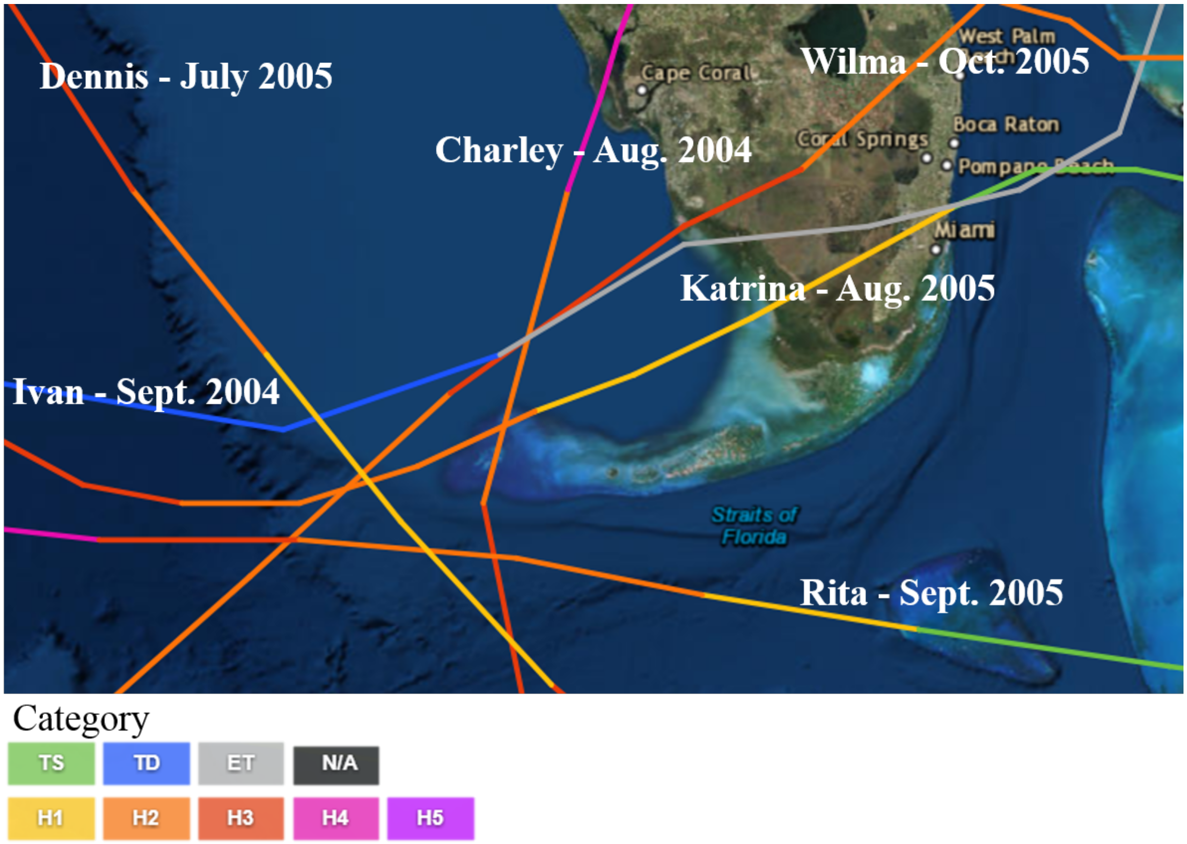


Figure 11. Six tropical cyclones that occurred within 75 nautical miles of the Florida Keys study domain in 2004 and 2005. The color depicts the category of the storm: green (tropical storm), blue (tropical depression), grey (extratropical storm), yellow (hurricane category 1), orange (hurricane category 2), peach (hurricane category 3), magenta (hurricane category 4), and purple (hurricane category 5). Modified from the Office of Coastal Management, 2017.

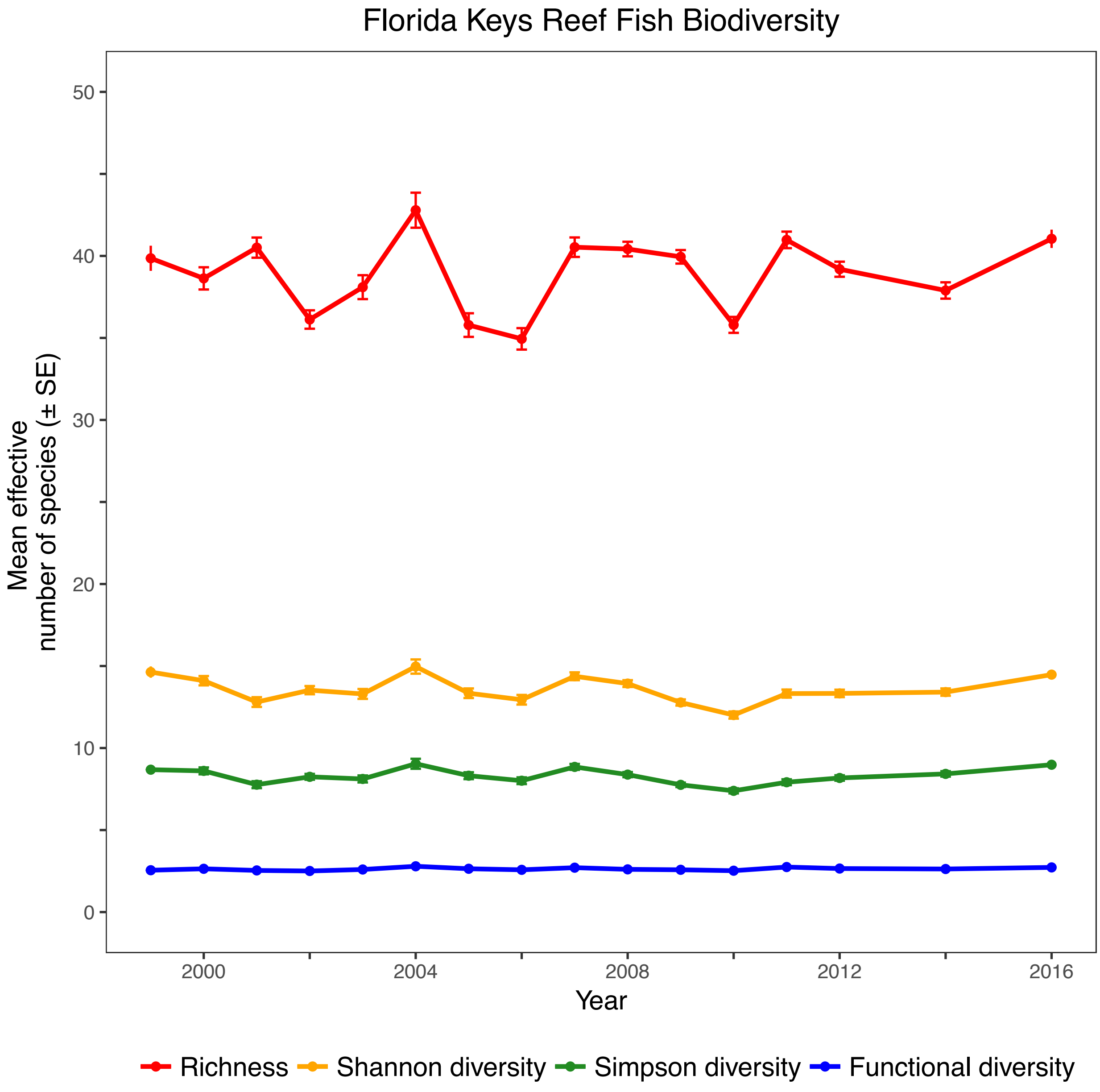


Figure 12. Species richness, Shannon diversity, Simpson diversity, and functional diversity across years. The data correspond to all sampling events in a given year including all levels of protection, strata, and subregion. The units are in mean effective number of species and error bars denote ± SE.

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APPENDIX

Table A1. Listing of families ranked by percent of total abundance observed in the reef visual census from the Florida Keys domain between 1999 – 2016. Between 1999 and 2016, 5 families accounted for 75% of all observed fish taxa: Labridae (20.5%), Pomacentridae (17.3%), Haemulidae (16.9%), Gobiidae (10.7%) and Scaridae (9.2%), and 55 families accounted for <1% of all observed fish taxa.

	Family	Percent
1	Labridae	20.45848
2	Pomacentridae	17.34617
3	Haemulidae	16.86045
4	Gobiidae	10.73944
5	Scaridae	9.23075
6	Atherinidae	5.69998
7	Lutjanidae	5.14526
8	Acanthuridae	4.56436
9	Carangidae	3.12332
10	Chaetodontidae	0.93839
11	Serranidae	0.92811
12	Pomacanthidae	0.87301
13	Kyphosidae	0.63886
14	Mullidae	0.58545
15	Clupeidae	0.40968
16	Tetraodontidae	0.36024
17	Engraulidae	0.27049
18	Sparidae	0.25775
19	Pempheridae	0.16889
20	Holocentridae	0.12913
21	Opistognathidae	0.12010
22	Sphyraenidae	0.10822
23	Sciaenidae	0.10235
24	Inermiidae	0.09228
25	Ptereleotridae	0.09056
26	Labrisomidae	0.07920
27	Aulostomidae	0.06358
28	Ostraciidae	0.06052
29	Balistidae	0.06032
33	Exocoetidae	0.05423
34	Ephippidae	0.04844
35	Priacanthidae	0.02413
36	Urolophidae	0.01979
37	Gerreidae	0.01915
38	Malacanthidae	0.01866
39	Diodontidae	0.01813
40	Muraenidae	0.01733
41	Scorpaenidae	0.01534
42	Chaenopsidae	0.01408
43	Ginglymostomatidae	0.01402
44	Apogonidae	0.01297
45	Echeneidae	0.00957
46	Elopidae	0.00857
47	Synodontidae	0.00542
48	Belonidae	0.00531
49	Myliobatidae	0.00371
50	Dasyatidae	0.00342
51	Cirrhitidae	0.00237
52	Centropomidae	0.00234
53	Congridae	0.00234
54	Carcharhinidae	0.00097
55	Tripterygiidae	0.00050
56	Callionymidae	0.00048
57	Fistulariidae	0.00045
58	Hemiramphidae	0.00045
59	Bothidae	0.00035
60	Grammatidae	0.00033
61	Sphyrnidae	0.00018
62	Paralichthyidae	0.00017

Table A2. Listing of species ranked by percent of total abundance observed in reef visual census from the Florida Keys domain between 1999 – 2016.

	Common Name	Scientific Name	Total abundance	Percent
1	Bicolor Damselfish	Stegastes partitus	240754	11.37
2	Bluehead	Thalassoma bifasciatum	224874	10.62
3	Masked Goby	Coryphopterus personatus	198573	9.38
4	Tomtate	Haemulon aurolineatum	121891	5.76
5	White Grunt	Haemulon plumierii	93382	4.41
6	Striped Parrotfish	Scarus iseri	86022	4.06
7	Reef Silverside	Hypoatherina harringtonensis	81552	3.85
8	Slippery Dick	Halichoeres bivittatus	70797	3.34
9	Yellowtail Snapper	Ocyurus chrysurus	61990	2.93
10	Redband Parrotfish	Sparisoma aurofrenatum	51623	2.44
11	French Grunt	Haemulon flavolineatum	49123	2.32
12	Bluestriped Grunt	Haemulon sciurus	47395	2.24
13	Yellowhead Wrasse	Halichoeres garnoti	41785	1.97
14	Ocean Surgeon	Acanthurus bahianus	39518	1.87
15	Hardhead Silverside	Atherinomorus stipes	39112	1.85
16	Clown Wrasse	Halichoeres maculipinna	38041	1.80
17	Sergeant Major	Abudefduf saxatilis	37482	1.77
18	Bar Jack	Caranx ruber	36493	1.72
19	Blue Tang	Acanthurus coeruleus	35927	1.70
20	Brown Chromis	Chromis multilineata	31941	1.51
21	Creole Wrasse	Clepticus parrae	30619	1.45
22	Gray Snapper	Lutjanus griseus	24400	1.15
23	Doctorfish	Acanthurus chirurgus	21179	1.00
24	Bridled Goby	Coryphopterus glaucofraenum	19819	9.36E-01
25	Blue Chromis	Chromis cyanea	19034	8.99E-01
26	Stoplight Parrotfish	Sparisoma viride	17887	8.45E-01
27	Smallmouth Grunt	Haemulon chrysargyreum	13969	6.60E-01
28	Bermuda Chub	Kyphosus sectatrix	13524	6.39E-01
29	Round Scad	Decapterus punctatus	13272	6.27E-01
30	Schoolmaster	Lutjanus apodus	13105	6.19E-01
31	Greenblotch Parrotfish	Sparisoma atomarium	11958	5.65E-01
32	Hogfish	Lachnolaimus maximus	11209	5.30E-01
33	Porkfish	Anisotremus virginicus	11127	5.26E-01
34	Cocoa Damselfish	Stegastes variabilis	10452	4.94E-01
35	Foureye Butterflyfish	Chaetodon capistratus	7901	3.73E-01
36	Mackerel Scad	Decapterus macarellus	7709	3.64E-01
37	Scaled Sardine	Harengula jaguana	7666	3.62E-01
38	Cottonwick	Haemulon melanurum	7633	3.61E-01
39	Sharpnose Puffer	Canthigaster rostrata	7442	3.52E-01

Table A2 continued. Listing of species ranked by percent of total abundance observed in reef visual census from the Florida Keys domain between 1999 – 2016.

	Common Name	Scientific Name	Total abundance	Percent
44	Dusky Anchovy	Anchoa lyolepis	5726	2.70E-01
45	Purple Reeffish	Chromis scotti	5514	2.60E-01
46	Redtail Parrotfish	Sparisoma chrysopterum	5505	2.60E-01
47	Princess Parrotfish	Scarus taeniopterus	5430	2.56E-01
48	Threespot Damselfish	Stegastes planifrons	5212	2.46E-01
49	Lane Snapper	Lutjanus synagris	5036	2.38E-01
50	Yellowtail Parrotfish	Sparisoma rubripinne	4897	2.31E-01
51	Saucereye Porgy	Calamus calamus	4841	2.29E-01
52	Dusky Damselfish	Stegastes adustus	4820	2.28E-01
53	Reef Butterflyfish	Chaetodon sedentarius	4501	2.13E-01
54	Neon Goby	Elacatinus oceanops	4426	2.09E-01
55	Rock Beauty	Holacanthus tricolor	4395	2.08E-01
56	Caesar Grunt	Haemulon carbonarium	4380	2.07E-01
57	Green Razorfish	Xyrichtys splendens	4379	2.07E-01
58	Graysby	Cephalopholis cruentata	4308	2.04E-01
59	Yellowtail Damselfish	Microspathodon chrysurus	4135	1.95E-01
60	Butter Hamlet	Hypoplectrus unicolor	3982	1.88E-01
61	Harlequin Bass	Serranus tigrinus	3970	1.88E-01
62	Blue Runner	Caranx crysos	3938	1.86E-01
63	Puddingwife	Halichoeres radiatus	3904	1.84E-01
64	Sunshinefish	Chromis insolata	3586	1.69E-01
65	Glassy Sweeper	Pempheris schomburgkii	3575	1.69E-01
66	Spanish Hogfish	Bodianus rufus	3464	1.64E-01
67	Yellow Jack	Caranx bartholomaei	3435	1.62E-01
68	Sailors Choice	Haemulon parra	3213	1.52E-01
69	Beaugregory	Stegastes leucostictus	3177	1.50E-01
70	Goldspot Goby	Gnatholepis thompsoni	3031	1.43E-01
71	Queen Angelfish	Holacanthus ciliaris	2884	1.36E-01
72	Striped Grunt	Haemulon striatum	2855	1.35E-01
73	Blackear Wrasse	Halichoeres poeyi	2573	1.22E-01
74	Yellowhead Jawfish	Opistognathus aurifrons	2502	1.18E-01
75	Blue Parrotfish	Scarus coeruleus	2410	1.14E-01
76	Mahogany Snapper	Lutjanus mahogoni	2166	1.02E-01
77	French Angelfish	Pomacanthus paru	2087	9.86E-02
78	Bluelip Parrotfish	Cryptotomus roseus	2005	9.47E-02
79	Rainbow Parrotfish	Scarus guacamaia	1983	9.37E-02
80	Boga	Inermia vittata	1954	9.23E-02
81	Mutton Snapper	Lutjanus analis	1870	8.83E-02
82	Midnight Parrotfish	Scarus coelestinus	1857	8.77E-02

Table A2 continued. Listing of species ranked by percent of total abundance observed in reef visual census from the Florida Keys domain between 1999 – 2016.

	Common Name	Scientific Name	Total abundance	Percent
87	Banded Butterflyfish	Chaetodon striatus	1635	7.72E-02
88	Black Grouper	Mycteroperca bonaci	1601	7.56E-02
89	Great Barracuda	Sphyraena barracuda	1584	7.48E-02
90	Blue Angelfish	Holacanthus bermudensis	1507	7.12E-02
91	Atlantic Trumpetfish	Aulostomus maculatus	1346	6.36E-02
92	Red Grouper	Epinephelus morio	1218	5.75E-02
93	Ballyhoo	Hemiramphus brasiliensis	1148	5.42E-02
94	Saddled Blenny	Malacoctenus triangulatus	1083	5.12E-02
95	High Hat	Pareques acuminatus	1076	5.09E-02
96	Atlantic Spadefish	Chaetodipterus faber	1025	4.84E-02
97	Cero	Scomberomorus regalis	1007	4.76E-02
98	Spanish Grunt	Haemulon macrostomum	1005	4.75E-02
99	Reef Croaker	Odontoscion dentex	899	4.24E-02
100	Longfin Damselfish	Stegastes diencaeus	894	4.23E-02
101	Seaweed Blenny	Parablennius marmoreus	862	4.07E-02
102	Colon Goby	Coryphopterus dicrus	812	3.84E-02
103	Smooth Trunkfish	Lactophrys triqueter	764	3.61E-02
104	Tobaccofish	Serranus tabacarius	743	3.51E-02
105	Rosy Razorfish	Xyrichtys martinicensis	738	3.49E-02
106	Gray Triggerfish	Balistes capriscus	732	3.46E-02
107	Scrawled Filefish	Aluterus scriptus	730	3.45E-02
108	Longspine Squirrelfish	Holocentrus rufus	720	3.40E-02
109	Southern Sennet	Sphyraena picudilla	691	3.26E-02
110	Lantern Bass	Serranus baldwini	612	2.89E-02
111	Horse Eye Jack	Caranx latus	588	2.78E-02
112	Rosy Blenny	Malacoctenus macropus	564	2.66E-02
113	Spanish Sardine	Sardinella aurita	507	2.39E-02
114	Redear Sardine	Harengula humeralis	500	2.36E-02
115	Black Margate	Anisotremus surinamensis	499	2.36E-02
116	Blue Hamlet	Hypoplectrus gemma	448	2.12E-02
117	Margate	Haemulon album	446	2.11E-02
118	Yellow Stingray	Urobatis jamaicensis	419	1.98E-02
119	Coney	Cephalopholis fulva	407	1.92E-02
120	Yellowfin Mojarra	Gerres cinereus	396	1.87E-02
121	Sand Tilefish	Malacanthus plumieri	395	1.87E-02
122	Ocean Triggerfish	Canthidermis sufflamen	386	1.83E-02
123	Rock Hind	Epinephelus adscensionis	375	1.77E-02
124	Barred Hamlet	Hypoplectrus puella	341	1.61E-02
125	Chalk Bass	Serranus tortugarum	324	1.53E-02

Table A2 continued. Listing of species ranked by percent of total abundance observed in reef visual census from the Florida Keys domain between 1999 – 2016.

	Common Name	Scientific Name	Total abundance	Percent
131	Scrawled Cowfish	Acanthostracion quadricornis	240	1.13E-02
132	Gag	Mycteroperca microlepis	225	1.06E-02
133	Rainbow Runner	Elagatis bipinnulata	216	1.02E-02
134	Spotfin Hogfish	Bodianus pulchellus	213	1.00E-02
135	Bigeye	Priacanthus arenatus	203	9.59E-03
136	Pallid Goby	Coryphopterus eidolon	197	9.31E-03
137	Emerald Parrotfish	Nicholsina usta	193	9.11E-03
138	Dash Goby	Ctenogobius saepepallens	192	9.05E-03
139	Hovering Dartfish	Ptereleotris helenae	190	8.95E-03
140	Sea Bream	Archosargus rhomboidalis	189	8.93E-03
141	Yellowtail Reeffish	Chromis enchrysura	186	8.79E-03
142	Dog Snapper	Lutjanus jocu	184	8.70E-03
143	Spotted Moray	Gymnothorax moringa	183	8.66E-03
144	Bandtail Puffer	Sphoeroides spengleri	181	8.57E-03
145	Tarpon	Megalops atlanticus	179	8.43E-03
146	Balloonfish	Diodon holocanthus	178	8.41E-03
147	Townsend Angelfish	Holocanthus sp.	177	8.37E-03
148	Red Hind	Epinephelus guttatus	177	8.36E-03
149	Scamp	Mycteroperca phenax	177	8.35E-03
150	Wrasse Blenny	Hemiemblemaria simula	168	7.94E-03
151	Sharksucker	Echeneis naucrates	167	7.87E-03
152	Nassau Grouper	Epinephelus striatus	153	7.25E-03
153	Yellowcheek Wrasse	Halichoeres cyanocephalus	143	6.76E-03
154	Seminole Goby	Microgobius carri	141	6.66E-03
155	Blackfin Snapper	Lutjanus buccanella	137	6.46E-03
156	Queen Triggerfish	Balistes vetula	133	6.27E-03
157	Twospot Cardinalfish	Apogon pseudomaculatus	132	6.24E-03
158	Pearly Razorfish	Xyrichtys novacula	129	6.09E-03
159	Spotted Drum	Equetus punctatus	128	6.05E-03
160	Orangespotted Filefish	Cantherhines pullus	126	5.97E-03
161	Jolthead Porgy	Calamus bajonado	123	5.80E-03
162	Blackbar Soldierfish	Myripristis jacobus	123	5.79E-03
163	Green Moray	Gymnothorax funebris	118	5.59E-03
164	Porcupinefish	Diodon hystrix	118	5.56E-03
165	Molly Miller	Scartella cristata	110	5.20E-03
166	Permit	Trachinotus falcatus	109	5.16E-03
167	Crevalle Jack	Caranx hippos	109	5.13E-03
168	Rainbow Wrasse	Halichoeres pictus	107	5.04E-03
169	Spotted Trunkfish	Lactophrys bicaudalis	103	4.87E-03

Table A2. Listing of species ranked by percent of total abundance observed in reef visual census from the Florida Keys domain between 1999 – 2016.

	Common Name	Scientific Name	Total abundance	Percent
175	Banner Goby	Microgobius microlepis	90	4.25E-03
176	Spottail Pinfish	Diplodus holbrookii	82	3.87E-03
177	Littlehead Porgy	Calamus proridens	81	3.83E-03
178	School Bass	Schultzea beta	81	3.83E-03
179	Lookdown	Selene vomer	81	3.80E-03
180	Spotted Eagle Ray	Aetobatus narinari	78	3.68E-03
181	Roughhead Blenny	Acanthemblemaria aspera	78	3.66E-03
182	Houndfish	Tylosurus crocodilus	75	3.52E-03
183	Honeycomb Cowfish	Acanthostracion polygonia	73	3.43E-03
184	Southern Stingray	Dasyatis americana	72	3.42E-03
185	Greater Amberjack	Seriola dumerili	64	3.02E-03
186	Greater Soapfish	Rypticus saponaceus	64	3.02E-03
187	Striped Burrfish	Chilomycterus schoepfii	64	3.00E-03
188	Spotted Scorpionfish	Scorpaena plumieri	62	2.92E-03
189	Flamefish	Apogon maculatus	61	2.88E-03
190	Tan Hamlet	Hypoplectrus tann	59	2.79E-03
191	Sand Perch	Diplectrum formosum	59	2.76E-03
192	Orange Filefish	Aluterus schoepfii	55	2.59E-03
193	Redspotted Hawkfish	Amblycirrhitus pinos	50	2.37E-03
194	Brown Garden Eel	Centropomus undecimalis	50	2.34E-03
195	Common Snook	Heteroconger longissimus	50	2.34E-03
196	Goldentail Moray	Gymnothorax miliaris	49	2.30E-03
197	Goliath Grouper	Epinephelus itajara	49	2.29E-03
198	Dusky Squirrelfish	Sargocentron vexillarium	46	2.19E-03
199	Almaco Jack	Lagodon rhomboides	45	2.13E-03
200	Pinfish	Seriola rivoliana	45	2.13E-03
201	Yellowfin Grouper	Mycteroperca venenosa	44	2.08E-03
202	Sheepshead Porgy	Calamus penna	44	2.05E-03
203	Yellowmouth Grouper	Mycteroperca interstitialis	42	1.98E-03
204	Leatherjack	Oligoplites saurus	41	1.94E-03
205	Jackknife Fish	Equetus lanceolatus	38	1.80E-03
206	Barred Cardinalfish	Apogon binotatus	36	1.70E-03
207	Redfin Needlefish	Strongylura notata	36	1.68E-03
208	Whitespotted Filefish	Cantherhines macrocerus	33	1.57E-03
209	Belted Cardinalfish	Apogon townsendi	33	1.54E-03
210	Cubera Snapper	Lutjanus cyanopterus	32	1.49E-03
211	Spanish Mackerel	Scomberomorus maculatus	30	1.39E-03
212	Remora	Remora remora	28	1.32E-03
213	Dusky Jawfish	Opistognathus whitehursti	27	1.28E-03

Table A2. Listing of species ranked by percent of total abundance observed in reef visual census from the Florida Keys domain between 1999 – 2016.

	Common Name	Scientific Name	Total abundance	Percent
219	Sheepshead	Archosargus probatocephalus	23	1.06E-03
220	Dwarf Wrasse	Doratonotus megalepis	21	9.68E-04
221	King Mackerel	Scomberomorus cavalla	20	9.29E-04
222	Atlantic Creolefish	Alphestes afer	20	9.21E-04
223	Mutton Hamlet	Paranthias furcifer	20	9.21E-04
224	Reef Squirrelfish	Sargocentron coruscum	19	8.98E-04
225	Barred Blenny	Hypleurochilus bermudensis	18	8.50E-04
226	Blackhead Blenny	Emblemariopsis bahamensis	18	8.27E-04
227	Cherubfish	Centropyge argi	17	8.03E-04
228	Longjaw Squirrelfish	Neoniphon marianus	17	7.79E-04
229	Guaguanche	Emblemaria pandionis	16	7.32E-04
230	Sailfin Blenny	Sphyraena guachancho	16	7.32E-04
231	Planehead Filefish	Stephanolepis hispidus	15	6.85E-04
232	African Pompano	Alectis ciliaris	14	6.38E-04
233	Banded Jawfish	Opistognathus macrognathus	14	6.38E-04
234	Fringed Filefish	Monacanthus ciliatus	13	6.14E-04
235	Orangespotted Goby	Nes longus	13	6.14E-04
236	Shy Hamlet	Hypoplectrus guttavarius	12	5.67E-04
237	Purplemouth Moray	Carcharhinus perezii	12	5.43E-04
238	Reef Shark	Gymnothorax vicinus	12	5.43E-04
239	Knobbed Porgy	Calamus nodosus	11	5.43E-04
240	Tiger Grouper	Mycteroperca tigris	11	5.35E-04
241	Red Porgy	Acanthemblemaria maria	11	5.20E-04
242	Secretary Blenny	Pagrus pagrus	11	5.20E-04
243	Indigo Hamlet	Enneanectes boehlkei	11	4.96E-04
244	Longsnout Butterflyfish	Hypoplectrus indigo	11	4.96E-04
245	Roughhead Triplefin	Prognathodes aculeatus	11	4.96E-04
246	Lancer Dragonet	Paradiplogrammus bairdi	10	4.80E-04
247	Bluespotted Cornetfish	Chriodorus atherinoides	10	4.49E-04
248	Hardhead Halfbeak	Fistularia tabacaria	10	4.49E-04
249	Palehead Blenny	Labrisomus gobio	10	4.49E-04
250	Spotfin Mojarra	Eucinostomus argenteus	9	4.41E-04
251	Whitefin Sharksucker	Echeneis neucratoides	8	3.78E-04
252	Papillose Blenny	Acanthemblemaria chaplini	8	3.54E-04
253	Fairy Basslet	Gramma loreto	7	3.31E-04
254	Silver Porgy	Diplodus argenteus	7	3.07E-04
255	Barfin Blenny	Elacatinus macrodon	6	2.83E-04
256	Hairy Blenny	Labrisomus nuchipinnis	6	2.83E-04

Table A2. Listing of species ranked by percent of total abundance observed in reef visual census from the Florida Keys domain between 1999 – 2016.

	Common Name	Scientific Name	Total abundance	Percent
262	Whitespotted Soapfish	Rypticus maculatus	5	2.36E-04
263	Bridle Cardinalfish	Apogon aurolineatus	5	2.13E-04
264	Bull Shark	Carcharhinus leucas	5	2.13E-04
265	Pigfish	Liopropoma eukrines	5	2.13E-04
266	Wrasse Basslet	Orthopristis chrysoptera	5	2.13E-04
267	Hybrid Hamlet	Epinephelus flavolimbatus	4	1.89E-04
268	Orangeside Goby	Gobiosoma dilepis	4	1.89E-04
269	Reef Scorpionfish	Hypoplectrus hybrid	4	1.89E-04
270	Yellowedge Grouper	Scorpaenodes caribbaeus	4	1.89E-04
271	Atlantic Bumper	Carcharhinus limbatus	4	1.65E-04
272	Blacktip Shark	Chloroscombus chrysurus	4	1.65E-04
273	Goldline Blenny	Liopropoma rubre	4	1.65E-04
274	Gulf Flounder	Malacoctenus aurolineatus	4	1.65E-04
275	Orangeback Bass	Oxyurichthys stigmalophius	4	1.65E-04
276	Peppermint Basslet	Paralichthys albigutta	4	1.65E-04
277	Spotfin Goby	Serranus annularis	4	1.65E-04
278	Dusky Blenny	Coryphopterus lipernes	3	1.42E-04
279	Ladyfish	Coryphopterus punctipectophorus	3	1.42E-04
280	Peppermint Goby	Elops saurus	3	1.42E-04
281	Spotted Goby	Malacoctenus gilli	3	1.42E-04
282	Vermilion Snapper	Rhomboplites aurorubens	3	1.42E-04
283	Checkered Puffer	Aluterus monoceros	3	1.18E-04
284	Leopard Goby	Dermatolepis inermis	3	1.18E-04
285	Marbled Grouper	Elacatinus saucrum	3	1.18E-04
286	Timucu	Enchelycore nigricans	3	1.18E-04
287	Unicorn Filefish	Sphoeroides testudineus	3	1.18E-04
288	Viper Moray	Strongylura timucu	3	1.18E-04
289	Eyed Flounder	Bothus ocellatus	2	1.10E-04
290	Great Hammerhead	Sphyrna mokarran	2	9.45E-05
291	Bonnethead	Apogon quadrisquamatus	2	7.09E-05
292	Honeycomb Moray	Chilomycterus atinga	2	7.09E-05
293	Marbled Blenny	Gymnothorax saxicola	2	7.09E-05
294	Sawcheek Cardinalfish	Paraclinus marmoratus	2	7.09E-05
295	Spotted Burrfish	Sphyrna tiburo	2	7.09E-05
296	Bandtail Searobin	Ahlia egmontis	1	4.72E-05
297	Conchfish	Antennarius ocellatus	1	4.72E-05
298	Goldspotted Eel	Astrapogon stellatus	1	4.72E-05
299	Key Worm Eel	Astroscopus guttatus	1	4.72E-05

Table A2. Listing of species ranked by percent of total abundance observed in reef visual census from the Florida Keys domain between 1999 – 2016.

	Common Name	Scientific Name	Total abundance	Percent
305	Reticulate Moray	Labrisomus filamentosus	1	4.72E-05
306	Silky Shark	Muraena retifera	1	4.72E-05
307	Yellowface Pikeblenny	Myrichthys ocellatus	1	4.72E-05
308	Yellowline Goby	Narcine bancroftii	1	4.72E-05
309	Yellowprow Goby	Prionotus ophryas	1	4.72E-05
310	Yellowtail Hamlet	Synodus synodus	1	4.72E-05
311	Belted Sandfish	Eucinostomus gula	1	2.36E-05
312	Giant Manta	Labrisomus bucciferus	1	2.36E-05
313	Puffcheek Blenny	Manta birostris	1	2.36E-05
314	Sharptail Eel	Myrichthys breviceps	1	2.36E-05
315	Silver Jenny	Serranus subligarius	1	2.36E-05
316	Scalloped Hammerhead	Sphyrna lewini	0.5	1.57E-05

Table A3. Contributions of individual traits to patterns in functional diversity in the Florida Keys.

Trait	R^2
Trophic group	0.594
Diel activity pattern	0.722
Preferred substrate	0.755
Trophic level	0.880
Water column position	0.929
Max length	0.932
Habitat complexity	0.978
Gregariousness	0.988

Table A4: Tested for differences between level of protection using the nonparametric Kruskal-Wallis rank sum test. * denotes not significantly different.

Metric	chi-squared	df	p-value
Abundance	83.908	1	2.2E-16
Biomass	172.69	1	2.2E-16
Evenness	1.2309	1	2.7E-01*
Richness	109.16	1	2.2E-16
Simpson	22.569	1	2.0E-06
Shannon	29.719	1	5.0E-08
Functional	15.991	1	6.4E-05

Table A5: Tested for differences across strata using the nonparametric Kruskal-Wallis rank sum test * denotes not significantly different.

Metric	chi-squared	df	p-value
Abundance	663.25	6	2.2E-16
Biomass	655.02	6	2.2E-16
Evenness	324.62	6	2.2E-16
Richness	1192.5	6	2.2E-16
Simpson	352.49	6	2.2E-16
Shannon	446.17	6	2.2E-16
Functional	663.1	6	2.2E-16

Table A6: Tested for differences across geographic subregion using the nonparametric Kruskal-Wallis rank sum test. * denotes not significantly different.

Metric	chi-squared	df	p-value
Abundance	17.443	2	1.6E-04
Biomass	28.286	2	7.2E-07
Evenness	17.196	2	1.8E-04
Richness	0.20689	2	9.0E-01*
Simpson	15.834	2	3.6E-04

Table A7: Dunn (1964) Kruskal-Wallis multiple comparison of abundance by strata. Inshore Patch Reef (INPR); Midchannel Patch Reef (MCPR); Offshore Patch Reef (OFPR); Forereef Shallow Linear Reef (FSLR); Forereef Medium Linear Reef (FMLR); Forereef Deep Linear Reef (FDLR); and High Relief Reef (HRRF). * denotes the strata are not significantly different.

Comparison	Z	P.unadj	P.adj
FMLR - OFPR	1.13E+00	2.59E-01	5.18E-01*
INPR - MCPR	-1.47E+00	1.43E-01	4.28E-01*
FDLR - HRRF	1.03E+00	3.05E-01	3.05E-01*
FSLR - MCPR	2.34E+00	1.90E-02	7.62E-02*
FSLR - OFPR	-2.89E+00	3.88E-03	1.94E-02
FSLR - INPR	2.98E+00	2.88E-03	1.73E-02
INPR - OFPR	-4.89E+00	9.87E-07	6.91E-06
MCPR - OFPR	-5.06E+00	4.21E-07	3.37E-06
FMLR - FSLR	5.21E+00	1.93E-07	1.74E-06
FMLR - INPR	6.37E+00	1.90E-10	1.90E-09
FMLR - MCPR	8.36E+00	6.38E-17	7.02E-16
FDLR - OFPR	1.11E+01	1.09E-28	1.31E-27
HRRF - OFPR	1.17E+01	2.00E-31	2.60E-30
FDLR - FMLR	1.27E+01	4.24E-37	5.94E-36
FDLR - INPR	1.36E+01	5.51E-42	8.27E-41
HRRF - INPR	1.39E+01	4.97E-44	7.95E-43
FMLR - HRRF	-1.45E+01	6.91E-48	1.17E-46
FDLR - FSLR	1.48E+01	1.32E-49	2.38E-48
FSLR - HRRF	-1.63E+01	1.98E-59	3.76E-58
FDLR - MCPR	1.72E+01	4.80E-66	9.59E-65
HRRF - MCPR	1.92E+01	4.16E-82	8.74E-81

Table A8: Dunn (1964) Kruskal-Wallis multiple comparison of biomass by strata. Inshore Patch Reef (INPR); Midchannel Patch Reef (MCPR); Offshore Patch Reef (OFPR); Forereef Shallow Linear Reef (FSLR); Forereef Medium Linear Reef (FMLR); Forereef Deep Linear Reef (FDLR); and High Relief Reef (HRRF). * denotes the strata are not significantly different.

Comparison	Z	P.unadj	P.adj
INPR - MCPR	-4.55E-01	6.49E-01	1.00E+00*
FMLR – INPR	-2.08E-01	8.35E-01	8.35E-01*
FMLR - MCPR	-1.21E+00	2.28E-01	6.85E-01*
INPR – OFPR	-2.22E+00	2.61E-02	1.05E-01*
MCPR - OFPR	-2.58E+00	9.78E-03	4.89E-02
FMLR - OFPR	-3.91E+00	9.17E-05	5.50E-04
FDLR – OFPR	4.70E+00	2.58E-06	2.06E-05
FSLR – INPR	-4.70E+00	2.65E-06	1.86E-05
FDLR – HRRF	-5.45E+00	5.13E-08	4.62E-07
FDLR – INPR	5.89E+00	3.77E-09	3.77E-08
FDLR - MCPR	7.69E+00	1.52E-14	1.68E-13
FSLR – MCPR	-7.86E+00	3.96E-15	4.75E-14
FMLR – FSLR	8.07E+00	6.75E-16	8.78E-15
FSLR – OFPR	-9.35E+00	8.53E-21	1.19E-19
FDLR – FMLR	9.52E+00	1.73E-21	2.60E-20
HRRF – INPR	1.07E+01	1.56E-26	2.49E-25
HRRF - OFPR	1.11E+01	1.41E-28	2.39E-27
FDLR – FSLR	1.40E+01	8.87E-45	1.60E-43
HRRF - MCPR	1.57E+01	1.05E-55	2.00E-54
FMLR - HRRF	-1.97E+01	1.19E-86	2.38E-85
FSLR – HRRF	-2.29E+01	3.94E-116	8.27E-115

Table A9: Dunn (1964) Kruskal-Wallis multiple comparison of evenness by strata. Inshore Patch Reef (INPR); Midchannel Patch Reef (MCPR); Offshore Patch Reef (OFPR); Forereef Shallow Linear Reef (FSLR); Forereef Medium Linear Reef (FMLR); Forereef Deep Linear Reef (FDLR); and High Relief Reef (HRRF). * denotes the strata are not significantly different.

Comparison	Z	P.unadj	P.adj
HRRF - INPR	4.84E-01	6.29E-01	1.00E+00*
FMLR - INPR	-1.02E+00	3.08E-01	9.24E-01*
FSLR - MCPR	2.02E-01	8.40E-01	8.40E-01*
INPR - MCPR	-2.39E+00	1.69E-02	6.75E-02*
FSLR - INPR	2.49E+00	1.29E-02	6.45E-02*
FMLR - HRRF	-2.60E+00	9.26E-03	5.56E-02*
FSLR - OFPR	-2.83E+00	4.58E-03	3.21E-02
HRRF - MCPR	-2.90E+00	3.70E-03	2.96E-02
FSLR - HRRF	3.00E+00	2.66E-03	2.40E-02
MCPR - OFPR	-3.09E+00	1.99E-03	1.99E-02
INPR - OFPR	-4.39E+00	1.15E-05	1.26E-04
HRRF - OFPR	-5.56E+00	2.69E-08	3.23E-07
FMLR - FSLR	-6.15E+00	7.93E-10	1.03E-08
FMLR - MCPR	-6.21E+00	5.42E-10	7.59E-09
FDLR - INPR	-8.10E+00	5.32E-16	7.98E-15
FMLR - OFPR	-8.59E+00	8.96E-18	1.43E-16
FDLR - FMLR	-1.13E+01	8.81E-30	1.50E-28
FDLR - HRRF	-1.18E+01	2.84E-32	5.11E-31
FDLR - FSLR	-1.43E+01	3.96E-46	7.53E-45
FDLR - MCPR	-1.44E+01	3.18E-47	6.36E-46
FDLR - OFPR	-1.57E+01	3.09E-55	6.49E-54

Table A10: Dunn (1964) Kruskal-Wallis multiple comparison of richness by strata. Inshore Patch Reef (INPR); Midchannel Patch Reef (MCPR); Offshore Patch Reef (OFPR); Forereef Shallow Linear Reef (FSLR); Forereef Medium Linear Reef (FMLR); Forereef Deep Linear Reef (FDLR); and High Relief Reef (HRRF). * denotes the strata are not significantly different.

Comparison	Z	P.unadj	P.adj
FMLR - OFPR	-3.57E-01	7.21E-01	7.21E-01*
FSLR - INPR	2.25E+00	2.47E-02	4.95E-02
FDLR - HRRF	-4.42E+00	9.94E-06	2.98E-05
FSLR - MCPR	-4.52E+00	6.24E-06	2.50E-05
INPR - MCPR	-5.28E+00	1.29E-07	6.43E-07
MCPR - OFPR	-6.39E+00	1.68E-10	1.01E-09
FMLR - MCPR	8.38E+00	5.29E-17	3.70E-16
FDLR - OFPR	8.83E+00	1.08E-18	8.67E-18
INPR - OFPR	-9.39E+00	6.03E-21	5.43E-20
FSLR - OFPR	-1.02E+01	3.20E-24	3.20E-23
FMLR - INPR	1.05E+01	1.45E-25	1.60E-24
FDLR - FMLR	1.13E+01	1.50E-29	1.80E-28
FMLR - FSLR	1.33E+01	2.92E-40	3.80E-39
HRRF - OFPR	1.47E+01	3.56E-49	4.99E-48
FDLR - MCPR	1.59E+01	6.89E-57	1.03E-55
FDLR - INPR	1.62E+01	9.93E-59	1.59E-57
FDLR - FSLR	1.93E+01	8.48E-83	1.44E-81
FMLR - HRRF	-2.05E+01	2.71E-93	4.89E-92
HRRF - INPR	2.10E+01	9.15E-98	1.74E-96
HRRF - MCPR	2.43E+01	6.15E-130	1.23E-128
FSLR - HRRF	-2.79E+01	4.68E-171	9.83E-170

Table A11: Dunn (1964) Kruskal-Wallis multiple comparison of Simpson diversity by strata. Inshore Patch Reef (INPR); Midchannel Patch Reef (MCPR); Offshore Patch Reef (OFPR); Forereef Shallow Linear Reef (FSLR); Forereef Medium Linear Reef (FMLR); Forereef Deep Linear Reef (FDLR); and High Relief Reef (HRRF). * denotes the strata are not significantly different.

Comparison	Z	P.unadj	P.adj
FMLR - FSLR	4.95E-01	6.20E-01	1.00E+00*
HRRF - OFPR	3.06E-01	7.59E-01	7.59E-01*
FDLR - INPR	-1.17E+00	2.43E-01	7.28E-01*
FSLR - MCPR	-3.06E+00	2.25E-03	9.00E-03
FMLR - MCPR	-3.25E+00	1.17E-03	5.84E-03
FSLR - INPR	4.40E+00	1.06E-05	6.35E-05
FMLR - INPR	5.07E+00	4.03E-07	2.82E-06
MCPR - OFPR	-5.20E+00	1.97E-07	1.57E-06
HRRF - MCPR	6.26E+00	3.83E-10	3.45E-09
INPR - MCPR	-6.50E+00	8.02E-11	8.02E-10
FDLR - FSLR	-7.20E+00	6.13E-13	6.74E-12
FSLR - OFPR	-7.73E+00	1.12E-14	1.34E-13
FMLR - OFPR	-8.55E+00	1.25E-17	1.62E-16
FDLR - FMLR	-8.64E+00	5.56E-18	7.79E-17
FSLR - HRRF	-9.05E+00	1.44E-19	2.15E-18
INPR - OFPR	-9.71E+00	2.86E-22	4.58E-21
FDLR - MCPR	-9.98E+00	1.93E-23	3.28E-22
HRRF - INPR	1.05E+01	7.78E-26	1.40E-24
FMLR - HRRF	-1.05E+01	5.44E-26	1.03E-24
FDLR - OFPR	-1.35E+01	2.89E-41	5.77E-40
FDLR - HRRF	-1.50E+01	5.18E-51	1.09E-49

Table A12: Dunn (1964) Kruskal-Wallis multiple comparison of Shannon diversity by strata. Inshore Patch Reef (INPR); Midchannel Patch Reef (MCPR); Offshore Patch Reef (OFPR); Forereef Shallow Linear Reef (FSLR); Forereef Medium Linear Reef (FMLR); Forereef Deep Linear Reef (FDLR); and High Relief Reef (HRRF). * denotes the strata are not significantly different.

Comparison	Z	P.unadj	P.adj
FMLR - MCPR	-1.60E+00	1.10E-01	2.20E-01*
FDLR - FSLR	-1.23E+00	2.17E-01	2.17E-01*
FDLR - INPR	2.70E+00	6.91E-03	2.07E-02
HRRF - OFPR	3.40E+00	6.83E-04	2.73E-03
FSLR - INPR	3.88E+00	1.04E-04	5.18E-04
MCPR - OFPR	-5.37E+00	7.73E-08	5.41E-07
FMLR - FSLR	5.35E+00	8.95E-08	5.37E-07
FDLR - FMLR	-5.75E+00	8.85E-09	7.08E-08
FSLR - MCPR	-5.85E+00	4.86E-09	4.38E-08
FDLR - MCPR	-6.25E+00	4.05E-10	4.05E-09
FMLR - OFPR	-7.39E+00	1.46E-13	1.60E-12
FMLR - INPR	7.43E+00	1.08E-13	1.29E-12
INPR - MCPR	-7.83E+00	4.95E-15	6.43E-14
HRRF - MCPR	1.00E+01	1.27E-23	1.78E-22
FDLR - OFPR	-1.02E+01	1.22E-24	1.83E-23
FSLR - OFPR	-1.03E+01	5.39E-25	8.63E-24
INPR - OFPR	-1.11E+01	1.81E-28	3.08E-27
FMLR - HRRF	-1.34E+01	8.06E-41	1.45E-39
HRRF - INPR	1.43E+01	3.55E-46	6.75E-45
FDLR - HRRF	-1.45E+01	2.07E-47	4.15E-46
FSLR - HRRF	-1.54E+01	1.10E-53	2.31E-52

Table A13: Dunn (1964) Kruskal-Wallis multiple comparison of functional diversity by strata. Inshore Patch Reef (INPR); Midchannel Patch Reef (MCPR); Offshore Patch Reef (OFPR); Forereef Shallow Linear Reef (FSLR); Forereef Medium Linear Reef (FMLR); Forereef Deep Linear Reef (FDLR); and High Relief Reef (HRRF). * denotes the strata are not significantly different.

Comparison	Z	P.unadj	P.adj
FDLR - HRRF	1.06E-01	9.15E-01	9.15E-01*
FMLR - INPR	-1.67E+00	9.55E-02	1.91E-01*
MCPR - OFPR	2.35E+00	1.90E-02	5.71E-02*
FDLR - MCPR	2.61E+00	9.15E-03	3.66E-02
HRRF - MCPR	2.97E+00	2.94E-03	1.76E-02
INPR - OFPR	-2.92E+00	3.47E-03	1.73E-02
FDLR - OFPR	4.36E+00	1.29E-05	9.01E-05
HRRF - OFPR	4.89E+00	1.02E-06	9.18E-06
INPR - MCPR	-4.87E+00	1.13E-06	9.06E-06
FDLR - INPR	6.31E+00	2.83E-10	2.83E-09
FSLR - INPR	-6.74E+00	1.61E-11	1.77E-10
HRRF - INPR	6.76E+00	1.41E-11	1.70E-10
FMLR - OFPR	-7.13E+00	1.01E-12	1.32E-11
FMLR - FSLR	9.32E+00	1.18E-20	1.65E-19
FMLR - MCPR	-1.19E+01	8.22E-33	1.23E-31
FDLR - FMLR	1.21E+01	7.35E-34	1.18E-32
FSLR - OFPR	-1.30E+01	6.84E-39	1.16E-37
FMLR - HRRF	-1.51E+01	1.65E-51	2.98E-50
FDLR - FSLR	1.72E+01	2.58E-66	4.89E-65
FSLR - MCPR	-1.76E+01	1.88E-69	3.76E-68
FSLR - HRRF	-2.02E+01	2.52E-90	5.30E-89

Table A14: Dunn (1964) Kruskal-Wallis multiple comparison of abundance by subregion (Upper Keys, Middle Keys, and Lower Keys). * denotes the subregions are not significantly different.

Comparison	Z	P.unadj	P.adj
Lower - Upper	-0.44759	0.654449	0.654449*
Middle - Upper	3.844107	1.21E-04	2.42E-04
Lower - Middle	-4.04764	5.17E-05	1.55E-04

Table A15: Dunn (1964) Kruskal-Wallis multiple comparison of biomass by subregion (Upper Keys, Middle Keys, and Lower Keys). * denotes the subregions are not significantly different.

Comparison	Z	P.unadj	P.adj
Lower - Middle	1.980602	0.047636	0.047636
Lower - Upper	-3.93466	8.33E-05	1.67E-04
Middle - Upper	-4.56579	4.98E-06	1.49E-05

Table A16: Dunn (1964) Kruskal-Wallis multiple comparison of evenness by subregion (Upper Keys, Middle Keys, and Lower Keys). * denotes the subregions are not significantly different.

Table A17: Dunn (1964) Kruskal-Wallis multiple comparison of Simpson diversity by subregion, Upper Keys, Middle Keys, and Lower Keys. * denotes the subregions are not significantly different.

Comparison	Z	P.unadj	P.adj
Lower - Upper	0.6314	0.527779	0.527779*
Middle - Upper	-3.57671	3.48E-04	6.96E-04
Lower - Middle	3.902137	9.53E-05	2.86E-04

Table A18: Dunn (1964) Kruskal-Wallis multiple comparison of Shannon diversity by subregion, Upper Keys, Middle Keys, and Lower Keys. * denotes the subregions are not significantly different.

Comparison	Z	P.unadj	P.adj
Lower - Upper	1.551028	0.120895	0.120895*
Middle - Upper	-4.09053	4.30E-05	8.61E-05
Lower - Middle	4.987365	6.12E-07	1.84E-06

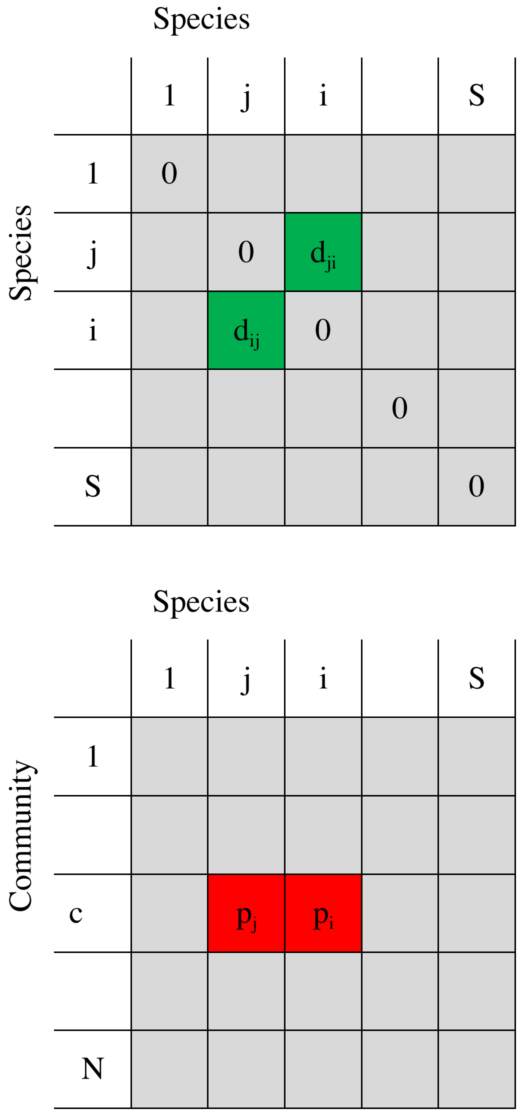
Table A19: Dunn (1964) Kruskal-Wallis multiple comparison of functional diversity by subregion, Upper Keys, Middle Keys, and Lower Keys. * denotes the subregions are not significantly different.

Comparison	Z	P.unadj	P.adj
Middle - Upper	-0.09993	0.920398	0.920398*
Lower - Middle	2.470237	0.013502	0.027005
Lower - Upper	3.748134	1.78E-04	5.34E-04

Table A20: Percent of sampling events in no-take marine zones across years by habitat strata.

Forereef Medium Linear Reef	33%
High Relief Reef	31%
Forereef Shallow Linear Reef	18%
Inshore Patch Reef	7%
Midchannel Patch Reef	7%
Offshore Patch Reef	4%
Forereef Deep Linear Reef	0%

Figure A1. Functional distance matrix example. d_{ij} = 1, when species i and species j are functionally distinct, and d_{ij} = 0 when species i and species j are functionally similar (top). Abundance matrix example. p_{jc} is the relative abundance of species j in community c (bottom).



Species

Species	1	j	i		S
1	0				
j		0	d_{ji}		
i		d_{ij}	0		
				0	
S					0

Species

Community	1	j	i		S
1					
c		p_j	p_i		
N					

$$Functional\ diversity\ (Rao's\ Q) = \left(\sum_{i=1}^{S-1}\sum_{j=i+1}^{S} d_{ij}p_ip_j\right)$$

I also plotted each index by subregion and grouped strata across years (Figure A2-A4). I grouped the strata into three main habitat classes: high relief reef or spur and groove (HRRF), forereef linear reef (FSLR, FMLR & FDLR) and patch reef (INPR, MCPR & OFPR) to better visualize differences among similar strata types. To better visualize the differences by strata across years, I also plotted the grouped strata for the Florida Keys domain across all years for each index (Figure A5).

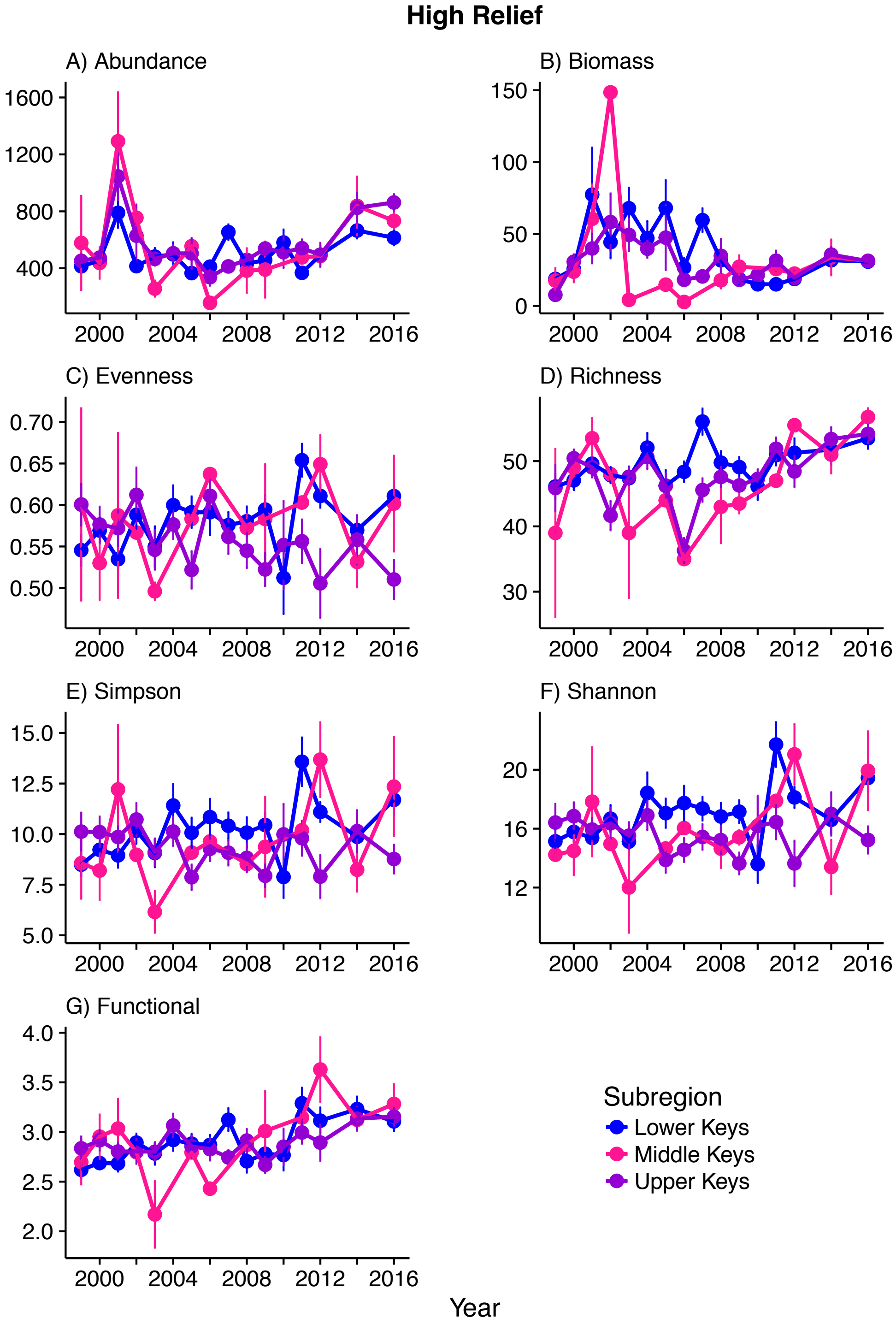


Figure A2. Plots of reef fish indices by subregion and grouped strata High Relief reef across years. The geographical subregions of the Florida Keys domain are Lower Keys, Middle Keys, and Upper Keys. The grouped strata High Relief reef correspond to the partitioned habitat classes grouped by High Relief reef (HRRF). The units for panel A is abundance, panel B is kilograms per 40,000 km^2, panel C is units ranging from 0 (maximally uneven) to 1 (maximally even), and panels D-G are in units of effective number of species. Error bars are ± SE.

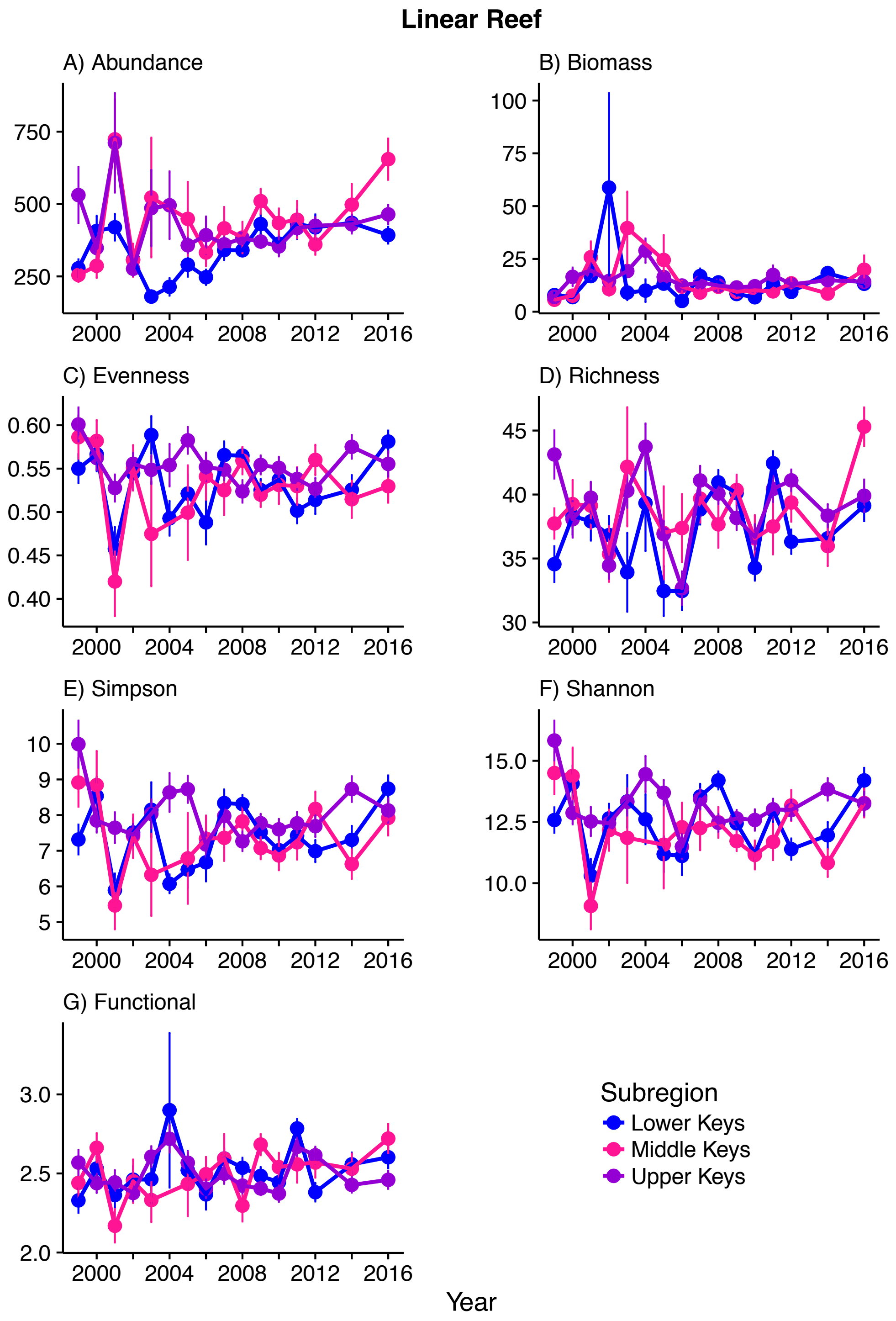


Figure A3. Plot of reef fish indices for each subregion and grouped strata Linear reef of the Florida Keys. The geographical subregions of the Florida Keys domain are Lower Keys, Middle Keys, and Upper Keys. The grouped strata Linear reef correspond to the partitioned habitat classes grouped by Forereef Deep Linear Reef (FDLR), Forereef Midchannel Linear Reef (FMLR), and Forereef Shallow Linear Reef (FSLR). The units for panel A is abundance, panel B is kilograms per 40,000 km^2, panel C is units ranging from 0 (maximally uneven) to 1 (maximally even), and panels D-G are in units of effective number of species. Error bars are ± SE.

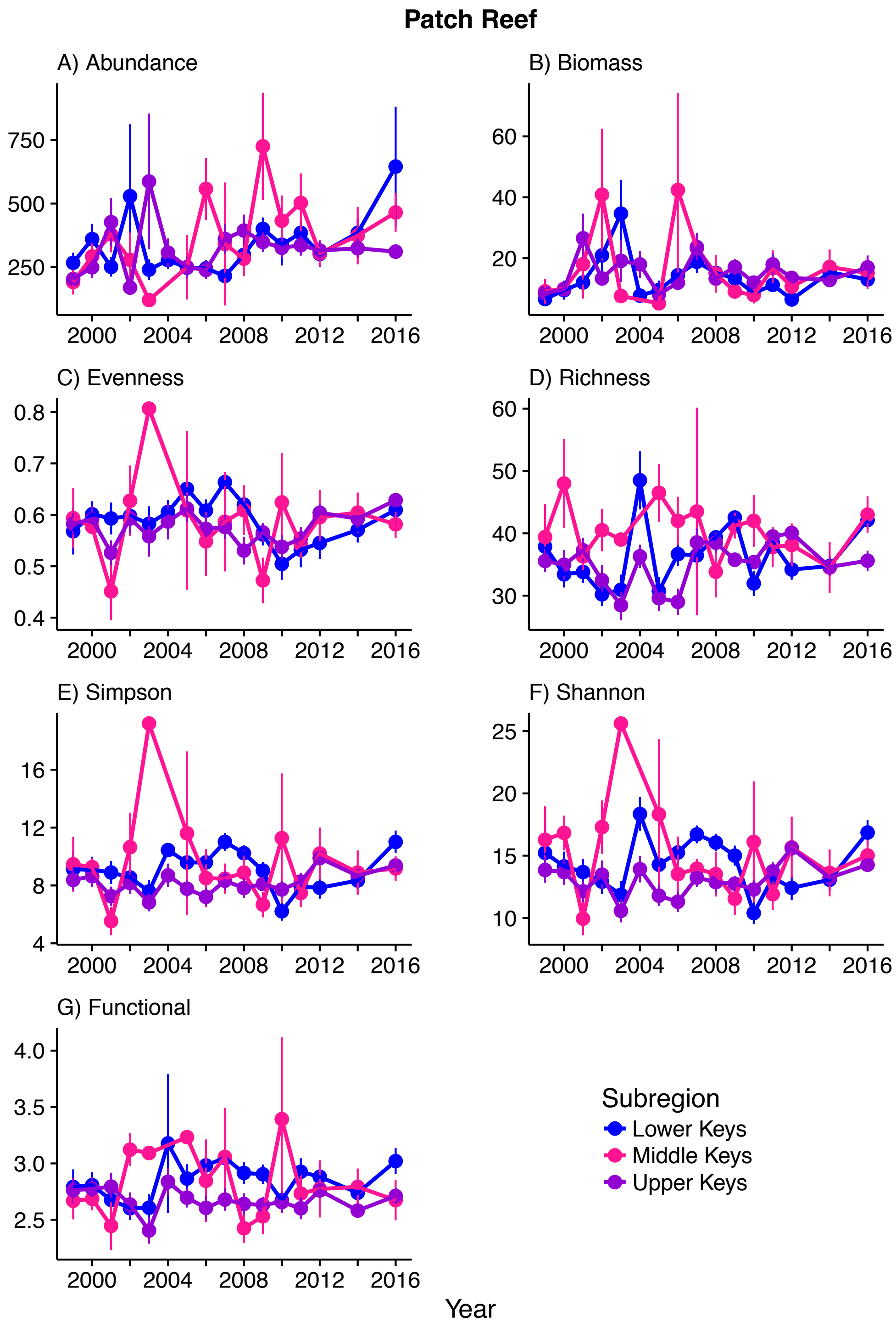


Figure A4. Plot of reef fish diversity for each subregion and grouped strata Patch reef of the Florida Keys. The geographical subregions of the Florida Keys domain are Lower Keys, Middle Keys, and Upper Keys. The grouped strata Patch reef correspond to the partitioned habitat classes grouped by Inshore Patch Reef (INPR), Midchannel Patch Reef (MCPR), and Offshore Patch Reef (OFPR). The units for panel A is abundance, panel B is kilograms per 40,000 km^2, panel C is units ranging from 0 (maximally uneven) to 1 (maximally even), and panels D-G are in units of effective number of species. Error bars are ± SE.

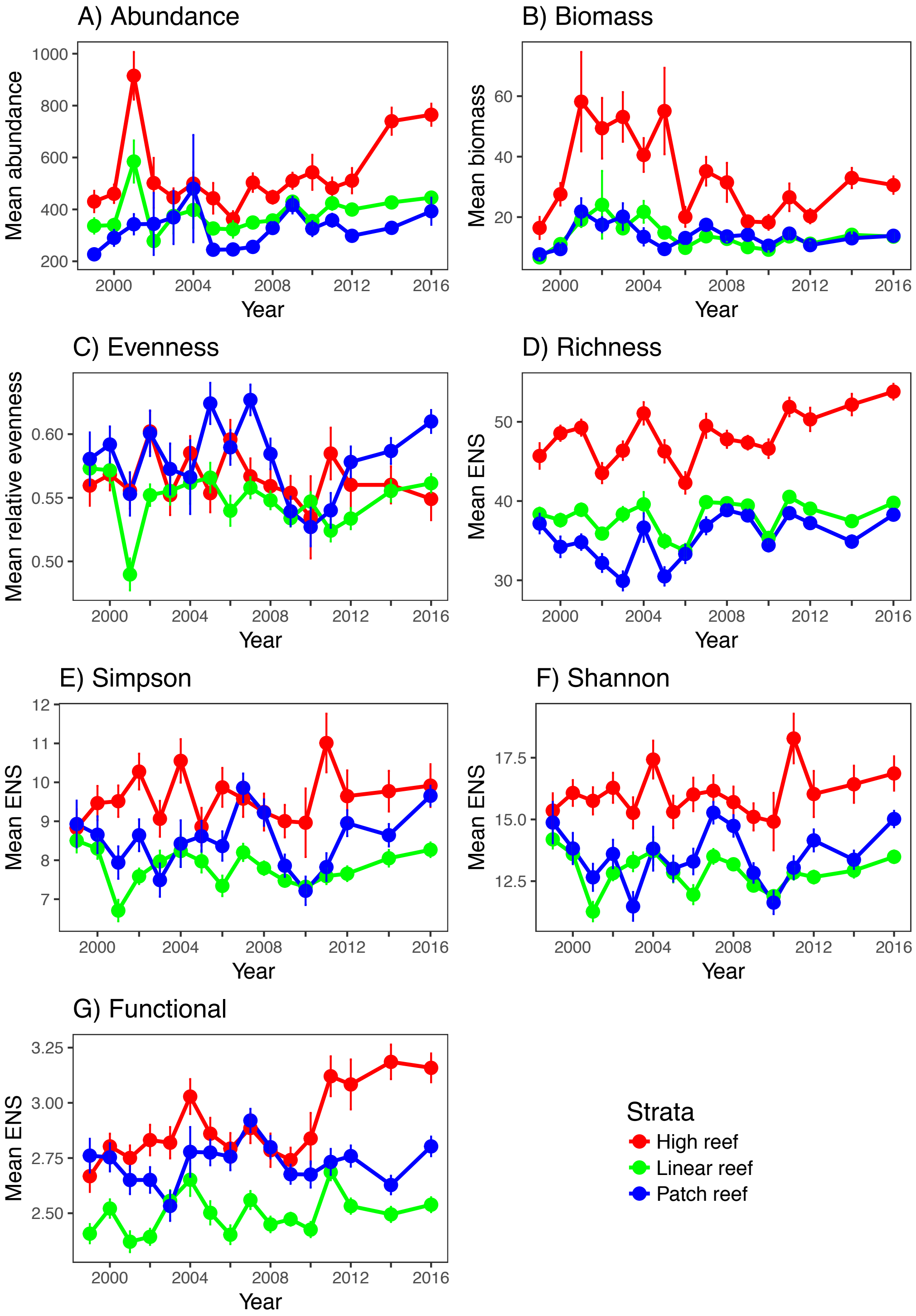


Figure A5. Plot of reef fish of the Florida Keys by grouped strata. The grouped strata correspond to the habitat classes grouped into High reef (High Relief Reef), Linear reef (Forereef Deep Linear Reef, Forereef Midchannel Linear Reef, Forereef Shallow Linear Reef), and Patch reef (Inshore Patch Reef; Midchannel Patch Reef; Offshore Patch Reef). The units for panel A is abundance, panel B is kilograms per 40,000 km^2, panel C is units ranging from 0 (maximally uneven) to 1 (maximally even), and panels D-G are in units of effective number of species. Error bars are ± SE.

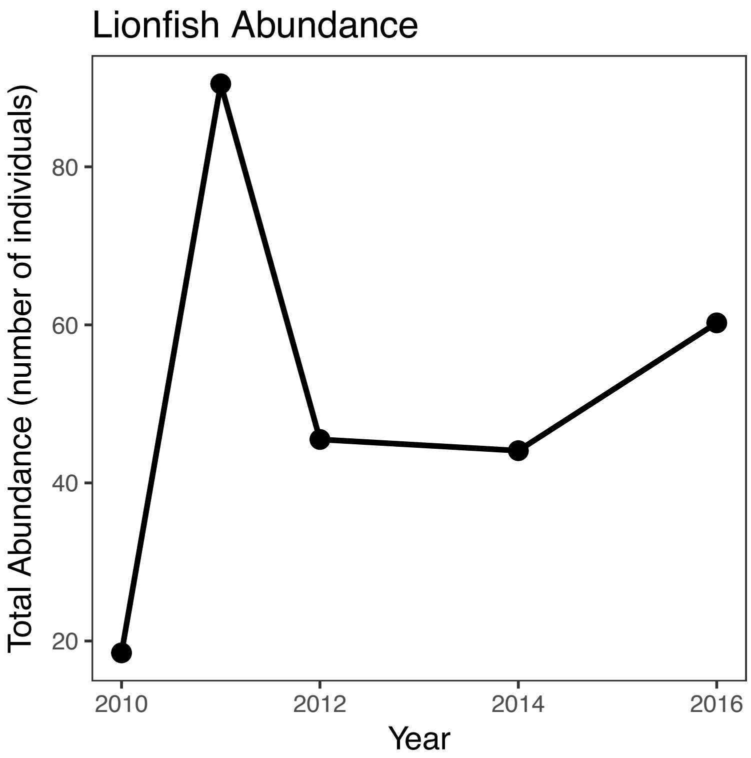


Figure A6. Total number of lionfish detected with the Reef Visual Census (RVC) from 2010 – 2016.