AN ABSTRACT OF THE DISSERTATION OF

Martha Patricia Rincón Díaz for the degree of Doctor of Philosophy in Fisheries Sciences presented on May 23, 2018.

Title: Functional Diversity: A Tool to Track Spatiotemporal Changes in the Trophic Organization of Reef Fish Assemblages

Abstract approved: _____

Selina S. Heppell

Biodiversity loss in highly diverse systems such as coral reefs has been linked to significant declines in the ecosystem functions and services provided by marine species. Ecological functioning of coral reefs and the resistance of coral reef fish communities to disturbance depend on the functional traits of species that promotes ecological resistance, as well as traits spatial and temporal abundance. Trait-based approaches are increasingly being used in marine ecology to predict impacts on ecosystem function and services from environmental change. Functional diversity (FD) metrics quantify the trait diversity in biological assemblages and act as a proxy for the diversity of ecological functions performed in the community. Analyses of FD offers a potentially useful tool to identify functional changes in diverse, complex, and disturbed marine ecosystems such as coral reefs, yet this metric is rarely applied to evaluate community change. Few studies have applied trait-based diversity metrics to understand the ecological roles that fishes play in the trophic dynamics in coral reef systems, neither for monitoring spatiotemporal changes in the trophic organization of fish assemblages to evaluate management strategies and resistance of fish assemblages to disturbances.

To better understand the trophic structure in fish communities and identify any knowledge gaps, we conducted an extensive literature review of six trophic functional traits for juvenile and adult stages of 274 marine fish species known to occur in the U.S.

Caribbean. Trait descriptions were more comprehensive for adult life stages than juveniles, and the trophic level was the most recorded trait, and social feeding behavior was the poorest recorded traits for species in adult and juvenile stages. From this review, we built a trait database that described fish trophic functions, but also gaps in trait knowledge in the Caribbean Basin.

In Chapter 3, we documented spatiotemporal variability in the trophic function of fish assemblages to identify changes in coral reef communities inside benthic habitats of the Buck Island Reef National Monument (BIRNM) in the U.S. Virgin Islands between 2002 and 2010. We combined six traits related to the trophic function of 95 fish species together with species biomass estimated from underwater surveys to calculate assemblage-level descriptors of functional richness, dispersion, and evenness. We found that coral reef and other hard bottom areas supported high levels of trophic functional richness and variation among habitat types, but with low functional redundancy evidenced by the unique trophic role that each fish species had within the functional trait space. Important temporal variations in functional trait composition during the last decade in the BIRNM, including change following a strong coral bleaching event in 2005, suggested that functional diversity descriptors are sensitive enough to track changes in the trophic organization of fish communities. In general, this chapter showed the utility of descriptors of functional diversity to evaluate changes in ecosystem functioning of heterogeneous habitats in the seascape.

In Chapter 4, we used descriptors of functional diversity and traits as tools to (1) evaluate the ecological performance of Marine Protected Areas (MPA); (2) study the association of fish functional diversity in ecosystem services such as production of fish standing biomass; and (3) identify the ecological resistance of fish communities to the coral bleaching event in 2005 in the U.S. Virgin Islands. We used four functional traits related to the trophic function of fish species and their biomass between 2002 and 2012 to calculate descriptors of functional richness, variation and evenness, community-weighted mean values of functional traits, and fish standing biomass inside and outside MPAs. We also used trait information to characterize trait values for tolerant and non-tolerant species to the coral bleaching event in 2005 that produced high mortality in coral reefs in the U.S.

Virgin Islands. First, we found that functional diversity descriptors and traits are sensitive to capture spatial and temporal differences in the functional organization of communities, and are an excellent addition to monitoring the ecological performance of marine reserves. Reserve effects were found only for the Buck Island National Reef Monument in St. Croix, and we consider that the lack of reserve effects in other MPAs is a consequence of their short establishment duration, the legacy of overfishing, and possible functional homogenization in fish communities. Second, we found an association of functional diversity and fish biomass, which indicated that high fish functional richness and variation, and low evenness covaries positively with the total fish standing biomass at all levels of habitat protection. This finding highlights the importance of protecting the diversity of ecological roles in reef fish assemblages to maintain ecosystem services. Finally, we identified indicators of fish functional diversity erosion and a low ecological resistance of fish species to the coral bleaching event in 2005. These indicators included (1) the reduction in fish functional richness; (2) the lack of return of fish functional richness to its original levels after seven years of survey; (3) the dominance of broader diets in fish assemblages; and (4) the reductions in the trophic levels of disturbance-tolerant fish species. Based on the tolerance of each fish species to the coral bleaching event in 2005, we built a database of ecological resistance to disturbance. Managers can use this database to enhance the intrinsic ecological resistance of fish assemblages or to better understand further trends in the trophic organization of fish assemblages in each evaluated MPA.

Functional Diversity: A Tool to Track Spatiotemporal Changes in the Trophic
Organization of Reef Fish Assemblages

by
Martha Patricia Rincón Díaz

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented May 23, 2018
Commencement June 2018

Doctor of Philosophy dissertation of <u>Martha Patricia Rincón Díaz</u> presented on <u>May 23, 2018.</u>

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Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Martha Patricia Rincón Díaz, Author

ACKNOWLEDGMENTS

CONTRIBUTION OF AUTHORS

For Chapter 2: Martha Patricia Rincon Diaz conducted the literature review, data compilation, verification, analysis, and coding, and wrote the manuscript. Simon J. Pittman provided data and academic guidance; and Selina S. Heppell provided guidance on data analysis. All coauthors provided editorial advice.

For Chapter 3: Martha Patricia Rincon Diaz conceived and designed the study, conducted the literature review, data compilation and verification of functional traits, conducted data analysis, and wrote the manuscript. Simon J. Pittman provided data and academic guidance; and Ivan Arismendi and Selina S. Heppell provided guidance on data analysis. All coauthors provided editorial advice.

For Chapter 4: Martha Patricia Rincon Diaz conceived and designed the study, conducted the literature review, data compilation and verification of functional traits, conducted data analysis, and wrote the manuscript. Simon J. Pittman provided data and academic guidance. Aaron Eager provided guidance on data analysis, and conducted the community species composition analysis; and Selina S. Heppell provided academic guidance. All coauthors provided editorial advice.

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Este trabajo está dedicado a mi familia: Blanca, Salvador y Juan. Ellos son mi apoyo y fortaleza para luchar por mis objetivos como madre y mujer latinoamericana en las ciencias.

Chapter 1: Introduction

1.1. Overview of functional traits, diversity and ecosystem functioning

   Ecosystem functions (processes) such as primary and secondary production, and associated services to humans such as fish standing biomass, depend on the functional traits of species and their spatial and temporal abundance (Hooper et al. 2005, Jax et al. 2005, Micheli et al., 2014). Functional traits are process-relevant attributes of organisms that make them bearers of functional roles, and thus supporters of ecosystem function (Jax et al. 2005). Traits can be morphological, behavioral, and physiological (Cadotte et al. 2011, Diaz and Cabido 2001, Petchey and Gaston 2006), and are connected to the environmental tolerance of organisms which influence the composition and organization of biological assemblages, but also ecosystem resilience (Boersma et al. 2014, Piacenza et al. 2015, Cadotte et al. 2015, Dee et al. 2016, Silva-Júnior et al. 2016). Resilience is crucial for ecosystems because it allows for the capacity of a system to persist or maintain function under disturbances through the system's ability to resist change and recover to its original functional state (Holling 1973, 1996, Folke et al. 2004, Mora 2015, Hodgson et al. 2015). Functional traits generate ecological resilience through the richness (diversification), but also the redundancy (overlapping) of the functional roles of species, which buffers the loss of ecological roles caused by biodiversity reduction due to human-induced and natural disturbances (Peterson et al. 1997, Smith et al. 2011, Mouillot et al. 2013, Dee et al. 2016, Duffy 2009, Micheli and Halpern 2005, Ricotta et al. 2016, Cernansky 2017). When implementing an ecosystem-based management approach, the diversity and redundancy of ecological roles of species are important indicators of change to track ecosystem functioning rather than counting the number of species (Cadotte et al. 2011).
   Trait-based approaches such as functional diversity analysis are increasingly being used in assessments of ecosystem conditions to predict impacts on ecosystem function and services due to environmental change and community responses to such change (Villéger et al. 2010, Luck et al. 2012, Michelli et al. 2014, Funk et al. 2016). Based on

species abundance and their functional traits, functional diversity provides a way to characterize the niche space used by each species, and the functional organization of biotic assemblages (Diaz and Cabido 2001, Petchey and Gaston 2006, Cadotte et al. 2011). Models of functional diversity describe how the relationship between species richness and functions delineates the values in the relationship between biodiversity and ecosystem function (BEF) (Fig. 1) (Cadotte et al. 2001). This relationship could be a positive or asymptotic curve called functional redundancy (Peterson et al. 1998, Elmqvist et al 2003, Micheli et al. 2014). The redundancy in species functions suggests that more than one species providing a specific ecosystem function is present at a single spatial and temporal scale (Peterson et al. 1998, Elmqvist et al 2003), which increases the resilience. Reducing biological diversity and species biomass reduces the ecological resilience of systems, increases their vulnerability to phase shifts caused by disturbances, and changes desired ecosystem services (Fig. 2) (Peterson et al. 1998). Even though functional diversity as a measurement of biodiversity is relatively new (Schleuter et al. 2010), functional diversity descriptors are considered to be simple, logical and repeatable metrics that can be comparable across multiple spatial scales (Carmona et al. 2016) to evaluate the change of the functional organization of communities and ecosystems.

Traditional descriptors of spatio-temporal changes in species diversity, including species richness, and trophic group richness and biomass (Gotelly and Colwell 2001, Colwell 2009, Maurer 2009, Vallès and Oxenford 2015, Loiseau and Gaertner 2015), can not capture the interspecific variability in species traits because they either ignore species-specific functional roles completely or clump species within trophic groups without sufficient knowledge of trait differences (Villéger et al. 2010, Micheli et al. 2014, Mouillot et al. 2013b, Boersma et al. 2014, 2016, Dee et al. 2016). Functional diversity descriptors consider the identity of species, interspecific variability and redundancy of functional roles (Villéger et al. 2008, 2010, Micheli et al. 2014, Boersma et al. 2014, 2016, Dee et al. 2016), roles played by rare species (Jain et al. 2014, Mouillot et al. 2013a, Leitao et al. 2016), and explanations of mechanisms of the functional organization under different levels of disturbance (Mouillot et al. 2013b). Even though the use of functional diversity as a measure of biodiversity is relatively new (Schleuter et al. 2010)

and a "good" level of redundancy in species function has not been established for ecosystem-based management, this metric is beneficial because it can vary spatiotemporally between disturbed and undisturbed habitats, which gives us a better understanding of the effect of protection levels of habitats on an ecosystem approach.

Figure 1. Relationships between species richness and functional diversity (FD), and their influence on biodiversity and ecosystem function (BEF) (From Cadotte et al. 2011). Positive relationship between species richness and FD leads to a positive BEF relationship (a) [Note: The magnitude of BEF depends on levels of FD]. When species in a community are functionally redundant, biodiversity does not influence ecosystem function (b). The lack of a relationship between species richness and FD leads to a range in ecosystem function, which is explained by functional diversity (c) (Cadotte et al. 2011).

Figure 2. Relationship between species richness, ecological function and ecosystem resilience (Modified from Peterson et al. 1998). In this example, the relationship between species richness and ecological function is represented by a linear trend in functional redundancy (A). Varying numbers in species richness leads to dissimilar levels of functional stability in the system. System stability is represented by the ball at the base of local stability pits at landscapes driven by species richness (B). Movement of the system between states is driven by the energy of a disturbance and its consequent changes in the landscapes of stability. System stability is measured by the slope and the resilience by the width of the pit in the current state (Peterson et al. 1998).

1.2. Functional diversity in coral reef fish assemblages

Fish exhibit a wide range of functional traits that perform complex ecological roles in coral reef ecosystems. Even though functional diversity studies provide an opportunity to understand changes in the functional organization of biological communities, these studies require an enormous effort to compile functional traits in areas of high biodiversity. In many regions, gaps in our understanding of functional traits throughout the life cycle of fishes could result in unreliable estimates of functional redundancy and biased conclusions about ecosystem resilience (Mora 2015, Nakazawa 2015, Sánchez-Hernández 2016). In the case of fishes associated with coral reefs, of which many undergo ontogenetic shifts in habitat and diet, functional redundancy at any location will be influenced by the space-use patterns of fishes and other trait changes throughout the life cycle (Nash et al. 2016, Kimierei et al. 2013, Lecchini and Galzin 2005). This leaves open the question: What ecological roles do juvenile fishes play in the complex trophic relationships of coral reef systems? Therefore it is important to understand the ecological roles that juvenile fishes play in the trophic relationships of coral reef systems and to

determine if the available information on functional traits is sufficient to identify changes in their function by life stages. The quality of information on functional traits for key functional groups of reef fish species is increasingly important because it impacts our ability to evaluate threats to coral reefs and predict their rates of recovery.

Coral reefs are highly biodiverse systems, however they are vulnerable to overfishing and climate warming, which results in the widespread degradation of the structure and function of reef fish assemblages worldwide (Pandolfi et al. 2003, D'agata et al. 2016b). The low resilience of reef fish assemblages to stressors has three explanations. The first is the limited redundancy in the functional roles of fishes within multiple functional groups (Bellwood et al. 2003, Micheli et al. 2014, Mouillot et al. 2014, D'agata et al. 2016, Rincon-Diaz et al. unpublished). The second is explained by the high vulnerability of unique functional roles performed by rare fish species that have low occurrence within communities (Mouillot et al. 2013, Leitão et al. 2016). The third is the increase in magnitude and frequency of disturbances which limits the resilience of coral reefs (Hughes 2010, Eakin et al. 2010, Hughes et al. 2018). Future resilience of coral reef communities to climatic change will depend on the capacity of species to resist disturbances through traits that help organisms to tolerate change and the protection of locations that show systematic ecological resistance to disturbances (Darling and Côté 2018). Studies that focus on the relationship between functional traits and resilience of reef fish communities are necessary to decrease the decline of ecosystem functions and ensure the survival and thriving of ecosystem services provided by coral reefs.

1.3. State of the research on fish functional diversity in the U.S. Virgin Islands

Recent studies about fish diversity in the in the U.S. Virgin Islands have focused on understanding the abundance and distribution of trophic groups and species richness within and outside Marine Protected Areas (MPAs) (Costa et al. 2009, 2012, Friedlander et al. 2013, Kendall et al. 2001, 2005, 2011, Monaco et al. 2008, 2009, Pittman et al. 2008, Zitello et al. 2009). However, despite the existence of vast information on fish species presence, distribution, and abundance, there is no information related to

functional diversity. Community composition and distribution of reef fish assemblages vary spatially in the U.S. Virgin Islands, even within similar habitats, because of the combined effects of differences in shelf size and fishing activities in this archipelago (Brandt et al. 2010). In general, due to fishing pressure fish assemblages in the U.S. Caribbean have experienced a depletion of large-bodied species such as groupers and parrotfish that resulted in a shift to small body species dominance such as coney grouper (*Epinephelus fulvus*) and rainbow parrotfish (*Sparisoma aurofrenatum*) (Pittman et al. 2010). The decline in species composition and biomass of fish communities in the U.S. Caribbean is due numerous factors that include: the lack of an early understanding of fish functional organization, a long history of overfishing (Garrison et al. 1998, 2004), damage from boats, hurricanes, bleaching events and diseases on coral reefs, and a weak enforcement against fishing activities inside MPAs (Rogers and Beets 2001, Pittman et al. 2014).

Comparisons of species-habitat relationships in areas inside versus outside MPAs show a variety of differences in the biomass of fish trophic guilds and abundance of individual species in the U.S. Virgin Islands. In St. John and the Buck Island Reef National Monument (BIRNM) in St. Croix, indexes of fish species richness are positively associated with reef context features such as patch adjacency to reefs and seagrasses inside the MPAs (Grober-Dunsmore et al. 2007, Pittman et al. 2008). In St. John, mobile invertebrate feeders and adult piscivores are related to seagrasses and reef habitat coverage respectively, and juvenile omnivores are associated with sources of ichthyoplankton in deep habitats (Grober-Dunsmore et al. 2007). In the Virgin Islands National Park (VIIS) in St. John, invertivore biomass was high in hard bottom habitats inside the MPA, and piscivores and planktivore biomass were higher outside it (Friedlander et al. 2013). Mesopredator release effects, due to the decline of larger groupers (Beets et al. 1994), are also observed in the VIIS since small mobile invertivores such as coneys (*Cephalopholis fulva*) are found in high densities but in small body sizes outside the MPA (Friedlander et al. 2013). The Buck Island Reef National Monument (BIRNM) in St. Croix exhibits a high biomass of herbivores in hard bottom habitats inside the MPA and of piscivores outside it (Pittman et al. 2008). Conversely, in the

BIRNM, coneys are found in high densities inside the MPA (Pittman et al. 2008). The observed short term variations in the biomass of fish trophic groups suggest that there is a spatial change in the food web structure of fish communities. This finding suggests a need to further study community-wide impacts under different protection levels in the U.S. Virgin Islands.

Important recommendations for management enforcement and modification of boundaries in MPAs of the U.S. Virgin Islands have been suggested to account for areas of higher coral reef complexity, healthiness, and redundancy of fish species richness (Friedlander et al. 2013, Monaco et al. 2009, and Pittman et al. 2008). The variability in responses of fish trophic guilds to habitat characteristics and their selection of reef patches need special consideration in MPAs' design (Grober-Dunsmore et al. 2007) since mechanisms behind fish species diversity operate in a habitat matrix that links habitats with different ecological functions under different fishing pressures and protection levels. Because the mechanisms of fish functional diversity are unknown in MPAs of the U.S. Caribbean, studies that contribute to the understanding of ecosystem changes in MPAs and impacts on the functional diversity of fish communities are needed to improve ecosystem-based management in this area.

1.4. Thesis outline

In the present work we use information on functional traits related to the trophic function of reef fish species, along with information on fish species abundance in the U.S. Virgin Islands to: (1) identify any knowledge gaps in the trophic traits of reef fish species; (2) validate functional diversity descriptors to understand the spatiotemporal changes in the functional organization of fish assemblages in coral reefs; and (3) evaluate functional diversity descriptors and traits as tools to monitor the ecological performance of MPAs and the ecological resistance of their reef fish communities in facing natural disturbances. In addition to this introduction (chapter 1), the dissertation is divided into three chapters:

Chapter 2: Information gaps in trophic functional traits of Caribbean reef fishes

This chapter was submitted as a data paper in Ecology (Rincon-Diaz et al. submitted).

To better understand trophic structure in fish communities and to identify any knowledge gaps, we conducted an extensive literature review of six trophic functional traits for juvenile and adult stages of 274 marine fish species known to occur in the U.S. Caribbean. We found that trait descriptions were more comprehensive for adult life stages than juveniles. A high percentage (62%) of species had no available information for juvenile stages which hinders our understanding of the ecosystem function required to support ecosystem-based management and conservation efforts in the Caribbean. Trophic level was the most recorded trait and social feeding behavior was the poorest recorded traits for species in adult and juvenile stages. We provide readers with a database of functional traits, but also with a current status of knowledge (which includes gaps) for reef fish species. This information can be used in other studies of functional diversity and ecosystem resilience in Caribbean marine ecosystems. This chapter was written in the format of a data paper, which includes metadata, accessibility, copyrights, citation, and files associated with this database.

Chapter 3: Functional diversity metrics show spatial and temporal changes in fish communities of a Caribbean marine protected area.

This chapter was accepted with minor revisions in Ecosphere (Rincon-Diaz et al. accepted).

In this chapter we document spatio-temporal variability in the trophic function of fish assemblages to identify changes in coral reef communities inside benthic habitats of the Buck Island Reef National Monument (BIRNM) in the U.S. Virgin Islands between 2002 and 2010. We combined 6 traits related to the trophic function of 95 fish species together with species biomass estimated from underwater surveys to calculate assemblage-level descriptors of functional richness, dispersion, and evenness. We found that coral reef and

other hard bottom areas supported high levels of trophic functional richness and variation among habitat types, but with low functional redundancy evidenced by the unique trophic role that each fish species had within the functional trait space. Important temporal variations in functional trait composition during the last decade in the BIRNM, including change following a strong coral bleaching event in 2005, suggest that functional diversity descriptors are sensitive enough to track changes in the trophic organization of fish communities. In general, this chapter shows the utility of descriptors of functional diversity to evaluate changes in ecosystem functioning of heterogeneous habitats in the seascape.

Chapter 4: Functional diversity: a tool for the ecological performance of MPAs and indicator of resistance in reef fish assemblages

This chapter was approved for all coauthors and will be submitted to the journal Ecology Progress Series.

In this chapter we validated the use of descriptors of functional diversity and traits as tools to (1) evaluate the ecological performance of Marine Protected Areas (MPA); (2) study the association of fish functional diversity in ecosystem services such as production of fish standing biomass; and (3) identify the ecological resistance of fish communities to the coral bleaching event in 2005 in the U.S. Virgin Islands. We used four functional traits related to the trophic function of fish species and their biomass between 2002 and 2012 to calculate descriptors of functional richness, variation and evenness, community-weighted mean values of functional traits, and fish standing biomass inside and outside MPAs. We also use trait information to characterize trait values for tolerant and non-tolerant species to the coral bleaching event in 2005 that produced high mortality in coral reefs in the U.S. Virgin Islands. First, we found that functional diversity descriptors and traits are sensitive to capture spatial and temporal differences in the functional organization of communities, and are a good addition to monitoring the ecological performance of marine reserves. We found reserve effects only for the Buck Island National Reef Monument. We consider the lack of reserve effects in other MPAs is a

consequence of their short establishment duration, long-term legacy of overfishing, and homogenization of trait composition in fish communities. Second, we found an association of functional diversity and fish biomass, which indicates that high fish functional richness and variation, and low evenness enhance total fish standing biomass at all levels of habitat protection. This finding highlights the importance of protecting the diversity of ecological roles in reef fish assemblages to maintain ecosystem services. Finally, we identified indicators of fish functional diversity erosion and a low ecological resistance of fish species to the coral bleaching event in 2005. These indicators include (1) the reduction in fish functional richness; (2) the lack of return of fish functional richness to its original levels after seven years of survey; (3) the dominance of broader diets in fish assemblages; and (4) the reductions in trophic levels of disturbance-tolerant fish species. Based on the tolerance of each fish species to the coral bleaching event in 2005, we built a database of ecological resistance to disturbance. Managers can use this database to enhance the intrinsic ecological resistance of fish assemblages, or to better understand further trends in the trophic organization of fish assemblages in each evaluated MPA.

Chapter 2: Information gaps in trophic functional traits of Caribbean reef fishes

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2.1. Abstract

Understanding the ecological roles that fishes play in the complex trophic relationships and dynamics of coral reef systems depends on our knowledge of fish feeding ecology and our ability to detect changes in community composition and function. The functional redundancy of fishes in different habitats is highly influenced by species composition and ontogenetic shifts in diets and feeding behavior across species, as evidenced by different patterns of habitat use and migrations during different life stages. To better understand trophic structure in fish communities and to identify any knowledge gaps, we conducted an extensive literature review of trophic functional traits of 274 marine fish species known to occur in the U.S. Caribbean. We also present the quality of trait information for each species based on the location of studies, date of publication, and sample sizes. Fish traits were extracted for juvenile and adult fish stages separately and selected based on: water column feeding position, social feeding behavior, time of feeding, habitat use for feeding, trophic levels, and diet breadth. Trait descriptions were more comprehensive for adult life stages than juveniles. Trophic level was the most recorded trait for species in adult and juvenile stages (96 and 30%, respectively). The poorest recorded traits for adults were social feeding behavior and feeding grounds (57%,

respectively), and very little was known about social feeding behavior for juveniles (8%). A high percentage (62%) of species had no available information for juveniles. Significant gaps in our knowledge of the trophic roles of juvenile fishes in the U.S. Caribbean, and throughout the Caribbean region, hinder our understanding of ecosystem function required to support ecosystem-based management and conservation efforts. We recommend increasing research efforts to describe functional roles of non-commercial, cryptic and rare fish species to understand changes in the functional redundancy and diversity of Caribbean marine ecosystems. This data set can be used in studies that link fish functional diversity to resilience of Caribbean coral reefs to natural and anthropogenic disturbances, as well as those focused on predicting transmission of parasitic infections in fishes by using behavioral traits related to feeding ecology of reef fishes.

Keywords: food webs/trophic structure; fishes; coral reef; Caribbean Islands; trophic roles; functional diversity; ontogenetic shifts; functional traits.

2.2. Introduction

Fishes exhibit a wide range of functional traits that together play complex ecological roles in coral reef ecosystems. Functional traits, or measurable features of an individual that affect its ecological role, can be physical, biochemical, or behavioral (Cadotte et al. 2011). Trait-based approaches are increasingly being used in marine ecology and in assessments of ecosystem condition to predict impacts on ecosystem function and services from environmental change and community responses to such change (Villéger et al. 2010, Luck et al. 2012, Michelli et al. 2014, Funk et al. 2016).

Functional diversity, a measure of the variety of functional traits exhibited by species within a community, is an ecologically meaningful approach for evaluating changes to ecosystem integrity and resilience, and requires accurate information on species ecology throughout their life history (Petchey and Gaston 2006, Stuart-Smith et al. 2013). For

instance, the impact on ecosystem integrity as a consequence of the decline and loss of a species from the community will depend on the degree of overlap with the functional roles of other species (Micheli and Halpern 2005, Ricotta et al. 2016), as well as of specific life stages of a species (Nakazawa 2015, 2016, Rudolf and Rasmussen 2013). Functional diversity accounts for similarities and differences among species based on their functional traits (Diaz and Cabido 2001, Cadotte et al. 2011). Models of functional diversity describe the relationship between species richness and species functions as a positive and asymptotic curve called functional redundancy (Peterson et al. 1998, Elmqvist et al. 2003). Functional redundancy is thought to increase the resilience of a system, or its degree of self-organization, to resist departures from equilibrium states following disturbances (Holling 1973, Folke et al. 2004). Even though functional diversity studies provide an opportunity to understand changes in functional organization of biological communities, these studies require of an enormous effort to compile functional traits of species in areas of high biodiversity.

Coral reefs are among the most biodiverse systems on Earth, but are vulnerable to disturbance from human activities which have resulted in widespread degradation of ecosystem structure and function worldwide (Pandolfi et al. 2003). This low resilience of coral reefs to stressors has been explained by observations of limited redundancy in the functional roles of fishes within multiple functional groups (Bellwood et al. 2003, Micheli et al. 2014). In the Caribbean, loss of functional groups of fishes and low functional redundancy in fish communities, together with multiple stressors, has resulted in especially high vulnerability of coral reefs to disturbance (Roff and Mumby 2012). As such, the quality of information on functional traits for key functional groups of species is increasingly important in our ability to evaluate threats to coral reefs and predict rates of recovery. In many regions, gaps in our understanding of functional traits throughout the life cycle of fishes could result in unreliable estimates of functional redundancy and biased conclusions about ecosystem resilience (Mora 2015, Nakazawa 2015, Sánchez-Hernández 2016). In the case of fishes associated with coral reefs, of which many undergo ontogenetic shifts in habitat and diet, functional redundancy at any location will be influenced by the space-use patterns of fishes and other trait changes throughout the

life cycle (Nash et al. 2016, Kimierei et al. 2013, Lecchini and Galzin 2005). Therefore it is important to understand the ecological roles that juvenile fishes, as well as adults, play in the complex trophic relationships of coral reef systems and to determine if the available information on functional traits is sufficient to identify changes in their function by life stages.

As part of a large effort to understand the complex roles that fish species have in coral reef areas we identified the trophic structure in fish communities of the U.S. Caribbean through the description of trophic roles of fish species by life stages. We also conducted an analysis of quality on compiled information for each species based on location, time of publication, and sample size of the studies reviewed. Information generated by this study can be also useful in studies of functional diversity in coral reef areas through the Caribbean region.

2.3. Metadata

2.3.1. Class I. Data set descriptors

A. Data set identity: Information gaps in the trophic roles of Caribbean reef fishes
B. Data set identification code: fish_traits_adults.csv, fish_traits_juveniles.csv, information_gaps_adults.csv, information_gaps_juveniles.csv, references.csv.
C. Data set description
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Abstract: Understanding the ecological roles that fishes play in the complex trophic relationships of coral reef systems depends on our knowledge of fish trophic ecology

and our ability to detect changes in community composition and function. To better understand trophic structure in fish communities, we conducted an extensive literature review of trophic functional traits of 274 marine fish species in the U.S. Caribbean. In this database we register the presence of the following fish traits for juvenile and adult fish stages separately: water column feeding position, social feeding behavior, time of feeding, habitat use for feeding, trophic levels, and diet breadth. We also present the quality of trait information for each species based on a gap analysis that considered location of studies, date of publication, and sample sizes.

D. Key words: Caribbean; 2001-2012; trophic roles; reef fishes; ontogenetic changes; functional traits.

2.3.2. Class II. Research origin descriptors

2.3.2.1. Overall project description

Identity: Information gaps in the trophic roles of Caribbean reef fishes

Originator: Same names and addresses as above.

Period of study: 2001-2012

Objective: The aims of this study were to identify the trophic structure in fish communities of the U.S. Caribbean through the description of trophic roles of 274 fish species by life stages, and to conduct an analysis of quality on compiled information for each species based on location, time of publication, and sample size of the studies reviewed.

Abstract: Same as above.

Sources of funding: This study was supported by the fellowship for doctoral studies abroad of the Colombian Department for Science and Technology COLCIENCIAS, and the International Cultural Service Program scholarship from Oregon State University.

2.3.2.2. Specific subproject description

2.3.2.2.1. Site description

This study utilized data on fish communities from databases covering marine
protected areas (MPAs) and non-protected areas located at the southwest and
southeast of Puerto Rico, and the U.S. Virgin Islands (USVI) (Table 1). Habitat
composition of the studied sites included coral reef and colonized hard seafloor,
with secondary cover including seagrasses, emergent vegetation (mangroves),
macroalgae, and uncolonized seafloor such as reef rubble and bedrock. The
existence of a variety of habitats assured the representation of the fish community
and major habitat types used during fish ontogenetic shifts.

2.3.2.2.2. Research methods

Characterization of fish communities. Fish communities were surveyed by the
Caribbean Coral Reef Ecosystem Assessment and Monitoring Project coordinated by
the Biogeography Branch of the National Oceanic and Atmospheric Administration in
Puerto Rico, and the U.S. Virgin Islands from 2001 to 2012 (NOAA et al. 2007a,b,c).
A total of 6102 survey sites included habitats within and outside MPAs (Table 1).
Location of surveys were established by a random stratified sample design by habitat
type using a benthic habitat map, and conducted by following a standardized 15
minute underwater visual census along a 100 m^2 belt transect using SCUBA (25 m
long and 4 m wide). Information gathered during census included identification of
fish species, an estimation of the fork length at 5 cm classes up to 35 cm and an
estimate of the actual fork length for individuals larger than 35 cm, and species
abundance. Length was used to calculate fish biomass using length-weight
relationships (NOAA et al. 2007a,b,c).

Compilation of fish functional traits for the U.S. Caribbean. Fish traits related to
the resource use function, and most accurately describe the trophic function of marine

fish species in the U.S. Caribbean were populated in the database of 274 fish species recorded during fish surveys in all MPAs (Table 2). We selected traits based on ontogenetic diet shifts that fish species exhibit by migrating to different habitats, diet plasticity, trophic location in the food web, and habitat use (Stuart-Smith et al. 2013, Oliveira et al. 2012, Micheli et al. 2014). We extracted traits for juvenile and adult fish stages separately from a literature review of 200 publications that included peer-reviewed papers, Masters and Ph.D. theses, conference proceedings, book chapters, and fisheries agency reports from Puerto Rico and the U.S. Virgin Islands as main sources of information, and information from other Caribbean islands and the mainland Caribbean Region as second and third sources of information. The literature review included information from 1941 to 2015 published in English and Spanish. The trophic level was calculated for each species by using the TropLab software (Pauly et al. 2000) based on information about diet content analysis. Trait information for juveniles was extracted from (1) publications focused on juveniles' stages, and (2) those that included sizes smaller than one third of the maximum species length following the criteria for determining juveniles used by Dorenbosh et al. (2004, 2007) and Nagelkerken and van der Velde (2002). Information for adults was extracted from: (1) publications that included sizes higher than one third of the maximum species length; and (2) publications with data on the following stages: adults, subadults, collapsed (adults and juveniles together), and life stages not specified. Maximum lengths of species were extracted from fishbase.org (Froese and Pauly 2012). Presence of functional traits was recorded for water column feeding position, social feeding behavior, feeding time, and feeding grounds. Proportions of food items ingested by fish species were calculated or their presence was described based on information of diet composition (Table 3).

Table 1. Fish survey sites conducted by NOAA in Puerto Rico and the U.S. Virgin Islands, U.S. Caribbean.

Island	MPA	Years of survey	Surveys		Fish Species	Benthic habitats included in the surveys				
			Inside MPA	Outside MPA		Colonized hardbottom	Mangroves	Macroalgae	Seagrass	Uncolonized hardbottom
Puerto Rico	Guanica NR	2010-2012	26	287*	141	Yes	Yes	Yes	Yes	Yes
	La Parguera NR	2000-2012	1590		259	Yes	Yes	Yes	Yes	Yes
	Jobos Bay NR	2009	5	40	112	Yes	Yes	Yes	Yes	Yes
	Bahias Bioluminiscentes de Vieques NR	2007	4	71	110	Yes				Yes
USVI St. Croix	Buck Island Reef National Monument	2003-2012	1235	No	215	Yes	Yes	Yes	Yes	Yes
	St. Croix East End Marine Park	2003-2012	984	169	213	Yes	Yes	Yes	Yes	Yes
USVI St. John	Coral Bay APC	2003-2011	456	212*	180	Yes	Yes	Yes	Yes	Yes
	Virgin Islands National Park	2001-2011	445		244	Yes	Yes	Yes	Yes	Yes
	Virgin Islands Coral Reef National Monument	2001-2011	498		244	Yes	Yes	Yes	Yes	Yes

Table 1 (Continued). Fish survey sites conducted by NOAA in Puerto Rico and the U.S. Virgin Islands, U.S. Caribbean.

Island	MPA	Years of survey	Inside MPA	Outside MPA	Fish Species	Colonized hardbottom	Mangroves	Macroalgae	Seagrass	Uncolonized hardbottom
			Surveys			**Benthic habitats included in the surveys**				
USVI St. Thomas	St. James MRWS	2012	49	6	148	Yes	Yes	Yes	Yes	Yes
	Cas Cay–Mangrove Lagoon MRWS	2012	25	No	148	Yes	Yes	Yes	Yes	Yes

Notes: Marine Protected Areas (MPA) include Natural Reserves (NR), Reef National Monuments (RNM), Areas of Particular Concern (APC), National Parks (NP), and Marine Reserves and Wildlife Sanctuaries (MRWS). * denotes surveys shared by more than one MPA: Coral Bay, U.S. Virgin Islands National Park, and U.S. Virgin Islands RNM shared 212 surveys around St. John. Guanica and La Parguera Natural Reserves shared 287 surveys located between MPAs' boundaries. Benthic cover classes were established according to Kendall et al. (2001) classification.

Table 2. Functional traits used to study fish functional diversity.

Functional traits	Rationale	Traits
Water column feeding position (WCFP)	Location of feeding in the water column (Stuart-Smith et al. 2013)	Benthic (BEN; sitting on bottom), demersal (DEM; just over the bottom), midwater (MID; between surface and the bottom), and surface (SUR).
Social feeding behavior (SFB)	Intra and interspecific social interactions while feeding, such as predator avoidance strategies or reduction of energetic costs while searching for preys.	Species feeding in interspecific aggregations (AGR), as solitary individuals (SOL), in pairs (PAIR), or in mixed groups with other species (MIX)
Feeding time (FT)	Time of feeding and daily turnover of consumers within the fish community	Nocturnal (NOC), diurnal (DIU), crepuscular (CRE)
Feeding ground (FG)	Substrata used as feeding ground (Stuart-Smith et al. 2013). Note that open water are ocean surface habitats.	Substrates: coral reefs (COR), rocky reefs (ROC), sea grasses (SEA), algae beds (ALG), mangroves (MAN), sand (SAN), coral rubble (RUB), open water (OPE; ocean surface habitats), water column (COL: water column of any listed benthic bottom as feeding area), out of shelf (SHE; oceanic edge of the bank/shelf, where depth increases rapidly), surface (SURF: surface water of inshore habitats), and attached to other vertebrates (VER)
Trophic level (TL)	Trophic position in the community (Stuart-Smith et al. 2013, Oliveira et al. 2012). The trophic level is related to body size, and therefore can show ontogenetic shifts in diet by species within the fish community (Stuart-Smith et al. 2013, Micheli et al. 2014). Trophic level of each fish species was calculated by using the TropLab software (Pauly et al. 2000) based on diet content data.	Trophic levels go from 2.0 for herbivores up to 4.5 for piscivores
Diet breadth (DB)	The number of broad taxonomic groups consumed by a fish species. This trait described diet plasticity and trophic niche amplitude (Oliveira et al. 2012)	Prey taxonomic groups include: nekton (NEK), zooplankton (ZP), zoobenthos (ZB), detritus (DET), plants (PLA), sand (SAND), organic matter (OM), ectoparasites (ECT), and unidentified animal material (UAM).

Table 3. Definition of variables for functional traits of adult and juvenile fish stages.

Column header	Variable definition	Units	Data storage
Family	Taxonomic family name	N/A	Character
Species	Scientific species name	N/A	Character
Water column feeding position			
BEN	Benthic	Presence	Numerical
DEM	Demersal	Presence	Numerical
MID	Midwater	Presence	Numerical
SUR	Surface	Presence	Numerical
Social feeding behavior			
AGR	Aggregation	Presence	Numerical
SOL	Solitary	Presence	Numerical
PAIR	Pairs	Presence	Numerical
MIX	Mixed	Presence	Numerical
Feeding time			
NOC	Nocturnal	Presence	Numerical
DIU	Diurnal	Presence	Numerical
CRE	Crepuscular	Presence	Numerical
Feeding ground			
COR	Coral reefs	Presence	Numerical
ROC	Rocky reefs	Presence	Numerical
SEA	Seagrasses	Presence	Numerical
ALG	Algae beds	Presence	Numerical
MAN	Mangroves	Presence	Numerical
SAN	Sand	Presence	Numerical
RUB	Coral Rubble	Presence	Numerical
OPE	Open water	Presence	Numerical
COL	Water column	Presence	Numerical
SHE	Out of shelf	Presence	Numerical
SURF	Surface	Presence	Numerical
VER	Attached other vertebrates	Presence	Numerical
TL	Trophic level	Decimal number	Numerical

Table 3 (Continued). Definition of variables for functional traits of adult and juvenile fish stages

Column header	Variable definition	Units	Data storage
DB	Diet breadth	Integer	Numerical
NEK	Nekton	Integer or presence	Numerical
ZP	Zooplankton	Integer or presence	Numerical
ZB	Zoobenthos	Integer or presence	Numerical
DET	Detritus	Integer or presence	Numerical
PLA	Plants	Integer or presence	Numerical
SAND	Sand	Integer or presence	Numerical
OM	Organic matter	Integer or presence	Numerical
ECT	Ectoparasites	Integer or presence	Numerical
UAM	Unidentified animal material	Integer or presence	Numerical
INS	Insects	Integer or presence	Numerical
References	Publication code	Integer	Numerical

Notes: Presence of traits was recorded as 1. A semicolon [;] between values of trophic level, diet breadth, and references means that traits were calculated from two different publications. Asterisks [*] means that trait information was based on diet content analysis and notes about feeding behavior of fish species.

Quality analysis for trait information. We analyzed quality of trait information by using three qualitative criteria based on the location of study sites, time of publication, and sample size (Table 4). The last criterion was only applied to traits derived from diet content analysis of fish species. All criteria were used to classify species as having good, intermediate, and poor quality information, or no information by using equal intervals on the maximum score of information quality found for the total pool of species (Table 5 and 6). Species with good standing had scores equal to and above 29 (with a maximum of 42). This information class was characterized by species with up-to-date information on traits (between 2000 – 2015) for Puerto Rico and the U.S. Virgin Islands, and a relatively large sample size for diet content analysis (>10 samples). Species with intermediate quality of information had scores between 15 and 28, and species with poor quality had scores below 14. Species classified as having intermediate and poor quality trait information included fish species with trait information extracted from studies conducted in the three main general locations, with time of publication from 1979 to 2015, and

sample sizes for diet content analysis that included from feeding observations up to more than 10 diet content samples. Species with a score of zero were those for which trait data was not available.

Table 4. Criteria used for quality analysis of functional traits

| | Score | | | Criteria for each functional trait | |
Criteria	3	2	1	WCFP, SFB, FT, FG	TL, DB
Location	Puerto Rico and U.S. Virgin Islands	Other Caribbean Islands	Mainland Caribbean Region	x	x
Time of publication	2000 - 2015	1980 - 1999	1950 -1979	x	x
Sample size (# samples)	> 10	3 - 10	< 3 or observation		x
Maximum score per trait				6	9

Table 5. Quality analysis of information about functional traits for fish species in adult stages

| | | Number of species within the score | |
Quality of information	Score by species	Adult	Juvenile
No information	0	1	170
Poor	1-14	46	36
Intermediate	15-28	152	53
Good	29-42	75	15
Total species		274	274

Table 6. Variable definition for information gaps of adult and juvenile fish stages

Column header	Variable definition	Units	Data storage
Family	Taxonomic family name	N/A	Character
Species	Scientific species name	N/A	Character
Stage	Life stage of fish species: adult (A) or juvenile (J)	N/A	Character
WCFP	Water column feeding position	N = No information available	Character
SFB	Social feeding behavior		
TF	Time of feeding	P = Poor information	
FG	Feeding grounds	I = Intermediate information	
TL	Trophic level		
DB	Diet breadth	G = Good information	
SIQ	Species information quality		

Use of the data in previous publications. Data on diet content of fish species was recorded from published papers reviewed in this study, with the exception of unpublished data referred to Clark et al. (2009) which was provided by the authors directly. Clark et al. (2009) collected stomach content information on 688 fishes in Puerto Rico to quantify nutrient flow and trophodynamics based on cross-habitat movements of 71 species. We used the stomach content database as described by Clark et al. (2009) to characterize diet breadth and trophic levels of fish species in juvenile and adult stages.

Project personnel: This study is part of the doctoral dissertation of Martha Patricia Rincon Diaz. She conducted the literature review, data compilation, verification, analysis, and coding. Simon J. Pittman provided data and academic guidance; and Selina S. Heppell provided guidance on data analysis.

2.3.3. Class III. Data set status and accessibility

A. Status

    Latest update: January 2017

    Latest Archive date: January 2017

    Metadata status: January 2017, complete.

    Data verification: All data has been at minimum double-checked.

B. Accessibility

Storage location and medium: Original data is held by MPRD.

Contact person: Martha Patricia Rincon-Diaz, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331 (patricia.rincon-diaz@oregonstate.edu; princon7@gmail.com)

Copyright and proprietary restrictions: None. Please, contact the main author for the use of the data. Use the data only for non-commercial purposes, and cite this chapter when using this data in presenting and publishing works.

Costs: None.

Citation: Rincón-Díaz M.P., Pittman S.J., Heppell S.S. 2018. Chapter 2: Information gaps in trophic functional traits of Caribbean reef fishes. Doctoral dissertation. Department of Fisheries and Wildlife, Oregon State University.

2.3.4. Class IV. Data structural descriptors

A. Data set file: Data files can be downloaded as a single archive associated to this chapter of the dissertation, Chapter 1_FishFunctionalTraits.zip (37 KB).

(1) Functional traits for fish adult stages
Identity: fish_traits_adults.csv.
Size: 31 KB, 275 rows and 44 columns.
Format and storage mode: CSV text, comma delimited.
Content: Each row represents a single species, and columns show trait presence and references that support trait information. References for each set of functional traits are represented by numbers, and can be found in references.csv.
(2) Functional traits for fish juvenile stages
Identity: fish_traits_juveniles.csv.
Size: 23 KB, 275 rows and 44 columns.
Format and storage mode: CSV text, comma delimited.

Content: Each row represents a single species, and columns show trait presence and references that support trait information. References for each set of functional traits are represented by numbers, and can be found in references.csv.

(3) Information gaps for adults

Identity: information_gaps_adults.csv.

Size: 15 KB, 275 rows and 10 columns.

Format and storage mode: CSV text, comma delimited.

Content: Each row represents a single species, and columns show quality of trait information for adult stages of each species.

(4) Information gaps for juveniles

Identity: information_gaps_juveniles.csv.

Size: 17 KB, 275 rows and 10 columns.

Format and storage mode: CSV text, comma delimited.

Content: Each row represents a single species, and columns show quality of trait information for juvenile stages of each species.

(5) References for trait information

Identity: references.csv.

Size: 40 KB, 201 rows and 2 columns.

Format and storage mode: CSV text, comma delimited.

Content: References for trait information were coded with a corresponding number in column A. Complete citation can be found in column B.

1. Variable definition: please see Tables 5, 6, and 7 for specific details.

Table 7. Variable definition for references of trait information

Column name	Variable definition	Units	Data storage
Code	Publication code	Integer	Numerical
Reference	Citation for publications	N/A	Character

2.4. Acknowledgments

Chapter 3: Functional diversity metrics show spatial and temporal changes in fish
communities in a Caribbean marine protected area

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3.1. Abstract

Functional diversity (FD) metrics quantify the trait diversity in biological assemblages
and act as a proxy for the diverse ecological functions performed in the community.
Analyses of FD offers a potentially useful tool to identify functional changes in diverse,
complex, and disturbed marine ecosystems such as coral reefs, yet this metric is rarely
applied to evaluate community change. Here, we document spatio-temporal variability in
the trophic function of fish assemblages to identify changes in coral reef communities
inside the Buck Island Reef National Monument (BIRNM) in the U.S. Virgin Islands
between 2002 and 2010, which include an intense coral bleaching event in 2005. We
combined 6 traits related to the trophic function of 95 fish species together with species
biomass estimated from underwater surveys to calculate assemblage-level descriptors of
functional richness, dispersion, and evenness. We tested the effects of habitat type, time,
and their interaction on fish FD using a non-parametric permutational multivariate
analysis of variance. We found statistically significant differences for functional richness
and dispersion, suggesting that changes in trophic trait composition and abundance vary
by habitat and time. Coral reef and other hard bottom areas supported high levels of

trophic functional richness and variation among habitat types, but with low functional redundancy evidenced by the unique trophic role that each fish species had within the functional trait space. These results suggest that a significant decline in fish diversity in the BIRNM would likely result in loss of trophic functions from the community. Important temporal variations in functional trait composition during the last decade in the BIRNM, including change following the strong coral bleaching event in 2005, suggest that functional diversity descriptors are sensitive enough to track shifts in the trophic organization of fish communities. In addition, we show a new way to monitor resilience by plotting the centroid of the functional trait space formed by fish communities through time. Collectively, our findings demonstrate the utility of functional diversity descriptors to evaluate changes to the functional integrity of diverse and spatially heterogeneous habitats across the seascape.

Key words: Functional diversity; fish assemblages; trophic traits; resilience; Caribbean reefs; spatio-temporal variation.

3.2. Introduction

Understanding the spatial and temporal patterns and processes that influence the functional organization of species assemblages is an essential step for understanding ecosystem structure and function (Oliveira et al. 2012). Traditional descriptors of spatio-temporal changes in species diversity, including species richness, and trophic group richness and biomass (Gotelly and Colwell 2001, Colwell 2009, Maurer 2009, Vallès and Oxenford 2015, Loiseau and Gaertner 2015), are often insensitive to interspecific variability in species traits because they either ignore species-specific functional roles completely or clump species within guilds or trophic groups without sufficient knowledge of trait differences (Villéger et al. 2010, Micheli et al. 2014, Mouillot et al. 2013b, Boersma et al. 2014, 2016, Dee et al. 2016). Diversity in the ecological roles of species in complex trophic relationships may be a more important indicator of change for

monitoring programs to track than simple number of species when implementing an ecosystem-based management approach (Cadotte et al. 2011).

Functional diversity metrics have emerged as alternative descriptors of spatio-temporal patterns in community organization that respond to changes in environmental gradients (Villéger et al. 2010, Boersma et al. 2014, Piacenza et al. 2015, Dee et al. 2016). Based on species abundance and their functional traits, these descriptors provide a way to characterize the niche space used by each species. A functional trait is a measurable feature that describes the ecosystem role of an individual or species, and can be morphological, behavioral, and physiological (Cadotte et al. 2011, Diaz and Cabido 2001, Petchey and Gaston 2006). These traits are highly related to environmental tolerance of organisms, which in turn shapes community composition and organization (Boersma et al. 2014, Piacenza et al. 2015, Dee et al. 2016, Silva-Júnior et al. 2016), allowing us to understand changes in the ecosystem function of biotic communities and their resilience to perturbations.

For assemblages of organisms, descriptors of trait diversity allow for the inclusion of rare species commonly excluded from community analysis and which can perform unique functional roles (Jain et al. 2014, Mouillot et al. 2013a, Leitao et al. 2016). Trait diversity descriptors are sensitive tools to capture interspecific variability in functional roles of species because they capture the variability and redundancy in species traits (Villéger et al. 2010, Micheli et al. 2014, Mouillot et al. 2013b, Boersma et al. 2014, 2016, Dee et al. 2016). Trait redundancy, a measure of overlap in ecological function, can be used to estimate how biodiversity loss can influence ecosystem function and services provided by biotic communities (Peterson et al. 1998, Elmqvist et al. 2003, Folke et al. 2004, Cadotte et al. 2011). For instance, high functional redundancy implies high ecosystem resilience i.e., the degree of self-organization of a system to resist departures from steady states following disturbances (Holling 1973, 1996, Folke et al. 2004). In terrestrial systems, it has been found that high functional redundancy of drought resistance and trophic traits in invertebrate communities buffer against functional changes in their arid-land streams communities even during habitat contraction and fragmentation induced by severe drying (Boersma et al. 2014). In contrast, studies indicate that

nearshore marine ecosystems, including high diversity coral reef fish communities, have relatively low functional redundancy (Bellwood et al. 2003, Micheli and Halpern 2005, Mouillot et al. 2014). In application, functional diversity descriptors are considered to be simple, logical and repeatable metrics that can be comparable across multiple spatial scales (Carmona et al. 2016) to evaluate performance of functional organization of communities and ecosystems.

Measures of functional diversity offer great potential as an effective tool to monitor and evaluate shifts in the trophic function of fishes and to predict subsequent changes in ecosystem function. However, these metrics need further evaluation to determine if they are ecologically meaningful in complex, high diversity systems such as coral reef ecosystems. In Caribbean coral reefs, a low functional redundancy in the trophic role of fish assemblages suggests that small decreases in species richness could lead to loss of ecosystem functions and fish biomass production (Halpern and Floeter 2008, Micheli et al. 2014, Mouillot et al. 2014). Functional redundancy in the trophic function of reef fish communities should be highly influenced by species composition, but also by the specific life stages that affect their ontogenetic shifts in diets (Nakazawa 2015), habitat use, and migrations (Helfman et al. 2009, White 2015). Yet, there is a paucity of published information on the functional traits of reef fishes, especially of juvenile life stages, which may have a different ecological role in the community (Rincon-Diaz et al., public communication).

The use of descriptors of functional diversity and redundancy has great potential to evaluate the resilience of communities to perturbations and management interventions such as marine reserves where extractive activities are prohibited. Monitoring and measuring the status and trends in the functional diversity of coral reef fish communities is central to ecosystem-based management because functional diversity is linked to ecosystem-level functions and the provisioning of economically important ecosystem services attributed to coral reefs (Micheli et al. 2014). These metrics are useful to evaluate the resilience of coral reefs following trophic cascades caused by disturbances, such as: overfishing of high trophic guilds (sharks, groupers, or snappers) (Heaithus et al. 2008, Ruttenberg et al. 2011, Tyler et al. 2011, Valdivia et al. 2017), the effects of

changes in species presence and richness in trophic groups (Mumby et al. 2012, Estes et al. 2011, Bremner 2008, Nyström 2006), and the availability of food for fish species of commercial importance and human consumption (Smith et al. 2011, Dee et al. 2016). But to be a useful metric for monitoring systems, functional redundancy must be measurable and sensitive enough to detect change across the seascape and time scales to understand resilience of systems.

Here, we compile functional and behavioral traits related to the trophic function of fish species in Buck Island Reef National Monument (BIRNM) in the U.S. Caribbean to evaluate spatial and temporal changes in functional richness (FRic), functional dispersion (FDis), and functional evenness (FEve) of fish assemblages (Fig. 3). These descriptors were selected because they provide insights about different aspects of functional diversity within the community and can incorporate multiple categorical and numerical traits in multidimensional trait space (Villéger et al. 2008, Schleuter et al. 2010, Laliberté and Legendre 2010, Laliberté et al. 2015). We test the hypothesis that variation in fish functional diversity metrics is a function of habitat type and time, owing to changes in fish species and trait composition through time and differences in habitat structure, and shifts in life stage-and habitat-prey preferences. In addition, we test the hypothesis that each functional trait contributes differently to the variability of fish functional diversity descriptors. Our study provides information about functional traits for 95 marine fish species known to occur in the BIRNM, which represents an important contribution to knowledge on the trophic function of fish species in the Caribbean. We validate descriptors of functional diversity as important tools to be implemented in monitoring programs of marine biotic communities, and provide a visual tool to understand temporal changes in their functional organization to identify levels of ecosystem resilience.

Fish traits:

- Trophic level
- Diet breadth
- Social feeding behavior
- Feeding ground
- Time of feeding
- Water column feeding position

dimensionality reduction →

FRic   FDis   FEve

● Fish species   ○ Centroid of trait space

Modified from Villeger et al. (2008) and Liberte and Legendre (2010)

Figure 3. Functional diversity metrics used in the study. Fish functional traits are assigned to each fish species within a community, and are reduced in dimensionality to locate species in a two-dimensional trait space. Abundances of fish species are represented by sizes of black circles in the trait space. (A) Functional richness (FRic) measures how much of the niche space is occupied by species present in a community by estimating the convex hull volume occupied by species in the trait space (Schleuter et al. 2010, Stuart-Smith et al. 2013, Villéger et al. 2008). Species touched by the convex hull possess extreme values of functional traits. Functional richness covariates with species richness (Schleuter et al. 2010). (B) Functional dispersion (FDis) measures trait dispersion in a community by averaging species distances (D) to the centroid in the trait space (Laliberté et al. 2015, Laliberté and Legendre 2010). The location of the centroid is weighted by the species relative abundances (Laliberté and Legendre 2010). Functional dispersion gives insight about trait redundancy in the community. High values of functional dispersion indicate low trait redundancy due to a high variability of functional traits, suggesting that the ecosystem function performed by one species is exclusive within the community. In contrast, high functional redundancy in species functions suggests that more than one species is providing a specific ecosystem function (Peterson et al. 1998, Elmqvist et al 2003), and thus there is a high resilience of the system (Holling 1973, 1996, Folke et al. 2004). (C) Functional evenness (FEve) measures the abundance distribution of species in the niche space to effectively use the entire range of available resources (Mason et al. 2005, Mouillot et al. 2013b). Low values of functional evenness suggest that there are niche spaces under-utilized, which decrease productivity and increase probabilities for invasions (Mason et al. 2005).

3.3. Methods

3.3.1. Study site

We focused our functional diversity study on an extensive set of fish community data collected by NOAA's Coral Reef Ecosystem Monitoring and Assessment project (2002 to 2012) in shallow areas (< 30 m) inside the marine protected area of Buck Island Reef

National Monument (BIRNM) located in northeast St. Croix, U.S. Virgin Islands (USVI)
(Fig. 4). BIRNM encompasses 7695 hectares of land and marine areas, and is managed
by the U.S. National Park Service (NPS) (Pittman et al. 2008). Habitat composition of the
studied sites included coral reef and colonized hard bottoms, seagrasses, macroalgae, and
unconsolidated sediments (Kendall et al. 2001, Costa et al., 2012). This National
Monument is a permanent No-Take/No-Anchoring Zone established in 1961, and was
expanded in 2001 to protect coral reef building species such as Elkhorn coral (*Acropora
palmata)* (Rothenberger et al. 2008). In spite of the high level of protection, coral reef
communities in the BIRNM did not escaped from several natural disturbances that
reduced health of coral reefs during evaluated years of this study. A mass coral bleaching
in 2005 and subsequent disease outbreak in 2006 decreased 53% of reef-building species
in this MPA (Rogers et al. 2009). In 2008, Hurricane Omar and an extreme swell event
caused structural damages in coral reefs; and in the same year the ecological invasion of
the Indo-Pacific lionfish was recorded for the U.S. Virgin Islands (Pittman et al. 2014).
Finally, in 2010, Hurricane Earl produced high levels of sedimentation in coral reefs due
to its strong rains (Pittman et al. 2014). Providing park managers with scientifically
validated evidence of reserve performance and condition is not only essential to
informing resource management strategies, it is critical to building public support for
management plans. The analyses here address NPS strategic goals by providing new
information on the condition of the monuments marine resources.

Figure 4. Survey sites inside the Buck Island Reef National Monument.

3.3.2. Spatio-temporal characterization of fish abundance and size

Community species composition, abundance and size of fish species by habitat type were characterized in 835 survey sites by the Coral Reef Ecosystem Monitoring and Assessment project led by the Biogeography Branch of the National Oceanic and Atmospheric Administration (NOAA) within the BIRNM from 2002 to 2010 (NOAA et al. 2007; http://www8.nos.noaa.gov/bpdmWeb/queryMain.aspx). Surveys were conducted during winter and spring (January-April) and fall (August-November) each year to account for seasonal variation (Table A1). Survey locations were selected with a random-stratified sample design, whereby spatially random survey start points where allocated to hard and soft bottom strata on the NOAA benthic habitat map (Kendall et al. 2001) using a Geographical Information System. Trained scientific divers surveyed fish assemblages along a standardized 25 m long and 4 m wide (100 m2) belt transect during a 15 minute swim at constant speed. Survey locations were not repeated during 10 years of fish characterizations, providing statistical independence within each survey site.

Information gathered in each census included the identification of fish species, number of individuals, and an estimation of the fork length at 5 cm size class bins up to 35 cm to calculate fish biomass by life stages (Pittman et al. 2008). Surveys of unconsolidated sediments were omitted from our analysis because of low sample size during the surveyed years.

3.3.3. Compilation of fish functional trait

Traits related to the trophic function of 166 marine fish species, recorded by NOAA in the BIRNM were extracted from a database created from an extensive literature review of studies conducted in Puerto Rico and the U.S. Virgin Islands (Table 8). Where information was inadequate in the U.S. Caribbean, information from elsewhere in the Caribbean Sea was used as a secondary source of information (Rincon-Diaz et al. public communication). Traits were selected to include knowledge of ontogenetic diet shifts through the life cycle that typically coincide with changes in movement patterns (e.g., relocations from seagrass to coral reefs), social foraging behavior, feeding time, trophic location in the food web, and diet plasticity (Stuart-Smith et al. 2013, Oliveira et al. 2012, Micheli et al. 2014, Rincon-Diaz et al. public communication). Habitat use traits included water column feeding position (Stuart-Smith et al. 2013) and feeding habitat, which describe the location in the water column and sea bottom type used as the feeding habitat, respectively. Feeding habitat is a previously unexamined trait for functional diversity analysis of marine fish communities. Other traits unique to this study include social foraging behavior, which describes species social strategies that minimize predation and energetic costs while feeding, and feeding time, which accounts for diurnal and nocturnal use of feeding habitats by reef fish species, and also describes temporal fish species turnover within the assemblages (Randall 1967, Collette and Talbot 1972). Diet breadth was also a novel trait included in this study; it describes diet plasticity by considering the number of taxonomic groups consumed by a fish species (Oliveira et al. 2012). Trophic level was included because it describes the trophic position of a species within a community (Micheli et al. 2014, Oliveira et al. 2012, Stuart-Smith et al. 2013). Trophic

level was calculated by using the TropLab software (Pauly et al. 2000) based on information from diet content analysis reported in studies conducted primarily in the U.S. Caribbean (Randall 1967, Birkeland and Neudecker 1981, Turingan 1995, White et al. 2006, Clark et al. 2009, Liedke et al. 2013).

Table 8. Functional traits used to calculate fish functional diversity.

Functional traits	Traits
Water column feeding position	Benthic (BEN), demersal (BEN), midwater (MID), surface (SUR)
Social feeding behavior	Species feeding as solitary individuals (SOL), in pairs (PAIR), in interspecific aggregations (AGR), or in mixed groups with other species (MIX)
Feeding time	Diurnal (DIU), crepuscular (CRE), nocturnal (NOC)
Feeding ground	Species feeding on the following substrates: coral reefs (COR), rocky reefs (ROC), sea grasses (SEA), algae beds (ALG), mangroves (MAN), sand (SAN), coral rubble (RUB), open water (OPE), water column (COL), out of shelf (SHE), and attached to other vertebrates (VER)
Trophic level (TL)	Trophic levels go from 2.0 for herbivores up to 4.5 for piscivores.
Diet breadth (DB)	Number of prey taxonomic groups included in diet: nekton, zooplankton, zoobenthos, detritus, plants, sand, organic matter, ectoparasites, unidentified animal material, and insects.

Traits were extracted for juvenile and adult fish stages separately. Fishes were considered to be juveniles when they were smaller than one third of the maximum recorded species length (Dorenbosh et al. 2004, 2007; Nagelkerken and van der Velde 2002). Juvenile stages were ultimately excluded from analysis because so little information was found for all species (<30% of listed species had three or more traits). Binomial presence/absence of functional traits was recorded for this study because differences in quantitative trait measurements were assumed to vary among studies. The trophic level and diet amplitude of fish species were standardized by their maximum and ranged from 0 to 1. Only species with complete information were included in functional diversity analyses after evaluating the methodological issues with available trait information (Appendix A: Supplementary Methods and Results). A total of 95 fish

species representing 57% of all recorded species in adult stages had complete trait information and therefore were included in the functional diversity analysis.

3.3.4. Functional diversity metrics

We calculated functional richness (FRic), dispersion (FDis), and evenness (FEve) for each fish survey site and year following the methods of Laliberté et al. (2015) (Fig. 3). We used all proposed fish functional traits because we identified no significant levels of association among traits using the Cramer's V index (Appendix A: Supplementary Methods and Results, Table A3). We used fish species trait information and abundances expressed as biomass according to values calculated by NOAA (NOAA et al. 2007) in each surveyed site as inputs to calculate functional diversity metrics. A Gower (1971) dissimilarity matrix was calculated based on trait values among fish species because the majority of traits were categorical (Villéger et al. 2008). The Gower matrix was then used to conduct a Principal Coordinates Analysis (PCoA) to identify principal axes that explained more than 50% of variation in the functional trait space and to calculate locations of fish species in the multidimensional trait space. We used the first and second axis of the PCoA to explain variation of the functional trait space for fish assemblages in the BIRNM. The Gower matrix and PCoA were calculated by using the PAST program Version 3.08 (Hammer 2015). A functional matrix based on principal axis and a biomass matrix for fish species was used to calculate functional diversity metrics per survey site using the FD software package in R (Laliberté et al. 2015). We evaluated sample size effects on temporal patterns of functional diversity, and combined data by years to simplify patterns of fish functional diversity (Appendix A: Supplementary Methods and Results, Table A2. Fig. A1).

We also calculated species richness per survey site with the FD package, and conducted Spearman Rank correlation analyses (rho) among fish diversity metrics to examine the influence of this traditional metric on descriptors of functional diversity. Correlation analysis was conducted with the PAST Program Version 3.08 (Hammer 2015).

3.3.5. Spatial and temporal variation of fish functional diversity

A non-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008) was used to test the hypothesis that functional diversity metrics vary by habitat type and year of survey, allowing for interactions among these two factors. Statistical differences were established with the PERMANOVA analysis by p-values < 0.05 (Mateos-Molina et al. 2014). Analyses were conducted using the PAST Program Version 3.08 (Hammer 2015).

3.3.6. Sensitivity of functional diversity metrics to chosen traits

We identified functional traits that explained variation in functional diversity by dropping each trait from the calculations of each functional metric, and then, by using linear regressions, we compared those values with values calculated with the full pool of traits (Stuart-Smith et al. 2013). We compared coefficients of determination (r^2) between indexes calculated with all traits and dropped traits to identify the real contribution of traits to explain variation in functional diversity metrics (Stuart-Smith et al. 2013). Low coefficients of determination (r^2) with statistical significance represented a large gap in information, and indicated traits that contributed more to variation in functional diversity (Stuart-Smith et al. 2013).

3.3.7. Temporal variation in functional organization of fish assemblages

Temporal changes in fish functional organization were evaluated by describing species functional trait gradients, calculating centroids of convex hulls, and identifying hot spots of functional redundancy in the trait space through time. We created the functional trait space and convex hulls by plotting the first two coordinate's axis of PCoA used to calculate functional diversity metrics (Laliberté et al. 2015) because they explained more than 50% in fish trait variation.

Centroids of convex hulls were plotted in the trait functional space as a proxy to visualize temporal changes in fish functional organization for the BIRNM. Centroids of convex hulls were calculated by following the concept of 'center of mass', understood as the weighted relative location where a body is in equilibrium because distributed mass sums to zero (Levi 2009). In our study, a centroid was the location in the trait space in which distances from all species locations, weighted by species annual biomass, were the same (Fig. 3). These centroids were used as indicators of temporal trajectories in the trophic function of fish assemblages, and a potential indicator response of the communities following disturbance.

Temporal hotspots of functional redundancy were identified by plotting Kernel density maps calculated from species locations in the functional trait space by years. Density maps were calculated in the PAST Program Version 3.08 (Hammer 2015) by using the Gaussian function and locating nearby species within a radius of 0.02 within the trait functional space. Hotspots were formed by species with similar, but not equal functional traits.

3.4. Results

3.4.1. Spatio-temporal patterns of fish functional diversity

We successfully compiled information on 25 traits in 6 major categories related to the trophic function of adult stages for 95 fish species for the BIRNM in St. Croix, U.S. Virgin Islands (USVI). We combined these data with species biomass to obtain three descriptors of functional diversity (richness [FRic], dispersion [FDis], and evenness [FEve]) to describe and map spatio-temporal changes in the trophic function of fish assemblages in the BIRNM between 2002 and 2010. Our findings supported the hypothesis that functional diversity descriptors varied over time and habitat, with interaction between them for functional dispersion and evenness values ($p > 0.05$) (Table 9). Coral and colonized hardbottom habitats supported highest functional richness and variation among fish assemblages, with traits more evenly distributed after 2006 in the

multidimensional trait space of fish assemblages (Fig. 5 and 6). When data for the different habitats were combined, the largest change in functional diversity was observed in 2006 (Fig. 5). FRic values for 2006 were significantly higher than values of 2005 and 2009 (Mann-Whitney test; p-value <0.05), FDis values for 2006 were higher than values of 2002 and 2004 (Mann-Whitney test; p <0.05), and FEve values for 2004 were lower than values of 2006 and 2008 (Mann-Whitney test; p <0.05). The significant changes in functional descriptors between 2006 with 2004 and 2005 suggest a strong reorganization in the trophic function of fish assemblages in the BIRNM among these years, and show the utility of functional diversity metrics to capture shifts in the ecosystem function of biological assemblages.

Table 9. PERMANOVA on values of functional richness (FRic), dispersion (FDis) and evenness (FEve) for Caribbean fish assemblages (2002-2010).

Source of variation	FRic		FDis		FEve	
	df	F	df	F	df	F
Surveyed years	8	1.569**	8	1.650***	8	1.218**
Habitat type	1	27.473***	1	18.481***	1	1.173
Time of survey x Habitat type	8	-38.859	8	-37.439**	8	-36.401**
Residual	665		665		665	
Total	682		682		682	

Notes: From the total of 835 sites we excluded 153 sites from functional diversity analysis due to their low species richness (< 2 species). Convex hull volume for FRic, nor the values of FDis and FEve can be calculated with less than 2 species per site (Laliberté et al. 2015). ** denotes $p < 0.01$ and *** $p < 0.001$.

Figure 5. Spatio-temporal variation in functional diversity metrics by habitat type and years. Abbreviations: functional richness (FRic), functional dispersion (FDis), functional evenness (FEve). Total species richness by years is presented as numbers below averages of FRic. Note that there is a decline in functional richness, but an increase in functional dispersion in 2005. ** denotes Mann-Whitney test, p-value < 0.01 vs. FRic and FDis values for 2006, and FEve values for 2004.

Figure 6. Spatial distribution of fish functional richness (FRic), dispersion (FDis), and evenness (FEve) values.

There was a significant positive correlation between species richness and functional richness (Fig. 7 a), as well as a low positive correlation between species richness and functional dispersion, functional richness and dispersion, and functional dispersion and evenness (Fig. 7b,d,f). We did not observe a temporal trend in the relationship between

species richness with functional dispersion and evenness (Fig. 5). Functional richness indicators generally followed species richness whereas dispersion and evenness indicators did not. There was a low correlation between functional evenness with species richness and functional dispersion, suggesting that evenness and richness metrics provide independent evaluation of functional diversity (Fig. 7c,e).

Figure 7. Spearman rank correlation analysis (rho) between metrics of fish diversity. (A) Species richness vs. functional richness (FRic). (B) Species richness vs. functional dispersion (FDis). (C) Functional richness vs. functional dispersion. (D) Functional richness (FRic) vs. functional dispersion (FDis). (E) Functional richness (FRic) vs. functional evenness. (F) Functional dispersion (FDis) vs. functional evenness * denotes p < 0.05.

3.4.2. Importance of traits to explain variation in functional diversity metrics

We found that species traits contributed differently to explain variability in fish functional diversity (Table 10). Traits that explain the majority of variance in functional

diversity metrics were identified by their lowest coefficient of determination (r2) obtained when those traits were dropped from calculation of functional metrics (Stuart-Smith et al. 2013). Two traits, diet breadth and trophic level, were the most important for predicting functional diversity metrics. Diet breadth explained the most variation in functional richness (49%) and evenness (87%), and species trophic level best explained functional dispersion in the trait space of fish communities (31.5%).

3.4.3. Temporal variation in functional organization of fish assemblages

Although the functional organization in the fish functional trait space was visually similar for most years, the centroids from convex hulls did not always overlap (Fig. 8A,B). This result indicated that there were shifts in the trophic organization of fish assemblages during evaluated years. Functional organization of fish assemblages showed similar distribution of gradients in functional traits among years (Fig 8A). Variation in the functional trait space was explained better by the first coordinate axis (38% to 44%), followed by the second axis that explained between 25% and 27% of trait variation for all years. Traits associated with the first axis were trophic level, water column feeding position, and feeding habitats. Traits associated with the second axis were diet breadth, social foraging behavior, and time of feeding. Centroids in the functional space had different locations, but were mainly concentrated on the right side of the trait space where species with low trophic levels and specialist diet (herbivore fishes) were located (Fig. 8B). The exceptions were for years 2008 and 2010 where centroids were pulled by species of higher trophic levels in comparison to previous years.

Table 10. Real contribution of functional traits to explain variation in functional diversity metrics for Caribbean reef fishes.

Removed trait from calculation of metrics	FRic		FDis		FEve	
	r^2	Real contribution	r^2	Real contribution	r^2	Real contribution
Diet breadth	0.514***	0.486	0.832***	0.168	0.129***	0.871
Trophic level	0.649***	0.351	0.685***	0.315	0.189***	0.811
Feeding habitat	0.788***	0.212	0.896***	0.104	0.518***	0.482
Social foraging behavior	0.796***	0.204	0.901***	0.099	0.537***	0.463
Water column feeding position	0.843***	0.157	0.899***	0.101	0.477***	0.523
Time of feeding	0.881***	0.119	0.905***	0.095	0.483***	0.517

Notes: Coefficients of determination (r^2) for functional diversity metrics were calculated from sets of functional traits with one trait removed from the pool of traits. Bold values indicate traits that contributed more to variability in functional diversity metrics. Real contribution of a trait to explain variation in functional diversity metrics was identified by subtracting the maximum contribution of trait (equals to 1) from observed r2 calculated without the trait in question (1-r2). *** denotes $p < 0.001$.

Figure 8. Temporal changes in the fish functional trait space based on Principal Coordinates Analysis. (A) Functional trait space for 2002 shows the functional organization of fish assemblages in the BIRNM. Gradients of functional traits are shown for each coordinate axes. Fish icons close to labeled dots represent species with extreme trait values that delineate boundaries of the functional trait space in the assemblage for 2002. Locations of other fish species in the trait space are represented by labeled dots. Centroid of the functional trait space for 2002 is shown as the X symbol. (B) Centroids by years of survey in the functional space show trajectories of the functional organization over time.

Fish communities of the BIRNM had low levels of functional redundancy that varied highly through time, as shown by the configuration of the functional trait space in Kernel density maps (Fig. 9). Kernel density maps showed that no more than one fish species occupied the same location within the trait space, indicating that each fish species had a unique trophic role within the fish community. Functional redundancy tended to vary through time as hotspots were reduced after 2005 in the functional trait space, and never return to initial states (Fig. 9). Configuration of functional redundancy was similar for the four initial years, with hotspots of redundancy concentrated on specialist fishes with high and intermediate trophic levels. In 2005, density of species with similar traits diminished drastically in the trait space suggesting a reduction in fish functional redundancy. In 2006 and 2008, five hot spots of functional redundancy were observed with a high concentration of species of high and intermediate trophic levels. In 2007 and 2009, redundancy was concentrated in specialist species with intermediate and low trophic levels. Lastly, in 2010, two hotspots of functional redundancy were located on specialist species with high and intermediate trophic levels. However, like the centroid shift shown in Figure 6, the system failed to return to the state shown in the first 4 years of surveys by 2010 (Fig. 9). For all years evaluated, size of empty regions in the trait space varied, suggesting that there is a change in species composition which results in a change in trait distribution within the trait space over time. The observed temporal changes in configuration of functional redundancy confirmed that functional organization of fish communities was highly dynamic.

Figure 9. Temporal variation of functional redundancy in fish assemblages of the BIRNM. Plots maps show boundaries of the trait space, species location in the trait space as dots, hotspots of species with similar trophic function as reddish regions, and mean values of functional diversity descriptors in the upper side of the trait space. The scale bar gives an estimate of the number of species per area based on species distances within a radius of 0.02 within the trait functional space.

3.5. Discussion

3.5.1. Importance of functional diversity metrics to monitor reef fish assemblages

We have evaluated functional diversity metrics as ecological tools to map spatio-temporal changes in the trophic function of marine fish communities over time around Buck Island, in the U.S. Caribbean. Our results show that functional diversity metrics are sensitive enough to capture habitat effects and changes through time in fish functional diversity of tropical marine systems, supporting the use of functional richness, dispersion and evenness as ecological tools to monitor spatio-temporal trajectories of ecosystem function and resilience. Our results encourage the use of these metrics to identify sites that support high levels of functional diversity, as well as those with high functional redundancy that are likely to affect ecosystem resilience.

We postulate that functional diversity metrics can be used with traditional biodiversity metrics (Stuart-Smith et al. 2013), such as species richness, to monitor changes in the functional organization and resilience of natural assemblages. Functional diversity provides a deeper picture of ecological organization than species richness alone. For example, we found that after 2005, levels of trait redundancy in coral reef fish assemblages never return to initial states shown during the first four years of surveys. Likewise, we found low levels of trophic functional redundancy (high functional dispersion) in fish assemblages that had high species and functional richness in the BIRNM. This finding suggests that only a small number of fish species inhabiting coral reefs and hard bottoms share a similar trophic niche within the fish community. This weak relationship between functional richness and functional dispersion is also documented in studies that use functional variation metrics weighted by fish species abundance at global scales (Stuart-Smith et al. 2013), and support previous evidence of narrow functional redundancy in the trophic organization of fishes in other tropical coral reefs in the Caribbean and the Indo-Pacific (Mora et al. 2016). Fish trophic groups in coral reefs in the Bahamas (Micheli et al. 2014) and in high biodiversity areas of the Indo-Pacific (Bellwood et al. 2003, D'agata et al. 2016, Mouillot et al. 2014) also

exhibited low functional redundancy, with the majority of functional groups formed by one or two fish species, which represents a threat to multiple functional traits that would likely be lost under declines in species richness (Micheli et al. 2014). Although the study in Bahamas used a different methodology to characterize functional richness and redundancy than did our analysis, both studies showed that Caribbean coral reefs are highly vulnerable to the loss of trophic roles in diverse fish assemblages. This low overlap in functional roles means that coral reef systems experiencing harvesting of fish will have low capacity to replace the loss of key ecosystem functions resulting in greater fragility to stressors. Global studies on functional redundancy in coral reefs by Mouillot et al. (2014) conclude that "the promised benefits of functional insurance from high species diversity may not be as strong as we once hoped".

3.5.2. Habitat effects on fish functional diversity

We hypothesize that the high structural complexity and high diversity of trophic niches provided by coral reefs and similar hard bottom substrata drives the strong effect of habitat on levels of fish functional richness and dispersion observed in our analysis across the seascape. Recognition of the ecological importance of topographic complexity (e.g. rugosity), to coral reef fishes is not new (Luckhurst and Luckhurst 1978, Gladfelter et al. 1980, Gratwicke and Speight 2005, Graham and Nash 2013), but is now increasingly demonstrated at a range of spatial scales relevant to the movement neighborhoods of fishes using three-dimensional models of the seafloor (Pittman et al. 2007, Wedding et al. 2008, Pittman et al. 2009, Agudo-Adriani et al. 2016). For example, high resolution maps of the seafloor have linked high topographic complexity coral reefs in the U.S. Virgin Islands and Puerto Rico to fish diversity hotspots (Pittman et al. 2007, Pittman et al. 2009, Pittman and Brown 2011, Sekund and Pittman 2017). Thus, coral reefs with high structural heterogeneity supports a rich variety of physical habitats and niches occupied by diverse fish species and functional groups (Pittman et al. 2007, 2009, Pittman and Brown 2011), and include prey refuges (Hixon and Beets 1993) which increase functional trait richness and variation in fish assemblages. In the Indo-Pacific,

structural complexity of coral assemblages was the best predictor of the differences in fish functional richness and divergence among habitats, with branching coral habitat associated with highest functional richness (Richardson et al. 2017).

We believe that high levels of fish functional richness in coral reefs can also be explained by the habitat context and connectivity of reefs that increase local species richness through provision of food to species with different trophic roles. In other areas of the U.S. Virgin Islands, high fish species richness in coral reefs was explained by their proximity to seagrasses (Grober-Dunsmore et al. 2007a,b), which serve as nursery and foraging areas for many fishes (Randall 1967, Ogden and Gladfelter 1983, Nagelkerken et al. 2000). In our study, more than one third of fish species (36% of the 95 species) use seagrasses as their primary and secondary feeding habitat. These fish species represent all trophic levels, as well as specialist and generalist fishes. Seagrass beds offer a great abundance of prey biomass to reef fishes in Caribbean systems (Clark et al. 2009), which highlight the importance of protecting the ecological connectivity between marine habitats to enhance species diversity and abundance of trophic groups at the seascape level (Guillemot et al. 2011, Olds et al. 2012, 2013, 2016). This supports the need for connectivity among evaluated habitats in the BIRNM to maintain fish species trait diversity and biomass, as well as sites with high functional redundancy to avoid disruptions in the trophic function of fish assemblage.

3.5.3. Temporal variation in fish functional diversity

We analyzed annual changes in functional diversity descriptors and configuration of the trait space to understand the trophic organization of reef fish assemblages through time. The temporal variation that we found in fish functional redundancy and evenness in the trait space suggests that functional diversity metrics can be useful tools to track changes in the trophic organization of fish assemblages. Using centroids of the functional trait space, we captured temporal trajectories of fish functional diversity and changes in redundancy because the function of biotic assemblages is highly sensitive to trait presence, which is a function of temporal dynamics in species presence and abundance

(Stuart-Smith et al. 2013; Mouillot et al. 2013b). We found significantly higher values of functional richness in 2006 compared to 2005 due to an increase of species richness (Fig. 3). However, functional redundancy and evenness for 2006 were low and high, respectively, compared to previous years, which suggests that a strong reorganization in the functional trait space happened between 2004 and 2006. While the cause of these changes is difficult to pinpoint, we can monitor the functional metrics over time, compare them to known disturbances affecting the system, and potentially evaluate resilience by the gradual return to pre-disturbance functional conditions.

The reduction in fish trophic traits in 2005 coincided with a regional mass coral bleaching event that resulted in an estimated loss of 53% of reef-building species in the U.S. Virgin Islands, followed by coral diseases and macroalgal overgrowth during subsequent years (Miller et al., 2006, Mayor et al., 2006, Rothenberger et al., 2008, Rogers et at. 2009). Because the structural complexity of reefs is driven most by corals, changes in coral cover influence coral-associated fish communities (Garpe et al. 2006) by changing body size structure (Wilson et al. 2010), reef fish predator-prey dynamics (Graham et al. 2007), and community composition (Coker et al. 2012). We observed changes in species composition and reduction in the extent of functional redundancy hotspots formed by fish species of high trophic levels and specialist diets, which constitute medium-size classes in studied fish assemblages (Fig. 7). For example, the midwater piscivore *Scomberomorus regalis*, the pelagic piscivore *Caranx latus*, and the generalist carnivore *Alphestes afer*, disappeared from the trait space after the bleaching event in 2005. The structural erosion of coral reefs caused by bleaching events (Garpe et al. 2006) can explain the absence of medium-size fishes and changes observed in functional redundancy in the trait space. In general, reductions in reef structural complexity cause a consecutive reduction in microhabitats for habitat-specialist reef fishes of small-size that constitute prey for medium-sized piscivores (Graham et al. 2007). This reduction causes an indirect decline in piscivore numbers, and so changes sizes of functional redundancy hotspots for these species. Other evidence of reorganization in the trophic function of fish assemblages after 2005 is observed through the similar concentration of functional redundancy hotspots for 2006 and 2008, which

covered a wider area in the trait space in comparison to years prior to the bleaching event. For these two years, functional evenness was significantly higher in comparison to 2004, which suggests a change in species composition and abundance of functional traits. After 2005, trophic traits were more evenly distributed, and so more niches were exploited by reef fishes in the trait space.

Ecologists and managers have noted the need for metrics of resilience (Lam et al. 2017, Standish et al., 2014), particularly in light of the increasing disturbance regimes associated with climate change (Hughes et al. 2003, Bozec and Mumby 2015, Conversi et al. 2015). In our study, changes in the trait space revealed a signal of destabilization in the trophic function of fish assemblages in the BIRNM, and showed that the system did not return in five years to its original functional state (Fig. 7). While this research intended to describe potential mechanisms that explain changes in the trait space, we could not relate changes in functional diversity descriptors to variation in biotic benthic data. Future research should investigate the response of functional diversity metrics to abiotic environment characteristics, disturbances, or levels of habitat protection on the reef community, and identify the time lag that it takes for the system to return to its initial functional state.

3.6. Acknowledgments

academic guidance; and Ivan Arismendi and Selina S. Heppell provided guidance on data analysis. All coauthors provided editorial advice.

Chapter 4: Functional diversity: a tool for the ecological performance of MPAs and indicator of ecological resistance in reef fish assemblages

Functional diversity in reef fish assemblages

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4.1. Abstract

Ecological functioning of coral reefs and the resistance of coral reef fish communities to disturbance depend on the functional traits of resident species and their distribution and abundance through time and space. Developing and evaluating new process-oriented metrics for monitoring coral reef resilience is a high priority for adaptive management of coral reefs. Few studies have applied trait-based diversity metrics for monitoring the ecological performance of marine protected areas (MPA). Functional diversity metrics (functional variation and evenness, community-weighted mean values of functional traits, and total fish biomass production) were applied to understand spatio-temporal changes in the trophic structure of fish communities inside and outside No-Take and Multiple-Use MPAs in the U.S. Virgin Islands. We used this information to characterize trait values for tolerant and non-tolerant species to the coral bleaching event in 2005 that produced high

mortality in coral reefs in the U.S. Virgin Islands. We show that functional diversity metrics and traits are sensitive enough to capture spatial and temporal differences in the functional organization of fish communities. Reserve effects were detected only in a well-established No-Take MPA in St. Croix where fish functional richness, variation, and biomass were higher than the adjacent Multiple-Use MPA. We consider that the lack of a reserve effect in other MPAs is a consequence of their short time of establishment, long-term legacy of overfishing, and high habitat connectivity that allowed for homogenization of species and trait composition in fish assemblages. After the mass coral bleaching event, fish functional diversity had declined inside two MPAs and did not return to their original states after seven years. Fish assemblages increased their community values of diet breadth, and there was an immediate reduction in the mean trophic level of disturbance-tolerant species. Functional diversity metrics should be considered as complementary tools to monitor the performance of management actions such as MPAs and to monitor responses to disturbance. We provide a framework based on tolerance of reef fish species to a bleaching event to help managers determine which fish species and functional traits can promote short-term functional resistance and to predict further trends in the trophic organization of fish assemblages in managed areas.

4.2. Introduction

Marine biodiversity loss has been linked to significant declines in the ecosystem functions and services provided by marine species (Smith et al. 2011, Mouillot et al. 2013, Dee et al. 2016). Additionally, it has been shown that declines in ecosystem functioning are dependent not only on the taxonomic diversity of resident species but also on the functional diversity of ecologically relevant traits (Hooper et al. 2005, Jax et al. 2005). *Functional traits* are process-relevant attributes of organisms that make them bearers of functional roles (e.g., herbivores, piscivores), and thus determine how ecosystems operate (Jax et al. 2005). Linking functional traits to ecosystem functions provides a way to predict the consequences of species loss and to identify combinations of species that maximize ecosystem function (Nystrom 2006, Cadotte 2017).

Functional traits can be morphological, behavioral, or physiological (Diaz and Cabido 2001, Petchey & Gaston 2006, Cadotte et al. 2011). In addition to influencing the composition and organization of biological assemblages, they influence the ecological function of a community including emergent properties such as ecological resilience, i.e. resistance and recovery following disturbances (Boersma et al. 2014, Cadotte et al. 2015, Piacenza et al. 2015, Dee et al. 2016, Silva-Júnior et al. 2016). Resilience is crucial to ecosystem health because it allows for the capacity of a disturbed system to maintain (resist) or recover its functions and ecosystem services (Holling 1973, 1996, Folke et al. 2004, Hodgson et al. 2015, Mora 2015, Oliver et al. 2015). Functional traits generate ecological resilience through diversification and overlapping of functional roles performed by species (Peterson et al. 1997, Oliver et al. 2015). For example, the functional diversity of parrotfishes on coral reefs has been shown to positively influence coral reef resilience through complementary foraging of algae fostering the persistence of reef-building coral species (Roff & Mumby 2012, Edwards et al. 2013, Bonaldo et al. 2014, Mellin et al. 2014, Bozec et al. 2016). In addition, an understanding of the similarities and differences in prey preferences and foraging behavior of different parrotfishes aid in understanding the influence of this trophic group on coral reef community structure and functioning (Burkepile & Hay 2008, Bonaldo 2010). As such, tracking the spatial and temporal changes in the diversity (richness and evenness) and redundancy (overlapping niches) of the functional roles of species (Micheli & Halpern 2005, Duffy 2009, Ricotta et al. 2016, Cernansky 2017) may provide a suitable tool to monitor the resistance and recovery of ecological systems under different levels of disturbance.

Coral reef ecosystems are sensitive to disturbances such as heavy fishing pressure, invasion species, and climate change (Russ & Alcala 1989, Roberts 1995, Côté & Bruno 2015, Graham et al. 2017, Hughes et al. 2017). Even in well-managed marine reserves close to human populations, fish functional richness has been reduced with incomplete functional recovery (D'agata et al. 2016). An apparent low resistance and recovery to fishing on coral reefs is linked to at least three potential characteristics: 1.) a limited functional redundancy in the reef fish communities, characterized by having many

functional roles performed by just one species that once is lost cannot be replaced functionally by other species (Bellwood et al. 2003, Micheli et al. 2014, Mouillot et al. 2014, D'agata et al. 2016, Mora et al. 2016); 2.) a high vulnerability of unique functional roles performed by uncommon fish species that have low occurrence within communities and are prone to local extinction after disturbances (Mouillot et al. 2013a, Leitão et al. 2016); and 3.) the increased magnitude and frequency of disturbances on coral reefs, which limits their resistance and recovery time (Eakin et al. 2010, Hughes 2010, Hughes et al. 2018). Given the link between disturbances and declines in ecosystem resilience, the identification and evaluation of management strategies that address impairment of ecosystem functions and ensure the quality and flow of ecosystem services provided by coral reefs is needed.

Marine protected areas (MPAs) are a place-based strategy of ecosystem-based management typically established to mitigate the impacts of overfishing on both (1) commercial species and (2) the biodiversity and ecosystem function of marine habitats (Halpern 2003). However, more evidence is needed to support the capacity of MPAs to protect functional diversity. The successful reduction of fisheries pressure, especially by No-Take MPAs, has provided evidence of 'reserve effects' in the form of increased fish biomass and restoration of trophic integrity in coral reef areas (Micheli et al. 2004, Alcala et al. 2005, Tyler et al. 2011, Sala & Giankoumi 2010). In general, reserves promote higher levels of functional richness and redundancy in fish assemblages in tropical and Mediterranean areas (Micheli & Halpern 2005, Stelzenmuller et al. 2009, Villamor & Becerro 2012, Micheli et al. 2014). They also modify community trait-composition by protecting particular functional traits, such as living habits and mobility in benthic invertebrate communities in tropical coral reefs (Jimenez et al. 2017), and increase the abundance of species with original functional trait combinations in fish assemblages in the Mediterranean (Mouillot et al. 2008). While these results are promising, the positive effects of MPAs on marine functional diversity are not fully realized because the global MPA network protects only 17.6% of tropical fish species (Mouillot et al. 2015), which means that 82% of reef fishes and their functional roles are without protection. It is also difficult to monitor the community-level changes produced by the reduced fishing

pressure because the indirect responses on non-target species may take decades to reach detectable levels (Micheli et al. 2004, Babcock et al. 2010), requiring long-term enforcement and monitoring efforts which can be cost-prohibitive (Gaines et al. 2010).

Traditional metrics used to evaluate reserve effects on fish communities include temporal changes in species composition, trophic group richness, and biomass (Gotelly & Colwell 2001, Colwell 2009, Maurer 2009, Loiseau & Gaertner 2015, Vallès & Oxenford 2015). However, these metrics do not consider the identity of species, interspecific variability and redundancy of functional roles (Villéger et al. 2008, 2010, Mouillot et al. 2013b, Boersma et al. 2014, Micheli et al. 2014, Boersma et al. 2016, Dee et al. 2016), roles played by uncommon species (Mouillot et al. 2013a, Jain et al. 2014, Leitao et al. 2016), and explanations of mechanisms (e.g., predator-prey interactions, nutrient fluxes, competition) associated with functional organization under different levels of disturbance (Mouillot et al. 2013b). Recent studies suggest that future resilience of coral reef communities to climatic change will depend on the capacity of species to resist disturbances defined by traits that help organisms to tolerate disturbances and the protection of locations that show systematic ecological resistance to climatic disturbances (Darling & Côté 2018). By looking into species functional traits, we can assess the specific changes in the function of fish communities, and adequately monitor the ecological performance of MPAs based on shifts in trait values (Vandewalle et al. 2010, Villamor & Becerro 2012, Mouillot et al. 2013a,b, Micheli et al. 2014, D'agata et al. 2016). If we assume that functional diversity and redundancy in reef communities can promote their resilience to disturbance and enhance ecosystem services, it is logical to identify measurable indicators and thresholds for these metrics in monitoring and management programs. In highly impacted marine systems such as Caribbean coral reefs (Mora et al. 2016), No-Take MPAs may serve as reference areas to study the effects of protection levels on fish diversity and the redundancy of functional roles (Micheli et al. 2014).

In this study, we evaluated functional diversity metrics as tools to monitor: 1) the relative *ecological performance* of MPAs, defined as the capacity of different levels of protection to maintain or restore diversity features (Gaston et al. 2008); and 2) the

ecological resistance of reef fish communities to disturbances, defined as the trend of ecological functions to remain constant through broad-scale disturbance events (Oliver et al. 2015) such as coral bleaching events. To achieve the first goal, we compiled four functional traits related to the trophic ecology of reef fishes: habitat use during feeding, feeding time, trophic level, and diet breadth. We used the trait information, along with fish species abundance, to evaluate the spatial and temporal changes in functional richness (FRic), evenness (FEve), and dispersion (FDis), and community-level trait values among different levels of habitat protection in MPAs of the U.S. Virgin Islands. We evaluated No-Take MPAs (NTZ), Multiple-Use areas (MU), and areas open to fishing (NONE). We tested three main hypotheses to monitor the ecological performance of MPAs over time. (Table 11: H1, H2, H3). To achieve the second goal, we evaluated the ecological resistance of reef fish communities to disturbance by comparing trophic structure before and after the mass coral bleaching event in 2005 caused by extreme sea surface temperatures in the Caribbean basin (Eakin et al. 2010). We tested three main hypotheses to understand the ecological resistance of reef fish communities to a coral bleaching event (Table 11: H4, H5). Differences in descriptors of functional diversity and trait values will help us to identify components of functional diversity that are associated with the resilience of reef fish species to natural stressors. Our evaluations are relevant to the design of monitoring programs to assess the ecological performance of MPAs. We also provided useful information on the short-term resilience status and functional traits for 114 reef associated fish species to support future efforts to integrate trait-based approached to monitoring the adaptive management of coral reef ecosystems in the Caribbean region.

Table 11. Hypothesis and predictions for functional diversity metrics used to monitor the *ecological performance* of MPAs and ecological resistance of reef fish communities to a coral bleaching event.

	Metric	Hypothesis	Predicted response by protection level		
			NTZ	MU	None
H1	Functional richness (FRic) and dispersion (FDis)	Because fishing activities produce changes in fish species abundance and trait composition in the seascape, we expect spatial differences in metrics of functional diversity among levels of protection. Fish communities within No-Take MPAs will support higher ecological function by exhibiting high values of functional richness and redundancy (low dispersion) (Micheli et al. 2014) in comparison to areas with multiple uses and those open to fishing throughout all surveyed years.	Higher FRic and low FDis	Lower FRic and high FDis	Lower FRic and high FDis
H2	Community trait weighted mean values (CWM)	Spatial differences in fishing pressure among levels of protection will lead to differences in dominant fish functional traits at the community level. Below, we made trait predictions on the *dominant traits in fish assemblages* based on the most common commercially fished species (see Fig. 10) and shore-based fishing practices in shallow waters in the U.S. Virgin Islands:			
	a) Water column feeding position	Because fisheries primarily target benthic fish species (Mateo 2000, Holt & Uwate 2004, Kojis 2014, NOAA TRIP Program 2015, Goedeke et al. 2016), these species will be more dominant in fish communities within the No-Take MPAs than those zoned with multiple uses and unprotected areas.	Benthic feeding	Other feeding positions	Other feeding positions

Table 11 (Continued). Hypothesis and predictions for functional diversity metrics used to monitor the *ecological performance* of MPAs and ecological resistance of reef fish communities to a coral bleaching event.

	Metric	Hypothesis	Predicted response by protection level		
			NTZ	MU	None
H2	b) Feeding time	Because the fishing pressure by using traditional hand lines, bottom fishing and trolling in the U.S. Virgin Islands is concentrated in the mid-afternoon (14:00 - 17:00) and early evening (17:00 - 20:00) (Mateo 2000), and the most important commercial fish species feed during diurnal hours in adult stages (Fig.10), No-Take MPAs will include fish communities dominated by species that feed during diurnal and nocturnal hours.	Diurnal feeding	Other feeding times	Other feeding times
	c) Trophic level	Because local fisheries target medium and large size predatory fish (Mateo 2000, Pauly & Palomares 2005, and Goedeke et al. 2016) that represent medium and high trophic levels in fish assemblages (Fig. 10), fish communities within No-Take MPAs will be dominated by higher trophic levels.	High trophic levels	Low trophic levels	Low trophic levels
	d) Community diet breadth	Because fishing selects for specialist species in the U.S. Virgin Islands (Fig. 10), and reserves presumably protect them against or mitigate disturbance events (Devictor et al. 2008), fish communities within the No-Take and Multiple-Use MPAs will show narrow community diet breadths compared to unprotected areas.	Narrow diet breadth	Narrow diet breadth	Broad diet breadth
H3	Fish standing biomass	Because there is a positive association between functional richness and biomass in biological assemblages (Mora et al. 2011, Clark et al. 2012, Duffy et al. 2016, 2017), functional diversity will be positively associated with reef fish standing biomass at all levels of habitat protection. However, all areas that restrict fishing will exhibit higher biomass than MPAs with multiple uses and unprotected areas	Higher biomass	Lower biomass	Lower biomass

Table 11 (Continued). Hypothesis and predictions for functional diversity metrics used to monitor the *ecological performance* of MPAs and ecological resistance of reef fish communities to a coral bleaching event.

	Metric	Hypothesis	Predicted response by protection level		
			NTZ	MU	None
H4	Functional diversity descriptors and trait values	Ecological resistance of fish assemblages to the coral bleaching event in 2005 will be exhibited by the absence of temporary differences to original values of functional diversity descriptors and traits in the U.S. Virgin Islands. Since MPAs enhance fish functional diversity and ecological resilience of biotic communities to climatic disturbances (Micheli et al. 2012, Villamor & Becerro 2012, Micheli et al. 2014), No-Take MPAs will exhibit high ecological resistance in comparison to MPAs with Multiple Uses and unprotected areas.	High ecological resistance	Low ecological resistance	Low ecological resistance
H5	Functional trait values of disturbance-tolerant and non-tolerant species	Because high functional diversity and redundancy in fish assemblages promote ecosystem resilience, No-Take MPAs will have no significant differences in trait values of winner (tolerant) and loser (non-tolerant) species before and after the coral bleaching event in comparison to MPAs with Multiple Uses and unprotected areas.	No temporal differences in trait values of species	Temporal differences in trait values of species	Temporal differences in trait values of species

Figure 10. Functional trait values for commercially fished species from shallow waters in the U.S. Virgin Islands between 1974 and 2015 (n = 101 species). The list of fish species was a courtesy of Simon Pittman, and the functional trait data was a compilation by the corresponding author of this paper. Species list was compiled from the following sources: (1) the NOAA Trip Interview Program (TIP) in ports of the St. Croix and St. John between 2008 and 2015 (https://www.sefsc.noaa.gov/interview/); (2) historical reports of ex-vessel prices for fish species from 1974-75 to 2003-04 (Holt and Uwate 2004); (3) reports of seafood prices between 2003 and 2004 (Kojis 2014); and (4) socio-economic characterizations of fisheries in the U.S. Virgin Islands (Mateo 2000, Goedeke et al. 2016).

4.3. Materials and methods

4.3.1. Study sites

Our study used a large set of fish community data collected from 2002 to 2012 by NOAA's Caribbean Coral Reef Ecosystem Assessment and Monitoring project. These data were collected in shallow coral reef areas (< 30 m) inside and outside established MPAs with different levels of protection from human activity in St. Croix and St. John,

the U.S. Virgin Islands (Table 12, Fig. 11). We focused our analysis on the No-Take MPA (NTZ) of Buck Island Coral Reef National Monument (BUIS), and a neighboring reference MPA zoned with Multiple Uses (MU), the East End Marine Park (EEMP), both located in northeast St. Croix. We also analyzed data from the No-Take MPA U.S. Virgin Islands Coral Reef National Monument (VICR), and the U.S. Virgin Islands National Park (VIIS), a MU with limited-take reference area, as well as neighboring unprotected areas around St. John (Fig. 11). MPAs were selected because of the high sampling effort conducted by NOAA in coral reef areas to evaluate the ecological performance of these reserves in the U.S. Virgin Islands (Table 12).

Even though anecdotal illegal fishing has been documented inside MPAs between 2008 and 2012 (Pittman et al. 2014), this study classified MPAs based on the intended protection levels established for MPAs to account for differences in management treatments, and also because there is insufficient information to reliably estimate ilegal fishing intensity inside these MPAs since their establishment. No-Take MPAs in St. Croix (BUIS) and St. John (VICR) are MPAs where resource extraction is prohibited throughout the area. The MPA zoned for Multiple Uses in St. Croix (EEMP) include specific zones (i.e., no-take, recreation, sea turtle preserve and open zones); and in St. John (VIIS) it has limited take that allows line fishing and trap fishing with traditional Antillean fish traps and prohibits non-traditional gears and spearfishing (NOAA, NOS 2009).

The selected MPAs have a minimum of 11 years of establishment, and different extensions (Table 12). The oldest MPA, the Muliple Use VIIS, was established in 1956; and the most recent one, the Multiple Use EEMP was established in 2003. The U.S. Government National Park Service manages the No-Takes BUIS and VICR, and the Multiple Use VIIS. The Multiple Use EEMP is locally managed by the U.S. Virgin Islands Department of Planning and Natural Resources with support from NOAA. The EEMP is the largest MPA, encompassing 14940.9 hectares of marine areas 80% of which is open to fishing, followed by the BUIS (7726.3 ha), VICR (5918.1 ha), and VIIS (5176.5 ha) (NOAA, NOS 2009).

Survey sites were located in coral reef areas with average depths between 9 and 17 m

and with a wide range of structural complexity (seafloor rugosity) (Table 12). In St. Croix, the No-Take BUIS had survey sites with significantly higher average structural complexity (seafloor rugosity) than the Multiple Use MPA EEMP (Mann-Whitney test, p-value <0.05). Around St. John, surveys inside the No-Take MPA VICR had the highest structural complexity among the three surveyed areas, followed by unprotected sites, and the Multiple Use MPA VIIS (Mann-Whitney test, p-value <0.05).

Figure 11. Survey sites inside and outside marine protected areas in St. John and St. Croix, U.S. Virgin Islands.

Table 113. Fish survey sites conducted by NOAA in marine protected areas (MPA) of the U.S. Virgin Islands.

Sources: NOAA, NOS 2009; Pittman et al. 2014. DOC et al. 2009, 2011. Abbreviations: No-Take Zones (NTZ), Multiple Use Area (MU), and Unprotected Areas (None). Notes: *Mean depth and rugosity index of surveys were extracted from available bathymetric data in a buffer area of 100 m around location of each survey site. Rugosity index was derived from bathymetric surface data with the extension Benthic Terrain Modeler 3.0 for ArcGis 10.x (Jenness 2002, 2004; Wright et al., 2005) at 30 m^2 and 3m^2 resolutions for St. Croix and St. John, respectively (NGDC et al. 2010, NOS & OCM 2001). Rugosity values near 1 represent flat terrain, and higher values reveal increasing terrain rugosity (DOC et al. 2009).

Table 13. Fish survey sites conducted by NOAA in marine protected areas (MPA) of the U.S. Virgin Islands.

Island	MPAs				Surveys				Shared species
	Name	Protection level	Establishment	Coral reef / Colonized hardbottom (km2)	Years of sampling	Depth (m)* (mean $\pm$ SE)	Rugosity Index * (mean $\pm$ SE)	No. surveys (No. species)	Shared species
St. Croix	Buck Island Reef National Monument	NTZ	1961; expanded in 2001	18.539	2002-2012	8.966 $\pm$ 0.216	1.0012 $\pm$ 0.0001	654 (143)	125
	St. Croix East End Marine Park	MU	2003	80.451	2003-2012	11.788 $\pm$ 0.311	1.0003 $\pm$ 2.406E-05	540 (149)	
St. John	U.S. Virgin Islands National Park	MU-LT	1956	1.921	2002-2011	9.467 $\pm$ 0.438	1.0030 $\pm$ 0.0002	183 (128)	
	U.S. Virgin Islands Coral Reef National Monument	NTZ	2001	8.157	2002-2011	17.421 $\pm$ 0.455	1.0039 $\pm$ 0.0002	406 (137)	108
	Unprotected areas	None	-	-	2002-2011	13.796 $\pm$ 0.445	1.0037 $\pm$ 0.0002	490 (150)	

4.3.2.   Fish survey design

Fish species composition, abundance, and body size were recorded at 1,194 (St. Croix) and 1,079 (St. John) survey sites across coral reefs and colonized hard seafloor by the NOAA Caribbean Coral Reef Ecosystem Assessment and Monitoring project. This project was led by the Biogeography Branch of the National Oceanic and Atmospheric Administration (NOAA) from 2002 to 2012 (NOAA et al. 2007, Table 12). Survey locations within each level of protection were randomly allocated to the coral reefs and hard seafloor strata on the NOAA benthic habitat map (Kendall et al. 2001). Surveys were conducted in both islands during winter and spring (January-April) and fall (August-November) each year to account for seasonal variation, with exception of surveys in 2002, 2003, 2005, 2010 and 2011 in St. John that were conducted only in July. Trained scientific divers surveyed fish assemblages along a standardized 25 m long and 4 m wide (100 m^2) belt transect during a 15-minute swim at a constant speed. Surveys were not repeated at any of the exact same coordinates during 11 years of sampling. Information gathered in each underwater census included the identification of fish species, number of individuals, and an estimation of the fork length at 5 cm size class bins up to 35 cm to calculate fish biomass (Pittman et al. 2008).

4.3.3.   Quantifying beta diversity and assemblage similarity

Prior to analyzing functional diversity we assessed the species composition of each protection level in St. Croix and St. John across all surveyed years by using the distance to centroid beta-diversity metric (Anderson et al. 2006). The distance to centroid metric for beta diversity first calculates a dissimilarity matrix using the fish abundance data; then it uses a principal coordinate analysis (PCoA) to represent those dissimilarities in multivariate space. Finally, the beta diversity is calculated as the distance to the centroid of the PCoA transformation in multivariate space (Anderson et al. 2006). We normalized fish abundances to account for a range in species richness across sites, and then we calculated the dissimilarity matrix using Euclidean distances by using the Vegan package in R (Oskanen et al. 2007). Sites with different levels of protection

in St. Croix and St. John were assessed for differences in dissimilarity between using a one-way ANOVA. Significant differences between levels of protection were established by p-values < 0.05.

4.3.4. Compilation of fish functional traits

Traits related to the trophic function of 175 and 170 adult marine fish species in the St. Croix and St. John regions, respectively, were extracted from a database created from an extensive literature review of studies conducted in the U.S. Caribbean, and elsewhere in the Caribbean Sea (Rincón-Díaz et al. unpubl. data). We classified individuals as adult when fish were bigger than two-thirds of the maximum recorded species length reported in FishBase.org (Nagelkerken & van der Velde 2002, Dorenbosh et al. 2004, 2007, Froese & Pauly 2009). Traits were selected based on changes in the water column feeding position, feeding time, trophic location in the food web, and diet plasticity. These traits have been used to study patterns of functional diversity in coral reef fishes worldwide (Oliveira et al. 2012, Stuart-Smith et al. 2013, Micheli et al. 2014, Rincón-Díaz et al. unpubl. data). We had a mix of ordinal and continuous traits to consider with water column feeding position and feeding time classified as ordinal traits, and trophic level and diet breadth as continuous traits (Table 13). Trait combinations within ordinal categories were also considered to account for intraspecific variation in trait expression. Trophic level was calculated by using the TropLab software (Pauly et al. 2000) based on information from diet content analysis reported in studies conducted primarily in the U.S. Caribbean (Randall 1967, Bikerland & Neudecker 1981, Turigan 1995, White et al. 2006, Clark et al. 2009, Liedke et al. 2013). Trophic levels ranged from 2.0 for herbivores to 4.5 for piscivores. Diet breadth, or diet plasticity, was considered as the number of broad taxonomic groups consumed by a fish species (Oliveira et al. 2012) and ranged from one to five. Prey taxonomic groups included in diets were broad and included nekton, zooplankton, zoobenthos, detritus, plants, sand, organic matter, ectoparasites, and unidentified animal material.

Table 12. Functional trophic traits, range and categories used to describe functional diversity and community weighted mean trait values in reef fish assemblages of the U.S. Virgin Islands.

Trait	Number or Range	Category
Water column feeding position	1	Benthic
	1.5	Benthic and demersal
	2	Demersal
	2.5	Demersal and midwater
	3	Midwater
	3.5	Midwater and surface
	4	Surface
	5	Whole water column
Feeding time	1	Diurnal
	1.5	Diurnal and crepuscular
	2	Crepuscular
	2.5	Crepuscular and nocturnal
	3	Nocturnal
	4	Feeding during 24 hours
Trophic level	2 to 4.5	2 for herbivores and 4.5 for piscivores
Diet breadth	1 to 5	1 for narrow diets, and 5 for broad diets

4.3.5. Fish functional diversity and trait composition analysis between protection levels

We calculated functional richness (FRic), evenness (FEve), and dispersion (FDis), as well as community level weighted mean of trait values (CWM) for each survey site within each protection level by region (St. Croix and St. John). We used fish species biomass calculated by

NOAA using length-weight relationships (NOAA et al. 2017) and compiled trait information for adults of each species. Descriptors of functional diversity were selected because they provide insights about different aspects of functional composition and organization within fish communities, and can incorporate multiple categorical and numerical traits in a multidimensional trait space (Villéger et al. 2008, Laliberté & Legendre 2010, Schleuter et al. 2010, Laliberté et al. 2015). Functional richness (FRic) measures how much of the niche space is occupied by species present in a community by estimating the convex hull volume occupied by species in the trait space (Villéger et al. 2008, Schleuter et al. 2010, Stuart-Smith et al. 2013). Species touched by the convex hull possess extreme values of functional traits, and high values of FRic indicate that there are more functional groups in the functional trait space (Villéger et al. 2008). Functional richness covaries with species richness (Schleuter et al. 2010). Functional dispersion (FDis) measures trait dispersion in a community by averaging species distances to the centroid in the trait space (Laliberté & Legendre 2010, Laliberté et al. 2015). The location of the centroid is weighted by the species relative abundances (Laliberté & Legendre 2010). Functional dispersion gives insight about trait redundancy in the community. High values of functional dispersion indicate low trait redundancy due to high variability of functional traits, suggesting that the ecosystem function performed by one species is exclusive within the community. In contrast, high functional redundancy in species functions suggests that more than one species is providing a specific ecosystem function (Peterson et al. 1998, Elmqvist et al. 2003), and this functional overlap indicates there is potential for higher resilience of the system (Holling 1973, 1996, Folke et al. 2004). Functional evenness (FEve) measures the abundance distribution of species in the niche space to effectively use the entire range of available resources (Mason et al. 2005, Mouillot et al. 2013b). Low values of functional evenness suggest that there is under-utilized niche space, which has been shown to decrease productivity and increase the probability of successful invasions (Mason et al. 2005). Finally, community-weighted mean (CWM) trait values (i.e., site-level trait values weighted by species abundance) represent the most dominant trait in a biological assemblage (Laliberté et al. 2015).

We calculated functional diversity descriptors and CWM trait values following the protocol by Laliberté et al. (2015). A Gower dissimilarity matrix between all species pairs within a region,

calculated with the binary trait values, was used in a Principal Coordinate Analysis (PCoA) to obtain coordinates of fish species in the functional trait space (Gower 1971, Villeger et al. 2008, Laliberté et al. 2015). We kept the first and second PCoA axis to plot species because they explain most of the variation in the functional trait space in both regions (>75%). A functional matrix based on principal axis and a biomass matrix for fish species were used to calculate functional diversity metrics per survey site in each region. CWM trait values represent the most dominant trait in a biological assemblage and were calculated for the four functional traits by considering all species and their weighted relative abundances in each survey site (Laliberté et al. 2015). The Gower matrix, PCoA, functional diversity metrics, and CWM trait values were calculated by using the dbFD and functcomp functions of the FD software package in *R* (Laliberté et al. 2015).

A non-parametric permutational multivariate analysis of variance with 9999 permutations (PERMANOVA; Anderson et al. 2008) was used to test the hypothesis that functional diversity metrics and CWM trait values vary by protection level and year of survey, allowing for interactions among these two factors. We also conducted a one-way PERMANOVA with 9999 permutations in order analyzed pairwise comparisons for significant factors. Statistical differences were established with the PERMANOVA analysis by p-values < 0.05 (Mateos-Molina et al. 2014). Analyses were conducted using the PAST Program Version 3.08 (Hammer 2015).

4.3.6. Evaluation of ecological resistance in coral reef fish assemblages

We used the approach by Mouillot et al. (2013b) to evaluate the use of community trait values as a proxy to understand the ecological resistance of the coral reef fish community under natural disturbances. The selected disturbance was a thermal stress that caused a mass coral bleaching event in 2005 in the U.S.V.I (Miller et al. 2006, Mayor et al. 2006, Rothenberger et al. 2008, Rogers et at. 2009). This bleaching event caused a tremendous structural erosion of coral reefs in the U.S. Virgin Islands resulting in the loss of 53% of reef-building species, and followed by coral diseases and macroalgal overgrowth since 2006 (Mayor et al. 2006, Miller et al. 2006,

Rothenberger et al. 2008, Rogers et at. 2009). Resistance status of the reef fish community per study area was identified by using the FSECChange function in R (Mouillot et al. 2013b) by considering the biomass, functional traits, and rarity of each species.

We calculated the mean biomass of each species per level of protection before (2004), during (2005), and after (2006) the coral bleaching event, and used this information along with the species functional traits to account for temporal differences in the functional structure of fish assemblages. The mean biomass of species was calculated to reduce the noise caused by potential differences in detecting reef fish species in each survey site, and also because resampling events did not occur. We also identified the rarity of species according to their occurrence in each region to account for the influence of particular functional roles of uncommon species in the temporal trophic structure of fish assemblages in the US. Virgin Islands (Fig. B1). Common species were present in more than 20% of surveyed years, and uncommon species in less than 20%.

Previous to the resilience analysis we evaluated temporal changes in habitat complexity within levels of protection among evaluated years to account for the comparability of surveyed areas. We used the seafloor rugosity index, derived from Lidar bathymetric surface data for St. John at 3 m^2 resolution (NOS & OCM 2001) and coastal bathymetric data for St. Croix at 30 m^2 resolution (NGDC et al. 2010), as a proxy for habitat complexity. We calculated the mean rugosity index in a buffer area of 100 m radius (0.031 km^2) around locations of fish survey locations in each region (Table 12). Then we performed a pairwise Mann-Whitney U test to look for temporal and spatial differences in habitat complexity among levels of protection within each region. We found no significant temporal differences in rugosity indices within protection levels (Mann-Whitney U test, $p < 0.05$), but among them within each region (Mann-Whitney U test, $p < 0.05$). Based on this analysis we concluded that results from resilience analysis would not be affected by temporal differences in habitat complexity of survey sites within protection levels.

The resistance status for each reef fish species was identified based on their tolerance to disturbances. First, fish species were classified as "winners" and "losers" to the disturbance. Winners were tolerant species as they showed an increase in at least 1% of their relative biomass in fish assemblages after the bleaching event occurred; and losers were non-tolerant species as

they lost more than 1% of their relative biomass in the fish assemblages (Mouillot et al. 2013b). Species observed during one year in the functional trait space, but not in the following year, were categorized as non-detected during pre and post-disturbance periods. A non-parametric Mann-Whitney U-test was used to identify temporal differences in values of functional traits for winners and losers species within and between protection levels. We ran this test for assemblages with and without uncommon species to account for their influence in the identification of fish functional traits associated with natural stressors on coral reefs. Statistical differences were established with the Mann-Whitney U-test by p-values < 0.05. Analyses were conducted in the R program.

4.4.Results

4.4.1. Fish species community composition among protection levels

Prior to the analysis of functional diversity we found significant differences in species community composition between the two levels of habitat protection evaluated in St. Croix (ANOVA test, p-value < 0.01), but not among the three levels of protection in the St. John (ANOVA test, p-value > 0.01) (Fig. 12, Table 14).

Table 135. One way ANOVA on dissimilarity distances in fish species composition among levels of habitat protection in evaluated cites of the U.S. Virgin Islands.

Site	df	F value	P-value
St. Croix	1	11.17	< 0.01
St. John	2	0.62	0.54

Figure 12. Principal Coordinate Analysis on fish species composition in MPAs around St. Croix (A) and St. John (B) between 2002 and 2012. The percentage of variation explained by each coordinate axis is denoted in parenthesis. Levels of protection in evaluated MPAs were: No-Take Zones (NTZ), Multiple Use Areas (MU), and Unprotected areas (NONE).

4.4.2. Fish functional diversity metrics to monitor the ecological performance of MPAs

Four functional traits related to the trophic function of adult stages were attributed to each 180 reef-associated fish species recorded around northeast St. Croix and St. John, U.S. Virgin Islands. These data were combined with species biomass to obtain three descriptors of functional diversity (richness [FRic], evenness [FEve], and dispersion [FDis]) to describe spatio-temporal changes in the trophic function of fish assemblages inside and outside marine protected areas between 2002 and 2012.

Our findings on functional diversity descriptors do not support the first hypothesis that all MPAs restricting fishing access exhibit high ecological resistance to disturbances through high values of functional richness and redundancy and low evenness in comparison to areas with Multiple Uses and open to fishing in the U.S. Virgin Islands. We found that only the No-Take

MPA BUIS supported a higher richness of trophic functions in fish assemblages than the neighboring Multiple Use MPA EEMP in 2008 and 2010 (One Way-Permanova, p-value <0.05); Table 15, Fig. 13a,b). BUIS also supported higher values of functional redundancy, with traits less evenly distributed in the multidimensional trait space of fish assemblages for 2004 (One-way Permanova, p-value <0.05) (Fig. 13c,d).

Unexpectedly, unprotected areas in St. John supported higher values of functional richness than MPAs (Fig. 13d-k). Unprotected areas supported significantly higher functional richness than the No-Take MPA VICR in 2004; and in 2004, 2006, 2007 and 2008 functional richness was also higher in areas outside the Multiple Use MPA VIIS (One-way Permanova, p-value < 0.05) (Fig. 13e,i). We found no visible patterns in spatial differences of functional dispersion between protected and unprotected areas in St. John (Table 15). Unprotected areas had no spatial differences in functional dispersion values in comparison with the No-Take MPA VICR (One-way Permanova, p-value < 0.05); except for the significantly lower values outside this MPA in 2007 (One-way Permanova, p-value > 0.05) (Fig. 13f). Conversely, these unprotected areas exhibited a lowered functional dispersion than the Multiple Use MPA VIIS, with significantly lower values in 2004 (One-Way Permanova, p-value <0.05) (Fig. 13j). Finally, only temporal differences in functional evenness were found between protected and unprotected areas in St. John (Table 15). Higher values of functional evenness were found outside the No-Take MPA VICR in 2005 and 2007, and in 2005 outside the Multiple Use MPA VIIS (One-Way Permanova, p-value <0.05) (Fig. 13g,k). In general, these changes show the utility of functional richness and dispersion to capture spatial variations in the ecosystem function of biological assemblages, even though there was not a clear pattern of greater functional diversity in No-Take MPAs.

When data for the different protection levels in St. Croix and St. John were combined, the significant changes in functional diversity descriptors were observed after 2004 (Fig. 14). In St. Croix, we found a significant erosion of the functional trait space after 2005. FRic values since 2005 were significantly lower than values from 2002 to 2004 (Mann-Whitney test; p-value <0.05) (Fig. 14b). FDis values for 2006 were higher than values of all evaluated years except for 2003 (Mann-Whitney test; p <0.05), and FEve values for 2004 were lower than values of all

evaluated years in this region (Mann-Whitney test; p <0.05) (Fig. 14c,d). Main temporal changes in functional diversity in St. John were found in functional richness with higher values in 2006 than in 2004, 2008, 2009, and 2010 (Mann-Whitney test; p <0.05) (Fig. 14f). Functional dispersion decreased after 2002 in this region (Mann-Whitney test; p <0.05), and changes in functional evenness had the highest values in 2008 among surveyed years (Mann-Whitney test; p <0.05) (Fig. 14g,h). The significant changes in descriptors of functional diversity after 2004 in St. Croix, and in 2006 in St. John, suggest a re-organization in the trophic function of fish assemblages in the U.S. Virgin Islands.

4.4.3. Fish functional traits to monitor ecological performance of MPAs

   We also rejected our second hypothesis that reserves select for community level differences in functional traits (Table 1: H2a,b). We did find differences in the community-weighted mean trait values at different levels of protection that showed particular spatial and temporal differences related to the ecological resistance of fish assemblages (Table 16). We found a higher average trophic level within the area with Multiple Uses compared to the No-Take MPA of St. Croix (Mann-Whitney U test, p-value < 0.05) (Fig. 15c). This pattern agreed with the high contribution of low trophic levels to the total fish biomass in the No-Take MPA BUIS (Fig. B2). In both MPAs in St. Croix there was a temporal trend of fish species towards broader diet breadths (> than 2 taxonomic groups) in 2005, 2006, and after 2010 (Mann-Whitney U test, p-value < 0.05) (Fig. 15d). Around St. John, fish assemblages in the No-Take MPA were dominated by higher trophic levels than the other protected and unprotected areas around the island, which coincides with the greater contribution of high trophic levels (4 – 4.5) to the total fish standing biomass in this MPA (Fig. 15g; B2). Fish assemblages in unprotected areas leaned towards more specialist diets that included less broad taxonomic groups (Mann-Whitney U test, p-value < 0.05) (Fig. 15h).

Table 146. Two-way PERMANOVA on values of functional richness (FRic), dispersion (FDis) and evenness (FEve) for Caribbean fish assemblages under different levels of protection (2002-2012).

Source of variation	St. Croix (2002-2012)					St. John (2002-2011)				
	df	SR	FRic	FDis	FEve	df	SR	FRic	FDis	FEve
Year of surveys	10	5.289***	7.698***	1.868**	1.945**	9	2.212***	2.269***	1.304*	1.803**
Management	1	7.445**	11.769***	2.678	0.660	2	6.144**	5.327***	2.313*	1.257
Time x Management	10	-15.126*	-16.008	-16.551	-14.502*	18	-11.626*	-10.373**	-11.791	-13.324
Residual	1134					1047				
Total	1155					1076				

Notes:* denotes p < 0.05, ** p < 0.01 and *** p < 0.001. Abbreviations: Species Richness (SR), Functional Richness (FRic), Functional Dispersion (FDis), and Functional Evenness (FEve).

Figure 13. Spatial change in functional diversity descriptors between levels of protection for St. Croix (A-D) and St. John (D-K). Evaluated diversity descriptors were: species richness (SR), functional richness (FRic), functional dispersion (FDis), and functional evenness (FEve). Evaluated levels of protection in MPAs were: No-Take Zones (NTZ), Multiple Use Areas (MU), and Unprotected areas (NONE). Positive changes indicate that diversity descriptors are higher in the NTZ than in the MU area in St. Croix, and in the NTZ and MU MPAs than unprotected areas around St. John. * denotes p-value < 0.05, ** p-value <0.01, *** p-value <0.001.

Figure 14. Spatio-temporal variation in functional diversity metrics by levels of protection and years in St. Croix (a,b,c,d) and St. John (e,f,g,h). Evaluated diversity descriptors were: species richness (SR), functional richness (FRic), functional dispersion (FDis), and functional evenness (FEve). Levels of protection evaluated were: MPAs with No-Take Zones (NTZ) and Multiple Use Areas (MU), and Unprotected areas (NONE). Letters above lines denote significant differences among evaluated years when all data was collapsed per region. Significant differences among groups were identified with p-values < 0.05.

Table 17. Two-way PERMANOVA on values of functional traits for Caribbean fish assemblages under different levels of protection (2002-2012).

		St. Croix (2002-2012)					St. John (2002-2011)			
Source of variation	df	WCFP	FT	TL	DB	df	WCFP	FT	TL	DB
Years of Survey	10	1.362	2.824***	1.014	3.307***	9	1.127	0.933	0.641	1.666*
Management	1	0.026	9.155***	26.516***	35.066***	2	2.863*	1.766	3.785**	7.594***
Time x Management	10	-16.456	-15.646	-16.074	-16.108	18	-12.722	-11.687**	-12.283	-11.085
Residual	1134					1047				
Total	1155					1076				

Notes:* denotes p < 0.05, ** p < 0.01 and *** p < 0.001. Abbreviations: Water Column Feeding Position (WCFP), Feeding Time (FT), Trophic Level (TL), and Diet Breadth (DB).

Figure 15. Spatio-temporal variation in community-weighted mean (CWM) trait values by levels of protection and years in St. Croix (a,b,c,d) and St. John (e,f,g,h). Evaluated traits were: water column feeding position (WCFP), feeding time (FT), trophic level (TL), and diet breadth (DB). Levels of protection evaluated were: MPAs with No-Take Zones (NTZ) and Multiple Use Areas (MU), and Unprotected areas (NONE). Trait values ranged from benthic (B) to demersal (D) areas for the WCFP, and from diurnal (D) to crepuscular hours (C) for the FT. Letters above lines denote significant differences among evaluated years when all data was collapsed per region. Significant differences among groups were identified with p-values < 0.05.

4.4.4. Influence of functional diversity and habitat protection in fish standing biomass

We accepted the hypothesis that fish biomass was positively associated with fish functional diversity at all levels of habitat protection. While species richness and functional richness in coral reef areas had a significantly and positive association with high fish standing biomass (Fig 16a,b,e,f), functional evenness showed a significant negative association (Fig 16d,h). Conversely, we did not find a significant trend in the association between functional dispersion and biomass among evaluated regions. While functional dispersion show a positive association with fish biomass in St. John (Spearman rank correlation, $p < 0.05$), it did not show any association with fish biomass in St, Croix (Spearman rank correlation, $p > 0.05$) (Fig. 16c,g).

When fish standing biomass was compared between levels of protection, we accepted the hypothesis that No-Take MPAs exhibit higher biomass only in St. Croix. The No-Take MPA in St. Croix supported higher fish biomass than fish assemblages inhabiting the MPA with Multiple Uses around this island (Fig 17a). We rejected our hypothesis regarding the effect of No-Take MPAs on fish standing biomass in St. John, where unprotected coral reefs had no significant differences in fish standing biomass when compared with the No-Take MPA VICR (Mann-Whitney test, $p > 0.05$), but with the Multiple Use MPA VIIS (Mann-Whitney test, $p < 0.05$) (Fig 17b). The lack of commonality in results of fish standing biomass by protection levels in the U.S. Virgin Islands suggests that there are site-dependent factors in the management of MPAs that are influencing this pattern.

Figure 16. Association between metrics of fish diversity and fish standing biomass per levels of protection in the U.S. Virgin Islands. The association analysis was conducted with a Spearman rank correlation analysis (rho) between species richness (SR) (a,e), functional richness (FRic) (b,f), functional dispersion (FDis) (c,g); and functional evenness (FEve) (d,h), with the logarithm of the total fish standing biomass in St. Croix (a,b,c,d) and St. John (e,f,g,h). Levels of protection evaluated were: No-Take Zones (NTZ), Multiple Use Areas (MU), and Unprotected areas (NONE). * denotes $p < 0.05$.** p-value < 0.01, *** p-value < 0.001.

Figure 17. Total fish standing biomass per levels of protection in St. Croix (A) and St. John (B).Dashed lines indicate the mean of the logarithm of the total fish standing biomass. Evaluated levels of protection in both islands were: No-Take Zones (NTZ), Multiple Use Areas (MU), and Unprotected areas (NONE). Counts denote the number of survey sites evaluated in each level of protection. Significant differences in fish standing biomass between levels of protection are denoted by * $p < 0.05$, ** p-value < 0.01, and *** p-value <0.001.

4.4.5. The resistance of fish assemblages to natural disturbances

We reject our fourth hypothesis about the ecological resistance of No-Take MPAs to natural disturbances. We found temporary differences in functional diversity for both MPAs in St. Croix exhibited by the erosion in functional richness after 2005 with no return to its original values after seven years of sampling (Fig.14b).

We reject our fifth hypothesis that after the mass coral bleaching event in 2005, No-Take MPAs had no significant differences in trait values of winner and loser fish species in comparison to MPAs with Multiple Uses and unprotected areas. Our results show that significant changes in the trophic structure of fish assemblages occurred within two MPAs of the U.S. Virgin Islands after the large coral bleaching event. We found a significant decrease in the trophic levels of winner species inside and outside

the No-Take MPA in St. Croix, and inside the Multiple Use MPA in St. John (Mann-Whitney test, p > 0.05) (Fig. 18, B3). Winner species in both MPAs had trophic levels with medians lower than 3.5 after the bleaching event, suggesting that trophic groups such as general carnivores and piscivores lost representativeness within fish assemblages immediately after this natural disturbance. Conversely, in St. John we did not find temporal differences in trophic levels of winner and loser species inside the No-Take MPA and unprotected areas. We found differences in general patterns of significant traits for winner and loser species between the set of species with and without uncommon species only for changes of trophic levels in the Multiple Use MPA in St. John (Fig. B3). In general, our results show that the trophic level of fish assemblages is a sensitive indicator of the tolerance of fish communities to natural disturbances.

Figure 18. Differences in functional trait values between winners and losers for the four functional traits in pre and post disturbance periods. Letters above box plots indicate groups with significant differences in trait values within each region (p-value < 0.05). Dotted line serves as reference of median values for trophic levels of winner species inside the No-Take MPA Buck Island Reef National Monument in St. Croix and the areas with Multiple Uses Virgin Island National Park in St. John before the coral bleaching event in 2005. Abbreviations: Buck Island National Reef Monument (BUIS), East End Marine Park (EEMP), Unprotected areas in St. John (Non); Virgin Islands National Reef Monument (VICR), and Virgin Islands National Park (VIIS).

4.5.Discussion

4.5.1. Fish functional diversity metrics to monitor the ecological performance of MPAs

We evaluated functional diversity metrics as ecological tools to track spatio-temporal changes in the trophic function of marine fish communities located both inside and outside of marine protected areas in the U.S. Caribbean. Even though we did not observe strong influence of all No-Take MPAs evaluated along all surveyed years, our results demonstrate that functional diversity metrics are sensitive indicators of spatial and temporal changes in the fish community under different management strategies. We encourage the use of functional richness and dispersion as metrics to monitor the ecological performance of MPAs to protect components of biodiversity, predict spatial trends in fish standing biomass, and understand the functional resistance of fish assemblages to fishing activities. Our analyses highlight that these metrics can be used to identify sites with high levels of functional diversity, fish standing biomass, and ecological resistance to disturbances. Sites can then be classified and their biophysical characteristics described to enable a link to be drawn between stressors, condition and predicted resilience.

Our results show that the use of functional diversity metrics to evaluate the effects of different management regimes revealed differences in the ecological organization of fish communities across space and time. We observed positive reserve effects on functional richness only within the No-Take MPA BUIS in the U.S. Virgin Islands. This No-Take MPA showed higher values of functional richness than the neighboring MPA with Multiple Uses in 2008 and 2010, despite not showing significant differences in species richness in those years. High levels of functional richness inside MPAs are documented as one of the desirable reserve effects also reported from other MPAs around the globe (Micheli & Halpern 2005, Stelzenmuller et al. 2009, Villamor & Becerro 2012, Micheli et al. 2014). This reserve effect is characterized by the support of high levels of functional richness and variation (Micheli et al. 2014), or the presence of particular combinations of functional traits in

fish assemblages within MPAs (Mouillot et al. 2008). Both patterns increase functional richness because more functional roles by fish species are included in the trait space, and so the volume occupied by a fish community increases.

Temporal reserve effects observed in the No-Take MPA in St. Croix are likely due to its high seafloor structural complexity which increases fish functional richness. The high structural complexity of coral reefs is associated with hotspots of fish diversity (Pittman et al. 2007, Pittman et al. 2009, Pittman & Brown 2011, Massicotte et al. 2014, Bellwood et al. 2017, Sekund & Pittman 2017). Habitat complexity also facilitates high functional richness in fish assemblages (Richardson et al. 2017). Coral reefs with high structural heterogeneity can support a rich variety of physical habitats and niche space occupied by diverse fish species and functional groups (Pittman et al. 2007, 2009, Pittman & Brown 2011, Coker et al. 2013) which increase functional trait richness and variation in fish assemblages. If our interpretation is correct, the high structural complexity found in coral reefs inside the No-Take MPA BUIS, and measured with geospatial data, could be supporting high levels of fish functional richness. Our findings suggest that this No-Take MPA could be supporting ecosystem functioning through its structural components and fish trait composition that provide some ecological resistance to the erosion of coral cover after 2006, and any illegal fishing that takes place inside this protected area. It is likely that increasing compliance with regulations and potentially also enforcement effort to end illegal fishing will be vital to progress to a more ecologically complete restoration of ecosystem functioning.

We believe that the reserve effect observed in the No-Take MPA in St. Croix can be explained by its smaller size, and more prolonged history of enforcement to reduce illegal fishing activities in comparison to the bigger MPA with Multiple Uses in this region.

Our results also showed that functional diversity metrics are useful tools to evaluate the established marine reserves. We found no reserve effects in the No-Take MPA VICR at St. John. In fact, we found that in some years unprotected areas in this region supported higher values of fish functional richness than both MPAs, and

showed no differences in functional redundancy with the No-Take MPA. The high functional diversity exhibited by unprotected areas can have four potential explanations.

First, functional richness covaries with species richness (Schleuter et al. 2010). In our study, we observed that high values in species richness coincided with years where values of functional richness were significantly higher in unprotected areas than inside the No-Take (2004) and Multiple Use MPAs in St. John (2004, 2006, 2007, and 2008). This difference in functional richness between unprotected and protected fish assemblages in St. John can be explained by a better quality of habitats outside the MPAs. Reef fish assemblages outside the No-Take MPA in St. John inhabit areas with higher cover of corals and bottom rugosity than assemblages inside the MPA, and exhibit higher species richness, abundance, and biomass (Monaco et al. 2007). The higher structural complexity exhibited by unprotected reefs in St. John can increase niche space, that are occupied by more fish species and that rise values of functional richness in these reefs.

Second, it is possible that this No-Take MPA in St. John is very young and requires more comprehensive surveillance to exhibit reserve effects on functional diversity. Prior to its establishment in 2001 (NOAA, NOS 2009), coral reef areas in St. John experienced a long history of overfishing (Garrison et al. 1998, 2004). This high fishing pressure has depleted large-bodied species such as groupers and parrotfishes in the U.S. Virgin Islands, resulting in a shift to smaller bodied species such as coney grouper (*Epinephelus fulvus*) and redband parrotfish (*Sparisoma aurofrenatum*) (Pittman et al. 2010). It is possible that overfishing and natural disturbances have caused a long-term homogenization of fish species and functional traits in St. John that hinder reserve effects on functional diversity by MPAs in St. John. In fact, we observed no differences in species composition of fish assemblages among all levels of protection evaluated in St. John, which suggest that the long-term legacy of overfishing on functional trait composition could overcome any efforts done to protect fish assemblages inside the MPAs. Other studies have arrived to similar conclusions for MPAs in St. John. No positive reserve effects were found in

20 metrics of fish and benthic components evaluated in the same survey sites used in our study between 2002 to 2010 (Pittman et al. 2014). In that evaluation, the authors suggested that positive reserve effects may emerge under continued and increased regulations on fishing so long as a suitable habitat quality exists to support fish population replenishment (Pittman et al. 2014). Our findings corroborate this hypothesis and recommendation, but we also suggest that evaluation of current boundaries of the No-Take MPA in St. John is needed to include unprotected areas that support high fish functional richness. In this study, it is difficult to specify the time lag that fish assemblages need to show higher functional diversity in MPAs with complete surveillance on illegal fishing in St. John. Further studies can benefit from our baseline results, and apply modeling tools to find appropriate levels of habitat protection required to increase fish functional diversity in this region.

Third, high functional richness in unprotected areas can be enhanced through their high habitat quality and ecological connectivity of habitats in St. John. This high connectivity allows for greater dispersal of fish species beyond the boundaries of MPAs in this island (Pittman et al. 2014). The broad movement patterns by reef fishes outside MPAs can produce temporal changes in fish species and functional trait community composition driving spatiotemporal patterns of functional diversity. Previous studies in St. John suggested that movement patterns of adult stages of reef fish species may have significant implications in fish biomass productivity, fisheries management, MPA zoning and ecological performance of established MPAs (Pittman et al. 2014). If the high habitat connectivity between coral reefs in unprotected and protected areas in St. John enhances fish functional diversity, then the protection of this ecological bridge is needed to maintain biodiversity and ecosystem functioning in the U.S. Virgin Islands. The evaluation of current levels of functional diversity in unprotected areas of St. John could help to justify changes in their levels of protection to maintain ecosystem functioning.

4.5.2. Influence of functional diversity and habitat protection in fish biomass production

Biodiversity is the primary driver of reef fish standing biomass worldwide (Duffy et al. 2016, 2017). High fish species richness and functional diversity, coupled with low fishing pressure, are known to increase reef fish biomass and serve as a buffer against climate variability (Micheli et al. 2014, Dee et al. 2016, Duffy et al. 2016). These components enhance the resilience of fish communities and improve the ecosystem service of the harvestable portion of fish production (Micheli et al. 2014, Dee et al. 2016, Duffy et al. 2016). We believe that functional diversity supports fish standing biomass in coral reef areas at all levels of habitat protection. We observed that coral reef areas with more fish species richness, functional trophic roles (functional richness) and variation in functional traits (functional dispersion), exhibited high fish standing biomass at all levels of habitat protection. The significant positive association between fish functional richness and dispersion with fish standing biomass observed in our study is explained by the low functional redundancy exhibited by tropical reef fish assemblages. In these fish communities, functional groups are comprised by few species, which reduce the overlapping of functional roles (Bellwood et al. 2003, Micheli et al. 2014, Mouillot et al. 2014, D'agata et al. 2016). Therefore, under the low levels of functional redundancy exhibited by reef fish assemblages, the complementary roles played by fish species is needed to maintain ecosystem functions and support fish standing biomass in coral reefs. The effects of niche complementarity on biomass production have also been documented in plant assemblages, in which plant biomass is enhanced by processes including multiple species (Cardinale et al. 2007).

Besides the complementarity of functional roles, we also observed that their dominance in the trait space (low functional evenness) positively covaried with fish standing biomass in coral reef systems. Studies on terrestrial systems have demonstrated that the contribution of both niche complementarity and selection effect is equally important to increase plant biomass production through biomass

contribution by multispecies and highly productive species (Cardinale et al. 2007, Cadotte 2017). It seems that our findings follow this explanation, suggesting that it is equally important to protect functional fish diversity, as well as to identify trait combinations in fish species that increase fish biomass in coral reefs. Further work on the relationship between fish trait combinations and fish biomass can improve management of fishing resources in coral reefs in the U.S. Caribbean.

Unexpectedly we found that unprotected coral reefs exhibited similar levels of fish standing biomass to the reefs inside the No-Take MPA off St. John. We consider that this result can be related to (1) the high structural complexity of unprotected areas in St. John that enhances fish functional richness and variation; (2) significant temporal changes in species richness in unprotected areas that increase fish functional richness; (3) high ecological connectivity of habitats in St. John that allows movement of fish species from protected ones towards unprotected areas; and (4) the lack of effectiveness of the No-Take MPA, perhaps due to poaching. Our results suggest that fish communities inhabiting coral reefs in unprotected areas could exhibit high ecosystem resistance to fishing pressure and environmental change evidenced by their high levels of fish functional richness and biomass production. If our interpretation is correct, then these high resilient areas need evaluation to determine their current levels of ecosystem function and to identify potential changes in their protection level.

To improve the management and ecosystem functioning of MPAs in the U.S. Virgin Islands, the evaluation, and control of illegal fishing within these reserves need to be a priority. Available information from the National Park Services (NPS) for three of the studied MPAs suggests that besides efforts to control illegal fishing, this activity occurred between 2008 and 2012 (Pittman et al. 2014). The MPA with most infractions was the U.S. Virgin Islands National Park (VIIS) (n = 37), followed by Buck Island Reef National Monument (BUIS) (n = 32), and the U.S. Virgin Island Coral Reefs National Monument (VICR) (n = 18) (Pittman et al. 2014). Anecdotal evidence from the National Park indicates that the number of documented infractions underestimates the actual number of illegal fishing events observed. Even though

MPAs in the U.S. Virgin Islands have essential habitat to increase their reserve effects, the high pressure by multi-species small-scale fisheries in the area (Garrison et al. 2004) need to be better managed to avoid decreases in fish functional groups and impacts on the food web and ecosystem functioning (Micheli et al. 2014).

4.5.3.   The resistance of fish assemblages to natural disturbances

We analyzed temporal changes in functional diversity descriptors, community-weighted mean trait values, and traits of tolerant and non-tolerant species of fish assemblages to understand the ecological resistance of fish assemblages to face disturbances. The significant temporal differences in fish functional richness and dispersion found in both MPAs in St. Croix after 2005, suggest these functional diversity metrics were useful to track a decline in the range of traits that comprise boundaries of the functional trait space in fish assemblages. Despite the significant increases in functional richness in 2008 and 2010 in coral reefs around the No-Take MPA BUIS, St. Croix experienced an important erosion of the functional trait space after 2005. These changes in the trait space coincided with the regional mass coral bleaching event and subsequent diseases that reduced drastically coral cover in the U.S. Virgin Islands in 2005 and 2006 (Mayor et al. 2006, Miller et al. 2006, Rothenberger et al. 2008, Rogers et at. 2009, Pittman et al. 2014). Habitat degradation in corals by natural disturbances leads to the loss of functionally similar species (functional redundancy), and the addition of unique disturbance-tolerant species (Brandl et al. 2016). Indeed, we observed alarming indicators of the erosion in ecosystem functioning in St. Croix after the coral bleaching event. We observed that (1) values of fish functional richness decreased and never returned to their original states after seven years of surveys in both MPAs; (2) fish assemblages changed their community diets breadth towards the use of more broad taxonomic groups in both MPAs; and (3) there was an immediate reduction in the trophic level of winner species inside the No-Take MPA. Our results agreed with the favoring of more generalist species after coral bleaching events because of their low susceptibility to

environmental perturbations, and decreased of intermediate and large piscivore species because of the reduction in their prey (Pratchett et al. 2011). In a previous study inside the No-Take MPA BUIS, we also found that functional redundancy of high trophic levels decreased, and more niche space was used by reef fishes after the coral bleaching event in 2005 (Rincón-Díaz et al. unpubl. data). The reduction in functional richness and trophic levels, plus the trend towards a the use of more taxonomic groups as preys by reef fish species are alarming indicators of the erosion in ecosystem functioning and of the low resistance and lack of short-term recovery of fish assemblages to big natural disturbances in MPAs of St. Croix.

The reduction of fish functional diversity found in MPAs of the U.S. Virgin Islands after the bleaching event agree with recent evidence on the lack of reserve effects under large disturbances caused by global warming on coral reefs. Even though there is vast evidence that well-designed and managed MPAs can protect fish functional diversity from fishing (Alcala et al. 2005, Micheli & Halpern 2005, Mouillot et al. 2008, Stelzenmuller et al. 2009, Tyler et al. 2011, Villamor & Becerro 2012, Micheli et al. 2014), recent evidence on the effects of global warming on coral reefs suggest that local protection of reefs had little or no resistance to the severe and large spatial extension of coral bleaching events and consequent coral cover declines (Jones et al. 2004, Hughes et al. 2017a,b). In addition, MPAs cannot protect biodiversity and ecosystem functioning if there are continued anthropogenic stressors inside these areas, and shortcomings in their implementation such as budget restrictions, enforcement issues, coastal development and pollution are not solved (Mora & Sale 2011). In our study, we need to consider that there was illegal fishing within all evaluated MPAs in the U.S. Virgin Island during surveyed years (Pittman et al. 2014), and that there is a long-term legacy of overfishing in reef fish assemblages of St. John (Garrison et al. 2004). We consider that these two factors have also degraded ecosystem resistance of fish assemblages against natural disturbances.

In this study, we proposed a framework that may help managers to determine which fish species and functional traits can promote short-term functional resistance

to coral bleaching events in each evaluated region (Fig. 19). In this framework we grouped species based on their pre and post-disturbance tolerance status and assigned a short-term functional resistance status. For example, species that increased biomass between pre and post-disturbance periods were described as *highly tolerant* species. Species observed during pre-disturbance periods (winners and losers) that decreased abundance in post-disturbance periods are *tolerant species*. Species that were losing biomass during pre-disturbance periods, but then increased their biomass post-disturbance are *opportunistic* species. We also assigned this status to non-detected species previous to the disturbance, but that increased in biomass after the disturbance. Species observed during pre-disturbance periods but not observed in post-disturbance were characterized as *undetected* species.

We created a list of resistance status for each reef fish species in each surveyed area to the coral bleaching event that can serve managers as a tool to identify indicator species of erosion in functional diversity, and those that need of protection to enhance short-term ecosystem resistance (Table B1). For example, undetected species after the bleaching event in MPAs in St. Croix such as *Bothus lunatus, Hypoplectrus puella, Hypoplectrus unicolor, Hypoplectrus chlorurus, or Aulostomus maculatus* can serve as indicators of functional restoration because they possess functional traits that were present previous to the bleaching event. These species had high trophic levels and their diets rely on few broad taxonomic groups. Therefore, their protection can help to return these systems to their original values in functional diversity. On the other hand; if managers want to enhance the intrinsic resilience of assemblages through protecting traits that increase tolerance of species to disturbances (Darling & Côté 2018), efforts can be focused on tolerant species. In St. Croix, tolerant species such as *Lutjanus mahogoni, Epinephelus guttatus, Malacoctenus macropus, Stegastes diencaeus,* and *Scarus vetula* were characterized by being common species with a wide range of trophic levels and feeding activities. Highly tolerant species such as *Halichoeres garnoti* will be also important to increase resistance in both MPAs in St. Croix. However, this species will not help the system to return its original states because of the intermediate trophic level and high number

of broad taxonomic groups included in the diet. Therefore, depending on goals established by managers to recover ecosystem functioning in fish assemblages of the U.S. Virgin Islands, we consider that this list can be an important resource to focus protection efforts on certain groups of species.

One important aspect to consider by managers when selecting species for increasing resilience or putting it back to original states is the potential conflict with local fisheries because of any change in species protection. At least 52% of the fish species comprising our analysis of ecological resistance between 2004 and 2006, have a commercial importance for local fisheries in the U.S. Virgin Islands. We consider that by looking into differences in resistance status within each surveyed area, feasible agreements with the fisheries to protect target species, and a complete surveillance in MPAs, managers will benefit of trait information to enhance ecosystem resilience or understand further trends in the trophic organization of novel fish assemblages in evaluated areas.

Figure 19. A conceptual framework to assign short-term resistance status to reef fish species based on pre and post-disturbance tolerance and species establishment.

4.6. Further directions

Compiling trait information of highly diverse assemblages such as reef fish communities represents an enormous and important effort to improve the knowledge in the trophic ecology of reef fishes. Even though we could not include all fish species registered in sites sampled by the NOAA, we consider that included fish species and traits are a good representation of the evaluated fish assemblages and show differences in the trophic ecology of reef fish species in the U.S. Caribbean. We included four functional traits related to the general trophic function of 180 reef fish species encompassing the maximum of fish species with complete trait information in the U.S. Virgin Islands. People can argue that four traits are not enough to show differences in functional diversity of fish assemblages. However, we included functional traits such as the habitat use and trophic level that have been successfully used to explain spatial differences in functional diversity among reef fish assemblages worldwide (Mouillot et al. 2013 a,b, Micheli et al. 2014, D'agata et al. 2016, Brandl et al. 2016). We also introduced the feeding time and community diet breadth as new traits in studies of functional diversity in coral reef fish communities. In the third chapter of this dissertation, we showed the importance of the trophic level and community diet breadth as the traits that better explains the spatiotemporal variability in functional diversity and organization of fish assemblages in the U.S. Virgin Islands. In addition, prior to start the fourth chapter of this dissertation, we conducted a sensitivity analysis with species that had complete information for four and six traits, and did not find differences in general spatiotemporal patterns of fish functional diversity. In general, we consider that the fish species and trait data included in this chapter were very useful to understand spatiotemporal changes in fish functional diversity and the ecological resistance of fish assemblages to a coral bleaching event in the U.S. Virgin Islands. Further studies will benefit from our trait

data base, and also can test the importance of other functional traits to capture spatial and temporal differences of fish functional diversity in the seascape.

Even though we tried to relate documented disturbances on coral reefs with changes in the fish functional trait space, we could not include *in situ* data on the benthic biotic cover and structural habitat complexity of coral reefs in this study. Further works can benefit of the in situ data to understand better the relationship between expression of functional traits in biotic communities and changes in habitat quality to improve actions to recover ecosystem functioning.

4.7.Conclusions

Functional diversity metrics and traits showed spatiotemporal differences in the trophic organization of fish species and are a useful addition to monitor the ecological performance of marine reserves to protect biodiversity features in response to management actions and disturbances. By using functional diversity metrics, important associations in changes in fish standing biomass and ecological resistance of species to disturbances were identified inside and outside marine reserves. We found that high fish functional richness and variation, and low evenness had a positive association with fish standing biomass at all levels of habitat protection evaluated in this study. We also found that the reduction in values of fish functional richness, the lack of return of fish functional richness to its original states, broader diet breadths, and reduction in trophic levels of tolerant fish species to coral bleaching events indicate an erosion of fish functional diversity in two studied MPAs, suggesting a lack of ecological resistance of fish assemblages to coral bleaching events and other perturbations. Finally, we proposed a framework based on the use of functional traits of tolerant and non-tolerant fish species to the coral bleaching event in 2005 from which reserve managers will benefit to understand consequences and anticipate impacts from future disturbance events on reef fish assemblages.

4.8.Acknowledgments

5. Conclusions

This dissertation was focused on understanding the use of functional diversity as a tool to achieve four goals. The first goal was to understand the trophic structure in fish communities and identify any knowledge gaps (Chapter 2). The second goal was to understand spatiotemporal changes in the functional organization of reef fish assemblages in the seascape (Chapter 3). The third goal was to monitor the ecological performance of Marine Protected Areas (MPAs), and the fourth one was to identify traits related to the ecological resistance of their reef fish communities in facing natural disturbances (Chapter 4). Few studies in the marine realm have used information on functional traits related to the trophic role of reef fish species, along with information on fish species abundance, to achieve these four goals in the Caribbean Basin.

Compiling trait information of highly diverse assemblages such as reef fish communities represents an enormous and essential effort to improve the knowledge in the trophic ecology of reef fishes. In Chapter 2, we conducted an extensive literature review of six functional trophic traits for juvenile and adult stages of 274 marine fish species known to occur in the U.S. Caribbean to understand the trophic structure in fish communities and identify any knowledge gaps. Trait descriptions were more comprehensive for adult life stages than juveniles, which hinders our understanding of the ecosystem function required to support ecosystem-based management and conservation efforts in the Caribbean. Also, we found that important efforts need to be done to record behavioral traits such as social feeding behavior, which was the poorest documented trait in adult and juvenile stages of reef fish species. From this chapter, a critical trait database was built, and it is available for other researchers interested in functional diversity. Single traits were extracted from single or several references to prove trait presence in fish species improving the quality of our data. Readers can verify traits in our dataset by reviewing original references. Few published studies on fish functional diversity in the Caribbean (or worldwide) provide this level of

completeness supported by sources and evaluation of data quality. Few published studies on fish functional diversity in the Caribbean provide so much detail on sources used to extract trait information for fish species as we did to inform the reader about data quality.

In Chapter 3, spatiotemporal variability in the trophic function of fish assemblages was documented in the Buck Island Reef National Monument (BIRNM) in the U.S. Virgin Islands to identify changes in coral reef communities along the seascape. We found that coral reef and other hard bottom areas supported high levels of trophic functional richness and variation among habitat types, but with low functional redundancy, evidenced by the unique trophic role that each fish species had within the functional trait space. The temporal variations found in functional trait composition during the last decade in the BIRNM, including change following a strong coral bleaching event in 2005, suggested that functional diversity descriptors are sensitive enough to track changes in the trophic organization of fish communities. In general, this chapter showed the utility of descriptors of functional diversity to evaluate changes in ecosystem functioning of heterogeneous habitats in the seascape.

Finally, in Chapter 4, we used descriptors of functional diversity and traits as tools to 1.) evaluate the ecological performance of MPAs, 2.) study the association of fish functional diversity in ecosystem services such as production of fish standing biomass; and 3.) identify the ecological resistance of fish communities to the coral bleaching event in 2005 in the U.S. Virgin Islands. Functional diversity metrics and traits showed spatiotemporal differences in the trophic organization of fish species and were a useful addition to monitor the ecological performance of marine reserves to protect biodiversity features in response to management actions and disturbances. By using functional diversity metrics, important associations with changes in fish standing biomass and ecological resistance of species to disturbances were identified inside and outside marine reserves. We found that high fish functional richness and variation, and low evenness had a positive association with fish standing biomass at all levels of

habitat protection evaluated in this chapter. We also found a functional erosion of fish assemblages in two studied MPAs, suggesting a lack of ecological resistance of fish assemblages to coral bleaching events and other perturbations. Indicators of erosion in fish functional diversity to coral bleaching events included 1.) the reduction in values of fish functional richness, 2.) the lack of return of fish functional richness to its original values, 3.) trends toward broader diet breadths, and 4.) reductions in trophic levels of tolerant fish species after the coral bleaching event in 2005. Finally, we proposed a framework based on the use of functional traits of tolerant and non-tolerant fish species to the coral bleaching event in 2005 from which reserve managers will benefit to understand consequences and anticipate impacts from future disturbance events on reef fish assemblages.

In general, findings of this dissertation encourage the use of trait-based diversity metrics to understand spatiotemporal changes in the trophic organization of fish assemblages and resistance of fish assemblages to disturbances and to monitor the effectiveness of management strategies in marine ecosystems.

In this dissertation, we also faced and overcame important challenges by using functional diversity metrics in marine reef fish communities from the tropics. For us, it was essential to understand these limitations because they can lead to future directions in studies and management strategies associated with trait approaches in reef fish assemblages.

Understanding the ecological roles that juvenile fishes, as well as adults, play in the complex trophic relationships of coral reef systems determines if the available information on functional traits is sufficient to identify changes in their function by life stages. We emphasized that the primary goal of the second chapter was to compile and describe gaps in information for trophic traits of fish species recorded in Puerto Rico and the U.S. Virgin Islands (U.S. Caribbean). We focused on the U.S. Caribbean because this area is data rich about research on the trophic function in fishes, and the species recorded by the NOAA are also widespread across the broader Caribbean Basin, thus providing reliable

information of relevance to the broader region. Despite conducting a great effort by reviewing 337 studies to compile trait information for 274 reef fish species, we found gaps in knowledge of the trophic connections of fish species in different habitats, mainly on juvenile life stages and behavioral traits for both, adult and juvenile stages. In the third and fourth chapter of this dissertation, we had to exclude juvenile stages of reef fishes because trait information for these stages was scarce, and we were limited to use trait data from reef fish species that had complete information. Ecological roles of reef fishes in both adult and juvenile life stages are needed to understand their positions within multiple functional groups and to make forecasts of effects caused by species or biomass decline in coral reef systems (Micheli et al. 2014). We have recognized that the lack of knowledge in traits of juvenile stages is a limitation to monitor spatiotemporal changes of fish functional diversity in reef dynamics and to support ecosystem-based management and conservation efforts for juvenile stages in the Caribbean. We consider that there is a need to continue working on methods to characterize functional diversity under data poor scenarios. Fish families with complete trait information were primarily those with species of commercial importance, and those commonly included in the characterization of trophic functional groups in reef fish communities. Field characterizations and stable isotopic analysis that describe the trophic function of non-commercial and cryptic reef fish species in the Caribbean are needed to fill gaps in knowledge of the trophic roles of fish species for adult, as well as for juvenile stages at different habitats.

Functional diversity metrics are sensitive to available information about species' functional traits used to define ecosystem functioning. We included a variety of ecological traits related to the general trophic function of reef fishes such as trophic levels, closely related to fish body size, but also included levels of specialization in diet and behavioral traits that described fish trophic roles in terms of space (habitat type), time (time of feeding), and inter and intraspecific interactions. We consider that our approach to identify differences in the trophic role of fish species for assemblages in the U.S. Caribbean is accurate because trait

information was extracted mainly from studies conducted in this part of the Caribbean, and we accounted for geographic variation in trait values. For example, values of trophic levels and diet breadth for fish species depend on the local availability of prey items, and it varies within the Caribbean Region. We predominantly extracted diet information from studies conducted in the U.S. Caribbean to avoid trait generalization by including studies around the Caribbean Region. By filtering diet studies by location, we limited the number of references cited for trophic levels and diet breadths in our trait database, but increased accuracy in diet information, which is vital for researchers using our dataset in the U.S. Caribbean. We encourage researchers to describe the geographic scope of the trait values compiled in their studies because it may lead to different conclusions about the importance of traits to explain variation in functional diversity of reef fish assemblages at different spatial scales.

It is also known that the loss or addition of traits in functional diversity analysis may have effects on findings on ecosystem functioning of communities (Hillebrand and Matthiessen 2009). We found diet breadth and trophic level important to explain variation in functional diversity and dispersion among the traits used in chapter three. Other works in the Caribbean have found other traits such as the trophic group of fish species to be important to explain the variation of fish functional diversity worldwide (Stuart-Smith et al. 2013) and in the Caribbean (Michelli et al. 2014). These studies used other ecological traits such as diet (Halpern and Floeter 2008, Micheli et al 2014, Mouillot et al. 2014, D'agata et al. 2016), body size, adult mobility and habitat use to calculate species richness and evenness within functional groups (Micheli et al 2014, Mouillot et al. 2014, D'agata et al. 2016). We consider that further works can be focused on the standardization of methods to allow comparisons of particular ecosystem functions and functional diversity patterns at regional levels. These studies can consider selecting those traits that have contributed more to explain variation in the functional trophic organization of fish assemblages at the Caribbean basin.

Few sites are monitored in the Caribbean basin as thoroughly as evaluated areas by the NOAA in the U.S. Virgin Islands between 2002 and 2012. We had the advantage of using a large database of fish species presence and biomass that covered large extensions of coral reef areas in the U.S. Caribbean. Even though we could not include all fish species registered by the NOAA in the third and fourth chapter of this dissertation, we consider that included fish species and traits are a good representation of the evaluated fish assemblages, and that they showed differences in the trophic structure of reef fish assemblages in the U.S. Caribbean. We included six functional traits related to the general trophic function of 95 reef fish species in the third chapter, and four functional traits of 180 reef fish species in the fourth chapter by including the maximum of fish species with complete trait information in the U.S. Virgin Islands. Other researchers can argue that the number of traits or species included in this dissertation was not enough to show differences in functional diversity of fish assemblages. However, we included functional traits such as the habitat use and trophic level that have been successfully used to explain spatial differences in functional diversity among reef fish assemblages worldwide (Mouillot et al. 2013 a,b, Micheli et al. 2014, D'agata et al. 2016, Brandl et al. 2016). We also introduced the feeding time and community diet breadth as new traits in studies of functional diversity in these communities. In the third chapter, we showed the importance of the trophic level and community diet breadth as the traits that better explains the spatiotemporal variability in functional diversity and organization of fish assemblages in the U.S. Virgin Islands, and because of this importance, we included them in the fourth chapter of this dissertation. In addition, before starting this last chapter, we conducted a sensitivity analysis with reef fish species from the U.S. Virgin Islands that had complete information of four (n = 180 species) and six traits (n = 113 species) accounting for size effects from functional trait information on functional diversity metrics. We did not find significant differences in spatiotemporal patterns of fish functional diversity between these set of fish species, providing robustness to our decisions about the number of species and traits to be included

in the analysis. In general, we consider that the reef fish species and trait data included in these chapters were useful to understand spatiotemporal changes in fish functional diversity and the ecological resistance of fish assemblages to a coral bleaching event as we measured them in the U.S. Virgin Islands.

The inclusion of functional diversity descriptors of the trophic organization of fish assemblages in ecosystem-based management for coral reef areas or Marine Protected Areas (MPAs) implies the compilation of information about the functional roles and abundance of reef fish species. The compilation of this information is an outstanding effort that can be accomplished through collaborations between managers and academia since both can benefit from generated information about the ecological resilience of biotic communities. However, the understanding of functional diversity and its influence on ecological resilience of biotic communities requires of long-term information about natural and human disturbances on these communities. For example, even though we tried to relate documented disturbances on coral reefs with changes in the fish functional trait space, we could not include *in situ* data on the benthic biotic cover and structural habitat complexity of coral reefs in this study. Neither, we could include information about fishing intensity by levels of protection evaluated in the U.S. Virgin Islands, which could be useful to separate the effects of habitat structure, changes in biotic cover, and illegal fishing inside MPAs on fish functional diversity. Further works can benefit from the data on the benthic structure of coral reefs, as well as on disturbance intensity, to understand better the relationship between the expression of functional traits in biotic communities and changes in habitat quality to improve actions to recover ecosystem functioning in the Caribbean.

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APPENDICES

Appendix A. Supplementary material for Chapter 3

Table A 1. Temporal and spatial distribution of survey sites conducted by NOAA in the BIRNM.

	Year	2002		2003		2004		2005		2006		2007	2008		2009		2010
Habitats	Semester	1	2	1	2	1	2	1	2	1	2	2	1	2	1	2	2
Coral Reef and Colonized Hard bottom		37	37	43	39	28	44	42	48	46	49	51	42	46	39	47	42
Submerged Vegetation		23	18	24	13	4	8	10	8	6	8	1	3	7	7	6	10
Total		60	55	67	52	32	52	52	56	52	57	52	45	53	46	53	52

Supplementary Methods and Results

Methodological issues with available trait information for functional diversity analysis

Tradeoffs between species numbers and available trait information were identified to understand how many traits and species were needed to characterize the trophic function of fish assemblages in the BIRNM, but also to recognize potential issues to characterize the trophic function under data poor scenarios. Functional diversity metrics per habitat were calculated by varying levels of completeness in trait information for the 166 fish species registered during surveys between 2002 and 2010. Species were clustered in 3 groups: species with complete trait information (n=95 species), species with majority of trait information (n = 133 species), and species with incomplete trait information (n=165 species). The first group included species that had information for the six traits used in this study, and represented 57% of total registered fish species in the area. The second group included species with information of five or six traits, representing 80% of total fish species. The third group included species with information of at least 1 trait, and represented 100% of registered species.

Functional diversity metrics were calculated by using the PAST Program Version 3.08 (Hammer 2015) and FD package (Laliberté et al. 2015) available for R Project for Statistical Computing, and were described for each habitat type. A non-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008) was used to test for spatial and temporal variations in functional diversity indexes within species groups, and trends in functional diversity metrics were used to understand effects of trait availability on observed values of fish functional diversity. Analyses were conducted using the PAST Program Version 3.08 (Hammer 2015).

Functional diversity metrics and species richness varied by time and habitat type with no interactions between these factors at all groups, except for functional dispersion and evenness values calculated with species with complete, majority and incomplete trait information (Table A2). All levels of trait information showed that coral reefs and 2006

were the habitat and year with the highest values of species richness, functional richness,
dispersion and evenness (Fig. A1).

Table A 2. PERMANOVA results on functional diversity metrics calculated with
different levels of in trait information.

Trait information	Metrics	Time of survey	Habitat type	Time x habitat	Residual	Total
Complete	df	8	1	8		
	SR	2.314*	22.147*	-38.245	665	682
	FRic	1.569*	27.473*	-38.859	665	682
	FDis	1.65*	18.481*	-37.439*	665	682
	FEve	1.218*	1.173	-36.401*	665	682
Majority	df	8	1	8		
	SR	1.889*	44.836*	-38.895	701	718
	FRic	1.0314	50.424*	-39.844	701	718
	FDis	1.7235*	24.016*	-34.595*	701	718
	FEve	0.798	0.008	-36.093*	701	718
Incomplete	df	8	1	8		
	SR	1.753*	87.246*	-37.271	730	747
	FRic	3.051*	69.967*	-37.787	730	747
	FDis	2.897*	48.115*	-35.458*	730	747
	FEve	1.895*	4.339*	-29.893*	730	747

Notes: Evaluated metrics were species richness (SR), functional richness (FRic),
functional dispersion (FDis), and functional evenness (FEve). * denotes p-value < 0.05.

We observed similar spatiotemporal trends in functional diversity metrics at all levels
of completeness of functional trait information; however the magnitude of values varied
according to species number and completeness of trait information (Fig. A1). We
understand that variability in magnitude of metrics such as functional dispersion is an
artifact of gaps in species trait information, which were interpreted as equal trait values
among species in the analysis. These gaps reduced the variability in the trophic function
of species groups with incomplete and majority of trait information producing sub
estimation in functional dispersion values. After this analysis we decided to work with

species that had complete trait information to avoid overestimations of functional redundancy and because trends of functional diversity metrics for this group followed general patterns observed for all species groups.

Figure A 1. Functional diversity metrics calculated with different levels of fish functional trait information.

Association among functional traits

We used the Cramer's V index to analyze the level of association among functional traits, and to avoid trait redundancy in functional diversity calculations. This index is based on categorical values of nominal variables and calculates the intercorrelation between two variables. The statistical significance of Cramer's V indices is calculated

using the Pearson's chi-squared test (Cramer 1946). Cramer's values were calculated with PAST Program Version 3.08 (Hammer 2015). Pair of traits with Cramer's values higher than 0.50 indicated that two variables are probably measuring the same concept (Cohen 1988), and needed to be excluded from functional diversity calculations. We did not exclude any of our chosen traits because all pairwise comparisons showed Cramer's values < 0.5 and they were not statistically significant (Table A3). Traits with a tendency for association, such as vertical habitat associations and feeding grounds, were not excluded from functional diversity calculations because we considered that both traits describe better how fish perceive the variability in spatial contexts of marine habitats, and during their ontogenetic shifts. It is reasonable to keep these traits since marine fishes perceive a three dimensional heterogeneous area comprised by habitat patches, horizontally and vertically distributed, within continuous or discontinuous spatial gradients (Pittman and Olds 2015, Bouchet et al. 2015). We also kept these traits because the complexity in habitat use also influences spatial and temporal composition of species in fish assemblages, which directly influence functional diversity values.

Table A 3. Cramer's V indices for functional traits

	VHA	SFB	TF	FG	TL	DB
VHA		0.299	0.123	0.505*	0.274	0.150
SFB			0.077	0.196	0.227	0.161
TF				0.367*	0.339	0.170
FG					0.258	0.226
TL						0.304

Notes: Evaluated traits were vertical habitat association (VHA), social feeding behavior (SFB), time of feeding (TF), feeding grounds (FG), trophic level (TL), and diet breadth (DB). * denotes Significance level: p-value <0.001

Evaluation of sample size effects on temporal patterns of functional diversity

We conducted a bootstrapping analysis (Efron 1982) and Mann-Whitney pairwise comparisons on mean values of functional diversity metrics for 4, 10, and 20 survey sites per habitat type to evaluate the effects of different sample sizes among surveyed periods. Means of functional diversity metrics were calculated per habitat and surveyed time from a total of 999 sampling events without replacement. We excluded surveyed periods with less than 4 samples and bootstrapped means calculated from the same set of 4, 10 or 20 samples from sampling size analysis. Mann-Whitney comparisons between calculated mean values for same surveyed periods indicated that there was not sample size effect on means of functional diversity metrics (p-values > 0.05). Trends from bootstrapped data and the whole dataset were visually compared to evaluate if observed temporal patterns in fish functional diversity were consistent. Bootstrapped mean values of FRic, FDis and FEve supported observed trends in raw data, indicating that observed temporal trends in functional diversity metrics within and between habitats were not biased by sample size (Fig. A2). Bootstrapping was conducted by using the R Project for Statistical Computing, and Mann-Whitney pairwise comparisons were conducted using the PAST Program Version 3.08 (Hammer 2015).

We conducted Mann-Whitney pairwise comparisons by surveyed periods to identify temporal changes in functional diversity metrics within years in raw data. No differences between semesters within the same year were found, so we combined data by years to simplify patterns of fish functional diversity (Mann-Whitney test; p-value >0.05). Mann-Whitney pairwise comparisons were conducted using the PAST Program Version 3.08 (Hammer 2015).

Figure A 2. Functional diversity metrics for fish assemblages by survey period (year-semester). Survey periods were indicated by numbers "1" for first and "2" for second semester of a year. Resampled mean values of functional diversity metrics were show

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Appendix B. Supplementary material for chapter 4

Figure B 1. Differences in functional trait values between common and rare species. Trait values for the column feeding position included benthic (B), demersal (D), midwater (M), surface (S) and all positions in the water column (All). Feeding times included diurnal (D), crepuscular (C), and nocturnal hours (N), as well as feeding activities along 24 hours (All).* denotes p-values <0.05, ** <0.01, and *** <0.0001. Differences in trait values were evaluated with pair-wise Mann-Whitney tests using the PAST Program Version 3.08 (Hammer 2015).

Figure B 2. Contribution of trophic levels to the total fish standing biomass in the U.S. Virgin Islands. Surveyed areas in St. Croix were the No-Take MPA Buck Island National Reef Monument (BUIS) and Area with Multiple Uses East End Marine Park (EEMP). Areas surveyed in St. John were unprotected areas (NONE), the No-Take MPA Virgin Islands National Reef Monument (VICR), and the area with Multiple Uses Virgin Islands National Park (VIIS).

Figure B 3. Differences in functional trait values between winners and losers species in pre and post disturbance periods according to species rarity. (A-D) Trait values for all species, which included common and rare species at regional levels. (E-H) Trait values only for common species at regional levels. Letters with an asterisk above box plots indicate significant differences in trait values in comparison to single letters at each region (pair-wise Mann-Whitney test; p-value < 0.05). The dotted line serves as reference of median values for trophic levels of winner species inside the No-Take Zone Buck Island Reef National Monument (BUIS) in St. Croix and the Virgin Island National Park (VIIS) in St. John before the coral bleaching event in 2005. Surveyed areas in St. Croix were the No-Take MPA Buck Island National Reef Monument (BUIS) and Area with Multiple Uses East End Marine Park (EEMP). Areas surveyed in St. John were unprotected areas (Non), the No-Take MPA Virgin Islands National Reef Monument (VICR), and the area with Multiple Uses Virgin Islands National Park (VIIS).

Table B 1. Short term resistance of reef fish species to the coral bleaching event in 2005 in the U.S. Virgin Islands.

Note: Evaluated areas included the Buck Island Reef National Monument (BUIS) and East End Marine Park (EEMP) in St. Croix; and the Virgin Islands Reef National Monument (VICR), Virgin Islands National Park (VIIS), and unprotected areas (NONE) in St. John. Short term resistance status of reef fish species were assigned as highly tolerant (HT), non-observed (NO), opportunistic (O), and tolerant (T) species. Functional traits that described the trophic organization of fish assemblages are the water column feeding position (WCFO), feeding time (FT), trophic level (TL) and diet breadth (DB). Please refer to table 13 to understand trait categories assigned to each trait value.

Table B1. Short term resistance of reef fish species to the coral bleaching event in 2005 in the U.S. Virgin Islands.

Family	Species	Evaluated areas					Functional traits			
		BUIS	EEMP	VICR	VIIS	NONE	WCFP	FT	TL	DB
Acanthuridae	*Acanthurus bahianus*	O	O	HT	HT	HT	1	1	2	1
Acanthuridae	*Acanthurus coeruleus*	O	O	T	T	HT	1	1	2	1
Acanthuridae	*Acanthurus chirurgus*	T	O	T	O	O	1	1	2	2
Apogonidae	*Apogon townsendi*		NO				3	3	3.1	1
Aulostomidae	*Aulostomus maculatus*	NO	HT			O	1	1.5	4.3	2
Balistidae	*Melichthys niger*	O	O				2.5	1.5	2.4	4
Balistidae	*Balistes vetula*	T	HT	O	O	HT	1	1	3.9	4
Blenniidae	*Parablennius marmoreus*				O		1	1	2.34	2
Bothidae	*Bothus lunatus*	T	NO				1	2	4.5	2
Carangidae	*Carangoides ruber*	O	T	O	O	HT	3	4	4.39	3
Carangidae	*Caranx crysos*		O	O			5	4	4.4	4
Carangidae	*Decapterus macarellus*		O				3	4	3.4	2
Carangidae	*Trachinotus falcatus*					O	1	1.5	2.96	2
Chaenopsidae	*Acanthemblemaria maria*				NO		1	1	3.4	1
Chaetodontidae	*Chaetodon ocellatus*	NO					1	1	3.7	1
Chaetodontidae	*Chaetodon capistratus*	O	O	O	O	T	1.5	1	3.23	5
Chaetodontidae	*Chaetodon sedentarius*	O	O	T	NO	T	1	1	3.9	2
Chaetodontidae	*Chaetodon striatus*	O	O	T	T	T	1	1	3.2	4
Chaetodontidae	*Prognathodes aculeatus*					T	1	1	3.2	2
Cirrhitidae	*Amblycirrhitus pinos*	T				O	1	1	3.2	2
Diodontidae	*Diodon holocanthus*		O				2	4	3.45	2
Echeneidae	*Echeneis naucrates*			NO			3	4	3.1	3
Gerreidae	*Gerres cinereus*	HT	O				1	4	3.3	1
Gobiidae	*Coryphopterus glaucofraenum*	HT	O	O	O	T	2	1	2.7	3
Gobiidae	*Coryphopterus dicrus*	NO			O	O	1	1	2.7	5

Table B1 (Continued). Short term resistance of reef fish species to the coral bleaching event in 2005 in the U.S. Virgin Islands.

Family	Species	Evaluated areas					Functional traits			
		BUIS	EEMP	VICR	VIIS	NONE	WCFP	FT	TL	DB
Gobiidae	*Elacatinus chancei*	NO		O		O	1	1	3.5	3
Gobiidae	*Elacatinus evelynae*	O	O	T	O	T	2	1	2.56	1
Gobiidae	*Gnatholepis thompsoni*	O	HT	O	O	T	1	1	2.3	4
Gobiidae	*Coryphopterus eidolon*				O	NO	1	1	2	3
Gobiidae	*Coryphopterus personatus/hyalinus*			T	O	T	2	1	3	1
Grammatidae	*Gramma loreto*	O	O	O	O	O	2.5	1	3.31	2
Haemulidae	*Haemulon plumierii*	HT	T	T		HT	1	3	3.4	3
Haemulidae	*Haemulon carbonarium*	O		O	HT	T	1	3	3.3	2
Haemulidae	*Haemulon flavolineatum*	O	O	O	O	T	1	3	3.3	1
Haemulidae	*Haemulon melanurum*	O					1	1	2.2	1
Haemulidae	*Haemulon sciurus*	O	T	HT	O	O	1	3	3.28	4
Haemulidae	*Anisotremus virginicus*					HT	1	3	3.4	3
Holocentridae	*Myripristis jacobus*	HT	T	NO	NO	T	3	3	3.6	2
Holocentridae	*Sargocentron vexillarium*	O					1	3	3.5	3
Holocentridae	*Holocentrus adscensionis*	T	O	NO	O	O	1	3	3.5	1
Holocentridae	*Holocentrus rufus*	T	HT	T	O	T	1	3	3.5	2
Holocentridae	*Neoniphon marianus*					O	1	3	3.6	2
Labridae	*Halichoeres garnoti*	HT	HT	O	O	T	1	1	3.5	3
Labridae	*Halichoeres pictus*	NO		T	T	T	3	1	3.5	1
Labridae	*Halichoeres radiatus*	NO		O			1	1	3.3	1
Labridae	*Bodianus rufus*	O	O	HT	O	T	1	1	3.4	1
Labridae	*Halichoeres bivittatus*	O	O	O	O	HT	1	1	3.3	2
Labridae	*Halichoeres cyanocephalus*	O					3	1	3.6	1
Labridae	*Halichoeres maculipinna*	T	O	O	O	T	1	1	3.3	2

Table B1 (Continued). Short term resistance of reef fish species to the coral bleaching event in 2005 in the U.S. Virgin Islands.

Family	Species	Evaluated areas					Functional traits			
		BUIS	EEMP	VICR	VIIS	NONE	WCFP	FT	TL	DB
Labridae	*Halichoeres poeyi*	T	HT	O	O	T	1	1	3.4	2
Labridae	*Clepticus parrae*			T		O	3	1	3.3	2
Labridae	*Lachnolaimus maximus*					NO	1	1	3.3	1
Labridae	*Thalassoma bifasciatum*		O	O	O	O	5	1	3.3	4
Labridae	*Xyrichtys martinicensis*		O				1	1	3.5	1
Labridae	*Xyrichtys splendens*		O				1	1	3.1	3
Labrisomidae	*Malacoctenus macropus*	T	T	O		T	1	1	3.5	1
Labrisomidae	*Malacoctenus triangulatus*	T	O	O	HT	HT	1	1	3.5	1
Labrisomidae	*Malacoctenus boehlkei*				NO	O	1	1	3.5	1
Lutjanidae	*Lutjanus apodus*	O		HT		HT	1	4	4.2	2
Lutjanidae	*Lutjanus analis*	T	O	T			5	4	3.57	3
Lutjanidae	*Lutjanus mahogoni*	T	T				1	4	4.4	2
Lutjanidae	*Ocyurus chrysurus*	T					5	4	4.28	2
Lutjanidae	*Lutjanus griseus*				O		1	3	4.24	4
Lutjanidae	*Lutjanus synagris*					O	1	3	3.6	2
Malacanthidae	*Malacanthus plumieri*	T	HT				1	1	3.6	2
Monacanthidae	*Cantherhines pullus*	O		HT	HT	O	2	1	2.6	3
Monacanthidae	*Cantherhines macrocerus*					NO	2	1	3	2
Monacanthidae	*Monacanthus tuckeri*					NO	2	1	2.7	3
Mullidae	*Mulloidichthys martinicus*	O	O	HT	NO	T	1	4	3.2	3
Mullidae	*Pseudupeneus maculatus*	O	O	O	HT	T	1	3	3.5	3
Opistognathidae	*Opistognathus aurifrons*	T	HT	O		HT	1	1	3	3
Opistognathidae	*Opistognathus macrognathus*		NO				1	1	3.6	1
Ostraciidae	*Lactophrys triqueter*	T	HT				1	4	3.3	4

Table B1(Continued). Short term resistance of reef fish species to the coral bleaching event in 2005 in the U.S. Virgin Islands.

Family	Species	Evaluated areas					Functional traits			
		BUIS	EEMP	VICR	VIIS	NONE	WCFP	FT	TL	DB
Pempheridae	*Pempheris schomburgkii*		NO				3	3	3.1	2
Pomacanthidae	*Holacanthus tricolor*	O	O	O		T	1	1	3	2
Pomacanthidae	*Pomacanthus arcuatus*	O		T	O	T	1	1	2.9	4
Pomacanthidae	*Pomacanthus paru*	O	O	HT		T	1	1	2.9	3
Pomacanthidae	*Holacanthus ciliaris*			HT	O	O	1	1	3	2
Pomacentridae	*Stegastes adustus*	O	T	HT	O	HT	1	1	2.5	5
Pomacentridae	*Stegastes leucostictus*	O	HT	T	T	T	2	1	3.1	5
Pomacentridae	*Stegastes partitus*	O	HT	O	O	T	2	1	2	2
Pomacentridae	*Stegastes planifrons*	O	HT	T	O	T	1	1	3.3	5
Pomacentridae	*Stegastes variabilis*	O	O	O	O	O	1	4	2.5	3
Pomacentridae	*Abudefduf saxatilis*	T	HT		O	O	3.5	1	3.8	5
Pomacentridae	*Chromis cyanea*	T	O	O	O	HT	3	1	3.1	2
Pomacentridae	*Chromis multilineata*	T	O	T	NO	HT	3	1	3	3
Pomacentridae	*Microspathodon chrysurus*	T	O	HT	O	HT	1	1	2.1	4
Pomacentridae	*Stegastes diencaeus*	T	T		T	O	1	1	2.5	5
Scaridae	*Scarus iseri*	O	O	O	O	HT	1	1	2	1
Scaridae	*Scarus taeniopterus*	O	HT	O	O	T	1	1	2	2
Scaridae	*Sparisoma rubripinne*	O	T	T	O	T	1	1	2	2
Scaridae	*Sparisoma viride*	O	HT	O	O	HT	1	1	2	2
Scaridae	*Scarus vetula*	T	T	T	T	T	1	1	2.1	2
Scaridae	*Sparisoma aurofrenatum*	T	O	O	O	T	1	1	2	2
Scaridae	*Sparisoma chrysopterum*	T	HT	T	O	HT	1	1	2	1
Scaridae	*Cryptotomus roseus*				NO		1	1	2	1
Scaridae	*Sparisoma radians*		O				1	1	2	1
Sciaenidae	*Equetus punctatus*	NO				O	1	4	3.5	3

Table B1(Continued). Short term resistance of reef fish species to the coral bleaching event in 2005 in the U.S. Virgin Islands.

Family	Species	Evaluated areas					Functional traits			
		BUIS	EEMP	VICR	VIIS	NONE	WCFP	FT	TL	DB
Serranidae	*Hypoplectrus chlorurus*	NO		O	O	HT	2	1	3.8	2
Serranidae	*Cephalopholis fulva*	O	O	O	T	O	2	4	4.1	2
Serranidae	*Serranus tabacarius*	O	HT	O	O	T	2	1	4.2	1
Serranidae	*Epinephelus guttatus*	T	T	O	HT	HT	1	4	3.9	2
Serranidae	*Cephalopholis cruentata*		O	O	T	O	2	4	4.3	2
Serranidae	*Hypoplectrus aberrans*			O	T	HT	2	1	3.7	2
Serranidae	*Hypoplectrus nigricans*		T	HT	T	T	2	1	3.97	2
Serranidae	*Hypoplectrus puella*		NO	HT	T	T	2	1	3.7	2
Serranidae	*Hypoplectrus unicolor*		NO	T		HT	2	1	4	2
Serranidae	*Serranus tigrinus*			O		NO	1	1.5	3.7	2
Serranidae	*Serranus tortugarum*			O		NO	2.5	1	3.1	1
Sparidae	*Calamus calamus*			O		HT	2	1	3.29	2
Sparidae	*Calamus pennatula*					NO	2	1	3.51	2
Sphyraenidae	*Sphyraena barracuda*	T	O	T		HT	3	1.5	4.5	1
Synodontidae	*Synodus intermedius*	O		O		T	1	1.5	4.5	1
Tetraodontidae	*Canthigaster rostrata*	T	HT	O	O	HT	1	1	3.1	4

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