

Molecular and Life Sciences

**Functional diversity, redundancy and vulnerability of reef
fish assemblages in the Galápagos Archipelago**

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**This thesis is presented for the Degree of
Master of Research (Environmental Science) of
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AUTHORS DECLARATION

To the best of my knowledge and belief, this thesis contains no material previously published by any other person except where due acknowledgment has been made.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

ANIMAL ETHICS

The research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council Australian code for the care and use of animals for scientific purposes 8th edition (2013). The research study received animal ethics approval from the Curtin University Animal Ethics Committee, Approval Number # AEC_2014_09. The research was conducted under Galápagos National Park Directorate permit PC-17-15 and PC-28-16 granted to Dr Pelayo Salinas-de-León.

Signature:

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THESIS ABSTRACT

Globally, marine biodiversity loss is increasingly affecting marine ecosystem functioning. Therefore, marine managers and researchers are adopting a broader management focus to maintain long-term ecosystem functioning and services, alongside the historical objective of maintaining species diversity and specific taxonomic groups. Functional diversity assessments integrate ecosystem functioning into data analysis by quantifying the diversity of functional roles within an assemblage through incorporation of the biological and ecological functional traits of resident species. Functional diversity can more accurately assess marine community structure across environmental gradients, and ecosystem resilience and responses to environmental disturbance than traditional descriptors such as species richness and biomass.

In the Eastern Tropical Pacific, the remote Galápagos Archipelago has unique marine biodiversity composition and distribution patterns. Galápagos reef fish functional diversity is distinctly high compared to other reef fish faunas globally. It is also located within a region that is highly vulnerable to reef fish functional diversity loss following species loss. However, no research at the Galápagos Archipelago has assessed the patterns in reef fish functional diversity and vulnerability, and their relationship to marine ecosystem functioning. Marine ecosystem functioning is important, and it is likely that it has already been altered by marine habitat degradation and species disappearances caused by climate change and overfishing. Anthropogenic impacts are predicted to continue.

My research investigates marine ecological patterns and the community structure of Galápagos reef fish assemblages by assessing their functional diversity and vulnerability. Surveys using Stereo Baited Remote Underwater Stereo-Video systems (stereo-BRUVs) sampled coastal reef fish communities. Relative abundance data was estimated for 121 reef fish species based on a total of 41,594 individual fish. Reef fish functional diversity was then described using key reef fish functional traits relating to body size, trophic ecology, ecological niche, and social behaviour. These functional traits were used in combination to calculate different functional diversity and vulnerability indices.

In the first data chapter, Chapter 2, reef fish functional diversity was described using the three primary components of functional alpha-diversity (i.e. richness, divergence and evenness), functional beta-diversity and its two additive components (i.e. turnover and nestedness). Spatial patterns were then assessed across the four main Galápagos bioregions and the 19 geographic strata within them.

There were differences in reef fish functional diversity between bioregions, but similarities between communities (distinct marine habitat types). Low functional alpha-diversity (richness) within assemblages, but moderate functional beta-diversity between assemblages has

culminated in the high regional functional diversity that is distinct among global biodiversity patterns. The low alpha-diversity (richness) of functional roles is supplemented by a high divergence where a few reef fish species in high abundance represent specialised functional roles and support a large proportion of the total reef fish abundance. However, most functional roles are likely represented by a single species and low abundance, making Galápagos marine communities vulnerable to functional diversity loss following any species loss.

In Chapter 3, reef fish functional vulnerability is further investigated by distinguishing reef fish functional entities and quantifying a combination of functional diversity and vulnerability indices. The influence of geographic position, environmental variability and human management on functional entity distributions and richness were also assessed. Galápagos reef fish assemblages were highly vulnerable to functional diversity loss following species loss due to a low redundancy and high sensitivity of reef fish functional roles. Many of the reef fish functional roles with redundancy and resilience to species loss included piscivores, leaving most of the functional roles of the lower trophic levels represented by a single species and vulnerable. Variables relating to latitudinal environmental variation (i.e. sea-surface temperature and macroalgae cover) and marine habitat conditions (i.e. macroalgae cover, bottom incline and exposure to ocean currents) were important drivers of reef fish functional entities.

The study of local Galápagos reef fish functional diversity and vulnerability patterns refined conclusions drawn by larger-scale global and regional studies and reflected the previous biogeographical species composition patterns. By relating reef fish assemblages to key aspects of ecosystem functioning, this research extends ecological understanding beyond traditional taxonomic structure. An understanding of the functional importance of reef fish species and the current trophic diversity provides a baseline for long-term Galápagos marine ecosystem functioning and future monitoring. Using a combination of species and functional diversity metrics in future research in the Galápagos will more accurately describe marine community variation and integrate ecosystem functioning into marine biodiversity studies.

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STATEMENT OF CONTRIBUTIONS

CHAPTER 2

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LIST OF ABBREVIATIONS

AIC	Akaike Information Criterion
AICc	Corrected Akaike Information Criterion
CAP	Canonical Analysis of Principal coordinates
Chlo-a	Chlorophyll-a
dbRDA	Distance-based Redundancy Analysis
DistLM	Distance-based Linear Modelling
ETP	Eastern Tropical Pacific
FE	Functional entity
GLM	Generalised linear model
GMR	Galápagos Marine Reserve
MSD	Mean Squared Deviation
PERMANOVA	Permutational Multivariate Analysis of Variance
PcoA	Principal Coordinates Analysis
RSS	Residual sum of squares
SE	Standard Error
SST	Sea-surface temperature
stereo-BRUV	Baited Remote Underwater Stereo-Video system
UPGMA	Unweighted pair group method with arithmetic mean clustering algorithm

CHAPTER 1

General Introduction

1.1 The Galápagos Archipelago

1.1.1 The Galápagos Archipelago

The Galápagos Archipelago is a series of islands and rock formations of volcanic origin located in the Eastern Pacific Ocean (Snell et al., 1996). The archipelago is located approximately 1000km west of mainland Ecuador on the equator ($01^{\circ}40'N-01^{\circ}25'S$ and $89^{\circ}15'W-92^{\circ}00'W$) (Snell et al., 1995). The Galápagos is renowned because of Charles Darwin's visit aboard the H.M.S Beagle in 1835. Darwin's observations of the iconic terrestrial fauna and flora species that had evolved in isolation for hundreds of thousands of years inspired the 'Theory of Evolution by Natural Selection, which revolutionised our understanding of the Earth's biodiversity (Darwin, 1859). Early European visitors also noticed a comparatively cool climate compared to other places on the equator (Dampier, 1729; Darwin, 1889; Snell & Rea, 1999). The El Niño Southern Oscillation (ENSO) was later found to strongly influence climatic and oceanographic conditions in the region (Snell & Rea, 1999). Nowadays, the Galápagos remains an important location to research Earth's biodiversity owing to its location on the equator, isolation from the mainland and distinct climate (Bensted-Smith, 2002). Research has focussed on the unique terrestrial biodiversity, including Galápagos giant tortoises and Darwin's finches (Schiller et al., 2015). Research also explores its marine ecosystems as a natural 'field laboratory' to study spatial and temporal biodiversity patterns and the impacts of climate change and ocean warming on marine ecosystem functioning and resilience in the Anthropocene (Bustamante et al., 2000; Edgar et al., 2010; Salinas-de-León et al., 2020).

1.1.2 Galápagos marine environments

The Galápagos exists in a tropical region. However, its climate ranges between subtropical and temperate (Trueman & d'Ozouville, 2010). It is the only archipelago in the world at the intersection of three major current systems. The Panama current, which supplies warm water from the north-east, the Peru current, which supplies cold water from the south-east, and the Cromwell current, which supplies cold water from the deep (Banks, 2002; Houvenaghel, 1978). Furthermore, an equatorial undercurrent rises in the south-west where strong seasonal upwellings drive nutrient-rich ocean water into the archipelago (Banks, 2002). The currents mix warm, cool and productive ocean waters, creating important sea surface temperature gradients from south to north ($\sim 10^{\circ}C$ to $24^{\circ}C$) with high environmental variability, even at small spatial scales (Edgar et al., 2004a; Wellington et al., 2001). Physical and biological parameters have been used to describe patterns in marine environmental variability from north to south,

resulting in between three and five distinct bioregions being identified (Abbott, 1966; Edgar et al., 2004a; Jennings et al., 1994; Wellington, 1975).

1.1.3 Galápagos reef ecosystems and biodiversity

The Galápagos reef ecosystems sit on a relatively shallow platform surrounded by deeper waters (Christie et al., 1992; Geist, 1996). These marine habitats are relatively homogenous, primarily being composed of rocky reef interspersed with sand (Bustamante et al., 2002). However, small coral reefs and seaweed colonies exist where environmental conditions permit (Bustamante et al., 2008). The Galápagos marine ecosystems support unique assemblages, including species characteristic of tropical (e.g. reef sharks and corals), temperate (e.g. sea lions and kelp) and sub-Antarctic (e.g. fur seals and penguins) environments (Edgar et al., 2004a). There is also a diversity of reef fish species, with the most recent diversity update documenting ~463 nearshore species from four main sources: the Indo-Pacific, Panamic, and the mainland Peruvian and Chilean region (McCosker & Rosenblatt, 2010). High degrees of local and regional endemism also exist (Edgar et al., 2004a; McCosker & Rosenblatt, 2010).

The most recent Galápagos bioregionalization study assessed the distributions of reef species across the archipelago, including reef fish. Based on reef fish species diversity Edgar et al. (2004) recorded four main bioregions. A tropical far-north, a north-south “transition zone”, a mixed centre-south and a highly endemic cold-west. Reef fish species compositions differ between the Galápagos bioregions, characterised by a decreasing species richness from the tropical north to the temperate south reef fish faunas (Edgar et al., 2004a). Geographically separated to the far-north of the main Galápagos islands, the marine ecosystems of Darwin and Wolf Islands are most characteristic of the tropics with the highest average ocean temperatures, most extensive coral development and highest species richness (Edgar et al., 2004a; Wellington et al., 2001). These reefs host large abundances of tropical reef fish, including coral-reef associated species that support pelagic predators, culminating in the largest reef fish biomass recorded globally to date (Edgar et al., 2004a; Hearn et al., 2010; Hearn et al., 2014; Salinas-de-León et al., 2016). Just north of the central Galápagos islands lie Pinta, Marchena and Genovesa Islands, whose marine ecosystems represent a north-south transition zone between the tropical and temperate affinities. These reefs host reef fish species from the tropical Indo-Pacific and Panamic species with northward geographic ranges (Edgar et al., 2004a). The central and southern islands comprise the largest bioregion by geographical area. These reefs host the largest regional reef fish diversity of the bioregions, including large numbers of Panamic species and more endemism than the northern regions (Edgar et al., 2004a). Finally, separated from the central islands on the western side of Isabella, the marine ecosystems of the cold-west bioregion are temperate with the lowest average ocean

temperatures, most seaweed habitats, lowest reef fish species richness and the greatest number of endemics (Edgar et al., 2004a; Wellington et al., 2001). Furthermore, the eastward equatorial undercurrent rises here, resulting in high primary productivity compared to the rest of the archipelago (Pak & Zaneveld, 1973). These reefs support reef fish species from Peruvian origins with southward geographic ranges and high degrees of local and regional endemism that peaks in the Elizabeth Bay area, a possible sub-region and sink for primary productivity (Edgar et al., 2004a). Testament to its regional marine biodiversity, the Galápagos is recognised as a global marine biodiversity hotspot, a Marine Natural World Heritage site and is one of the world's largest marine reserves ("GMR", 138,000km²) (Heylings et al., 2002).

1.2 Functional diversity and vulnerability

1.2.1 Functional diversity

Marine ecological research and management increasingly aims to maintain long-term ecosystem functioning and services to humans instead of focussing on specific taxa or taxonomic groups (Díaz & Cabido, 2001; Moberg & Folke, 1999; Naeem et al., 2012; Palmer et al., 2004). To do so requires an understanding of the complex ecological and biological interactions that make up marine ecosystem functioning. Historically, taxonomic descriptors such as species richness and trophic groupings were used to study marine ecosystems. However, such metrics ignore the complex roles and services that species contribute to an ecosystem's functioning, which can vary widely between similar taxa (Kotowska et al., 2010; Mouillot et al., 2013a; Steneck, 2001; Villéger et al., 2010). Functional diversity analysis objectively describes ecosystem functioning by quantifying the diversity of ecosystem services (i.e. functional roles) in an assemblage (Díaz & Cabido, 2001; Petchey et al., 2009; Petchey & Gaston, 2006). Each species functional role is measured by unique combinations of biological or ecological characteristics that are linked to or determined by life within an environment (i.e. functional traits) (Cadotte et al., 2011; Díaz & Cabido, 2001; Petchey & Gaston, 2006; Violle et al., 2007).

In marine ecological studies, functional diversity has been applied to various habitats and taxa (Brandl & Bellwood, 2014; Mouillot et al., 2014; Ramírez-Ortiz et al., 2017). Reef fish represent a diverse and widely distributed group that play vital roles in ecosystem functioning, primarily by regulating food webs and recycling nutrients (Duffy et al., 2016; Holmlund & Hammer, 1999; Stuart-Smith et al., 2013). Functional diversity studies of reef fish have highlighted global marine biodiversity hotspots (Stuart-Smith et al., 2013), evaluated the resilience of ecosystems to disturbance (Micheli & Halpern, 2005; Mouillot et al., 2014) and complemented historical biogeographical studies (Olivier et al., 2018; Quimbayo et al., 2019; Ramírez-Ortiz

et al., 2017; Violle et al., 2014). Reef fish functional diversity differs across environmental gradients from tropical to temperate ecosystems (Quimbayo et al., 2019; Ramírez-Ortiz et al., 2017; Stuart-Smith et al., 2013). It is also thought that reef fish functional diversity loss is increasingly likely in a biological age of extinction (Graham et al., 2011; Naeem et al., 2012). Therefore, an assessment of reef fish functional diversity can complement traditional descriptors in biogeographical studies to assess ecosystem health, resilience, and responses to environmental disturbance more robustly (Bellwood et al., 2004; Cadotte et al., 2011; Mouillot et al., 2011; Tilman et al., 1997).

1.2.2 Functional diversity analysis methods

The functional diversity of an assemblage is determined by the unique combinations of functional traits present (Mouillot et al., 2014; Violle et al., 2007). The functional diversity of traits in an assemblage are then represented by different functional indices depending on the research objective (Mouillot et al., 2014; Violle et al., 2007).

For the spatial study of functional diversity, functional alpha-diversity assesses different aspects of within-community variation, while functional beta-diversity assesses variation between communities (Mouchet et al., 2010; Pavoine & Bonsall, 2011; Scluter et al., 2010). The spatial study of marine ecosystems is important to understand differences in marine ecosystem and/or community functioning across environmental gradients. The use of a combination of functional alpha-diversity and beta-diversity components can effectively identify spatial functional diversity patterns for a comprehensive regional functional diversity assessment while also prioritising conservation management efforts (Devictor et al., 2010a; Loiseau et al., 2017; Mason & De Bello, 2013).

For the study of community resilience, functional vulnerability assessments use the concepts of functional redundancy and sensitivity to estimate the likelihood that functional diversity loss will occur following species extinctions and predict likely community and ecosystem responses to different environmental disturbances (Parravicini et al., 2014). Functional roles are resilient due to redundancy when more than one species represents them. However, they are sensitive when represented by only one species (Bellwood et al., 2003; Fonseca & Ganade, 2001; Graham et al., 2011; Mouillot et al., 2014). Assessing the distribution of species in a community by their functional traits can effectively identify spatial functional vulnerability patterns and important functional roles to prioritise for conservation (Bellwood et al., 2003; Micheli & Halpern, 2005; Parravicini et al., 2014). Ultimately, functional diversity analysis is a biodiversity assessment that is independent of taxonomic structure that more accurately describes marine ecological patterns and ecosystem functioning and resilience compared to traditional

descriptors (Bellwood et al., 2004; Cadotte et al., 2011; Mouillot et al., 2011; Tilman et al., 1997).

1.3 Research significance

1.3.1 Research gaps

The Galápagos is distinct from other regions globally and within the Eastern Tropical Pacific because it has high functional diversity in its reef fish assemblages, even where taxonomic diversity is low (Quimbayo et al., 2019; Stuart-Smith et al., 2013). However, applied functional diversity studies within the Galápagos to date have been limited to categorising species into functional groups for further analysis. Functional group approaches have been used to distinguish macroinvertebrate and herbivore species in studies of subtidal environments (Brandt et al., 2012; Carr et al., 2018; Vinueza et al., 2006, 2014) or reef fish species according to trophic level in a modelling study of Floreana island (Bustamante et al., 2008; Okey et al., 2004). Existing spatial studies of Galápagos marine biodiversity primarily focus on the biology and ecology of species of 'greatest economic significance' to fisheries or tourism (Acuña-Marrero et al., 2018; Acuña-Marrero et al., 2017; Usseglio et al., 2015, 2016). The most comprehensive study of marine ecological patterns assessed coastal reef species distributions, including reef fish, and suggested that four main bioregions exist (Edgar et al., 2004a). However, to date no published study (but see Brandt, 2012) within the Galápagos has examined spatial variation in functional diversity, which is the basis of chapter 2 of my thesis.

Worldwide, reef fish assemblages have a high functional vulnerability (Mouillot et al., 2014; Parravicini et al., 2014). Furthermore, the Eastern Tropical Pacific region (where the Galápagos lies) is a reef fish functional sensitivity hotspot (Parravicini et al., 2014). Some studies in the Galápagos have focussed upon the vulnerability of threatened or endangered marine species (Edgar et al., 2008; Kaplan et al., 2014) or the effects of climate change and overfishing on marine habitats and species (Edgar et al., 2010; Glynn, 1988). However, patterns of functional vulnerability and the influence of environmental variation and human management on functional diversity within the Galápagos is a knowledge gap that remains. I address this gap in chapter 3.

1.4 Research aims and thesis structure

1.4.1 Research aims

The overarching aim of this thesis is to describe the functional diversity and vulnerability of marine fish communities throughout the Galápagos (Fig. 1.1). This objective will be investigated in two data chapters using a combination of functional diversity and vulnerability

analysis methods to assess coastal reef fish assemblages. Chapter 2 aims to quantify functional alpha-diversity and beta-diversity indices of reef fish assemblages and assess variation in functional diversity between bioregions and distinct marine habitat types with regions (Fig. 1.1). Chapter 3 aims to describe reef fish functional trait structure and vulnerability and to assess the influence of spatial and environmental variability and human management on functional diversity and vulnerability (Fig. 1.1).

1.4.1 Thesis structure

This thesis includes four chapters (Fig. 1): a general introduction (Chapter 1), two data chapters (Chapters 2 and 3) and a general discussion (Chapter 4). The two data chapters are written as stand-alone manuscripts. As a result, there is some repetition, particularly within the Methods sections. Chapter 2 has been peer-reviewed and published in the *Journal of Experimental Marine Biology and Ecology* (McKinley et al., 2022). Chapter 3 has been prepared for submission to the journal, *Diversity and Distributions*. Chapter 4 is a general discussion that draws together the outcomes of my research in terms of functional diversity of reef fishes in the Galápagos and globally and discusses the implications for marine conservation, spatial and fisheries management. Finally, I identify and discuss the opportunities and directions for future research that have arisen out of my thesis, in terms of both functional diversity patterns of the Galápagos, and functional diversity research methods. Chapters 1 and 4 are written from the first-person perspective (i.e. my research) while chapters 2 and 3 are written from the perspective of a collective of authors (i.e. “we collect”, “our research”).

Chapter 1 – General introduction

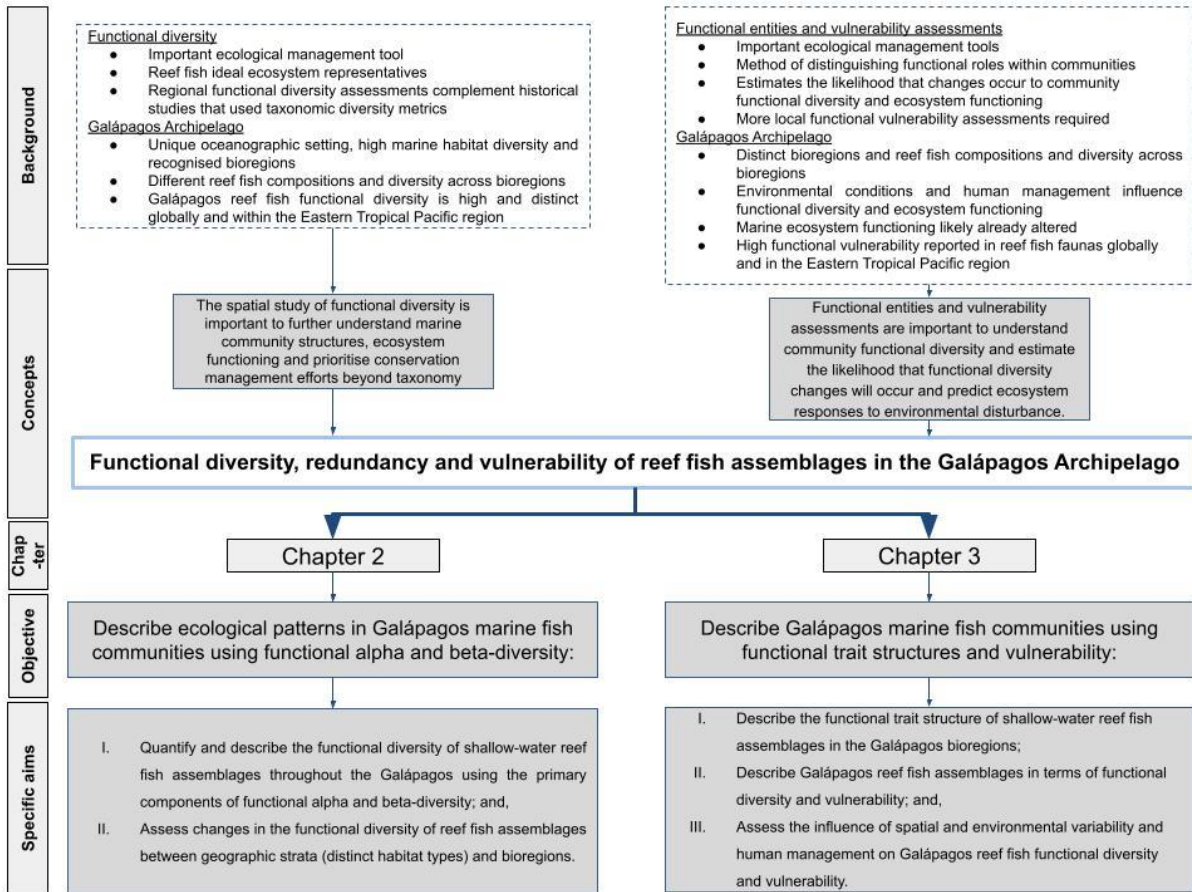


Figure 1.1. Conceptual diagram outlining the background, structure and aims of this research thesis.

CHAPTER 2

Functional diversity of reef fish assemblages in the Galápagos Archipelago

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This Chapter has been peer-reviewed and published in the Journal of Experimental Biology and Ecology (<http://doi.org/10.1016/j.jembe.2022.151695>) and is therefore formatted to their specific guidelines. However, for the consistency and readability of this thesis, the text, figures, and tables from the published manuscript are pasted under thesis headings and sub-headings.

2.1 Abstract

The Galápagos Archipelago's unique reef biodiversity and distribution patterns are relatively well understood compared to the study of local functional diversity processes. We investigated functional diversity patterns in coastal reef fish communities using stereo Baited Remote Underwater Video systems (stereo-BRUVs). We collected relative abundance data based on 41,594 individual fish belonging to 121 reef fish species and assessed functional diversity using seven functional traits and a combination of functional alpha-diversity and beta-diversity indices. We found differences between bioregions; however, we observed no differences in reef fish assemblages between the geographic strata (distinct habitat types) within regions. Low functional alpha-diversity within assemblages but high environmental variability at small spatial scales has resulted in a consistent moderate functional beta-diversity between assemblages and high functional diversity at an archipelago-wide scale. While there is a low diversity of functional roles, the most abundant species represent a few distinct and supportive functional roles in Galápagos reef ecosystems. Such functional roles likely have redundancy; however, many other functional roles are likely under-represented and vulnerable. The variable functional diversity between Galápagos bioregions facilitates an ecological interpretation that supplements traditional species diversity indices. Therefore, we suggest a combination of species compositions and functional diversity metrics be used in the future management of Galápagos marine communities.

Keywords: alpha-Diversity, beta-Diversity, Bioregion, Reef fish, stereo-BRUVs, Functional vulnerability

2.2 Introduction

The spatial study of marine ecosystems and their resident biodiversity is important to understand different marine community structures, assess ecosystem health, and prioritise conservation management efforts. Increasingly, marine ecological management's goal is to maintain long-term ecosystem functioning instead of specific taxa or taxonomic groups (Díaz and Cabido, 2001; Bellwood et al., 2004; Naeem et al., 2012). In recent decades, the concept of functional diversity has developed and become an important ecological assessment tool for better informing ecosystem management (Bellwood et al., 2002; Rincón-Díaz et al., 2018). Historically, traditional descriptors such as species richness and trophic groupings were commonly used. However, such metrics ignore the complex roles and services that species contribute to an ecosystem's functioning, health and resilience (Villéger et al., 2010; Mouillot et al., 2013b; Micheli et al., 2014; Boersma et al., 2016; Dee et al., 2016; Rincón-Díaz et al., 2018). Functional diversity analysis was developed on this premise, providing an objective method of integrating ecosystem dynamics into analysis by quantifying an assemblage's ecosystem services (i.e. functional roles) through measurable biological or ecological parameters (i.e. functional traits) (Díaz and Cabido, 2001; Petchey and Gaston, 2006; Petchey et al., 2009). Therefore, it has been suggested that functional diversity can more accurately assess ecosystem health, resilience and response to changes than traditional diversity metrics (Tilman et al., 1997; Bellwood et al., 2004; Cadotte et al., 2011; Mouillot et al., 2011). In marine ecological studies, functional diversity has been applied to various habitats and taxa (Brandl and Bellwood, 2014; Mouillot et al., 2014; Ramírez-Ortiz et al., 2017). Reef fish represent a diverse and widely distributed group that are relatively easy to sample and that play vital roles in ecosystem functioning (Stuart-Smith et al., 2013; Duffy et al., 2016). Functional diversity studies of reef fish have highlighted global marine biodiversity hotspots (Stuart-Smith et al., 2013), evaluated the resilience of ecosystems to disturbance (Micheli and Halpern, 2005; Mouillot et al., 2014) and complemented historical biogeographical studies (Violle et al., 2014; Ramírez-Ortiz et al., 2017; Olivier et al., 2018; Quimbayo et al., 2019).

The functional diversity of an assemblage is determined by the unique combinations of functional traits present (Violle et al., 2007; Mouillot et al., 2014). Functional traits are any measurable feature of an individual or species linked to or determined by life within an environment (Díaz and Cabido, 2001; Petchey and Gaston, 2006; Cadotte et al., 2011). Such traits are commonly related to morphology, behaviour, physiology, or phenology (Petchey et al., 2009). The functional diversity of traits in an assemblage are then represented by functional indices (Violle et al., 2007; Mouillot et al., 2014). Several functional diversity indices

have been developed and are distinguished by the spatial scale they consider. While most indices assess aspects of within-community diversity (alpha-diversity), other indices examine diversity between communities (beta-diversity) and regional diversity (gamma-diversity) (Mouchet et al., 2010; Schleuter et al., 2010; Pavoine and Bonsall, 2011). Functional alpha-diversity includes three primary components – functional richness, evenness, and divergence (Mason et al., 2005; Mouillot et al., 2005; Villéger et al., 2008). The analysis of all three elements is considered a complete quantification of alpha-diversity, as each describes an independent but complementary aspect of within-community functional diversity (Mouchet et al., 2010). Functional beta-diversity is analogous to the commonly used taxonomic beta-diversity index (Baselga et al., 2012; Villéger et al., 2013). The functional beta-diversity index describes the percentage of functional dissimilarity between assemblages and is the sum of two important ecological components, functional turnover and functional nestedness. For a comprehensive regional functional diversity assessment, the use of a combination of alpha-diversity and beta-diversity components can effectively assess regional functional diversity while also prioritising conservation management efforts (Devictor et al., 2010b; Mason and De Bello, 2013; Loiseau et al., 2017).

The Galápagos Archipelago is renowned for its unique oceanographic conditions and high environmental and marine habitat variability at small spatial scales (Wellington et al., 2001; Palacios, 2004). Straddling the equator 1000 km west of the continental coast of Ecuador, the archipelago comprises various islands and rock formations of volcanic origin (Snell et al., 1996). These exist at the intersection of three major current systems: the Panama current, which supplies warm water from the north-east; the Peru current, which supplies cold water from the south-east; and the Cromwell current, which supplies cold water from the deep (Houvenaghel, 1978; Banks, 2002). This convergence and the resultant mixing of productive ocean water creates important sea surface temperature (SST) and environmental gradients from north to south, and a range of marine habitats, from tropical to temperate reefs, which occur in close proximity to each other (Wellington et al., 2001; Edgar et al., 2004a). These habitats support unique assemblages of marine biodiversity that are characteristic of tropical, temperate, and sub-Antarctic environments (Edgar et al., 2004a).

The shallow water environments of the Galápagos host an abundance of reef fish species with ~463 nearshore fish species from four primary regions – the Indo-Pacific, Panamic, mainland Peruvian and Chilean region (McCosker and Rosenblatt, 2010). Additionally, high degrees of local and regional endemism exist (Edgar et al., 2004a; McCosker and Rosenblatt, 2010). In the tropical north, the islands of Darwin and Wolf are reported to host the largest reef fish biomass recorded globally (Salinas-de-León et al., 2016). The most comprehensive study of

the Galápagos' shallow-water environments to date quantified reef fish assemblages to identify bioregions that later assisted management decisions regarding the permanent establishment of conservation zones (Danulat and Edgar, 2002; Edgar et al., 2004a). According to species compositions and diversity, the Galápagos is distinguished according to four major bioregions – the tropical far-north, the north-south “transition zone”, the mixed centre-south and the highly endemic cold-west. To improve the current understanding of marine community structures throughout the Galápagos and assist future management decisions, it is important to integrate ecological functioning into species diversity studies.

Compared to other regions globally, the Galápagos is distinct in that it has high functional diversity, even where taxonomic diversity is low (Stuart-Smith et al., 2013). The Galápagos' functional diversity is also distinct within the Eastern Tropical Pacific (Ramírez-Ortiz et al., 2017; Quimbayo et al., 2019). High benthic habitat diversity and seasonal upwellings support unique assemblages of marine biodiversity and species richness in the Galápagos which are known to differ between bioregions (Edgar et al., 2004a; Edgar et al., 2011). Therefore, we hypothesise the functional diversity of reef fish assemblages will be high across the Galápagos as a whole and differ between bioregions.

This study aimed to describe ecological patterns in Galápagos marine fish communities using functional alpha and beta-diversity. To do this, we aimed to:

- I. Quantify and describe the functional diversity of shallow-water reef fish assemblages throughout the Galápagos using the primary components of functional alpha-diversity and beta-diversity; and,
- II. Assess changes in the functional diversity of reef fish assemblages between geographic strata (distinct habitat types) and bioregions.

2.3 Methods

2.3.1 Fish community data

2.3.1a Study site

Galápagos reef ecosystems exist on relatively shallow platforms (<200 m) surrounded by deeper waters (>1000 m) (Christie et al., 1992; Geist, 1996). Generally, marine habitats are rocky reefs interspersed with sand on sloping lava fields that vary in steepness (Bustamante et al., 2008). However, benthic components differ from tropical to temperate marine ecosystems across bioregions (Harris, 1969; Wellington, 1975; Edgar et al., 2004a).

Geographically separated to the north of the central Galápagos islands are Darwin and Wolf Islands, which comprise the Far-North bioregion. Its marine ecosystems are most

characteristic of the tropics with the highest average ocean temperatures, most extensive coral development and highest species richness (Wellington et al., 2001; Edgar et al., 2004a). Just north of the central Galápagos Islands lie Pinta, Marchena and Genovesa Islands, the North bioregion. Its marine ecosystems are on a more gradual bathymetric gradient than other regions and represent a north-south transition between tropical and temperate reefs (Harpp et al., 2002; Edgar et al., 2004a). The Centre-South bioregion includes most of the main Galápagos Platform and central and southern Galápagos Islands. These marine ecosystems include the largest regional diversity of marine environmental conditions and biodiversity (Witman and Smith, 2003; Edgar et al., 2004a). Separated from the central islands on the western side of Isabela is the Cold-West bioregion. Its marine ecosystems are temperate with the lowest average ocean temperatures and most macroalgae habitats (Wellington et al., 2001; Edgar et al., 2004a).

2.3.1b Sampling design

Shallow-water reef fish assemblages throughout the Galápagos Archipelago were sampled using Baited Remote Underwater Stereo-Video systems (stereo-BRUVs) along the 20-m depth contour. Sampling was conducted over two months (March–April) in 2015 prior to an El Niño Southern Oscillation (ENSO) (September 2015–April 2016) and the associated sea-surface temperature anomalies.

This study used a spatially stratified random sampling design thoroughly detailed in Acuña-Marrero et al. (2018). The archipelago was divided according to the bioregions defined by Edgar et al. (2004). Within each bioregion, all geographic features (islands, pooled groups of nearby islets, and submerged reefs shallower than 20 m depth) with a perimeter greater than 5000 m were identified. The perimeter around these geographic features was redefined along the 20-m depth contour because stereo-BRUVs were deployed approximately at this depth. The 20-m contour was then divided into unique geographic strata (marine habitat types). The strata were defined by scientists with substantial knowledge of the Galápagos based on the orientation, bathymetry (proximity to the 1000 m isobath) and exposure to oceanic currents within bioregions (*sensu* Edgar et al., 2004a). There were 19 unique geographic strata (distinct marine habitat types) defined across the Galápagos (Acuña-Marrero et al., 2018).

Within each stratum, a sample of candidate sites were placed along the 20-m depth contour separated by a minimum of 4 km. Two sites were then randomly selected except for larger strata where more sites were randomly selected for adequate representation (e.g. N1, Fig. 1). This allowed for eight stereo-BRUVs to be deployed at each site, separated by 500 m, and

alternating between two positions in the water column: near the sea-bed, benthic (~25 m water depth) and 15 m above the sea-bed, pelagic (~10 m below the surface). All deployments were made during daylight hours, for a minimum bottom time of 100 min, allowing for the first and last five minutes to be discarded, thereby minimising boat disturbance. Three hundred and twenty deployments were made across 43 sites within the four bioregions (Far-North $n = 2$ sites, North $n = 4$, Centre-South $n = 28$, Cold-West $n = 9$) and 19 unique geographic strata. (Fig. 1). The number of sites that could be sampled in each bioregion was determined spatially by habitat availability and the requirement for independence between samples. As a result, fewer sites could be sampled in the Far-North and North bioregions than in the large Centre-South bioregion.

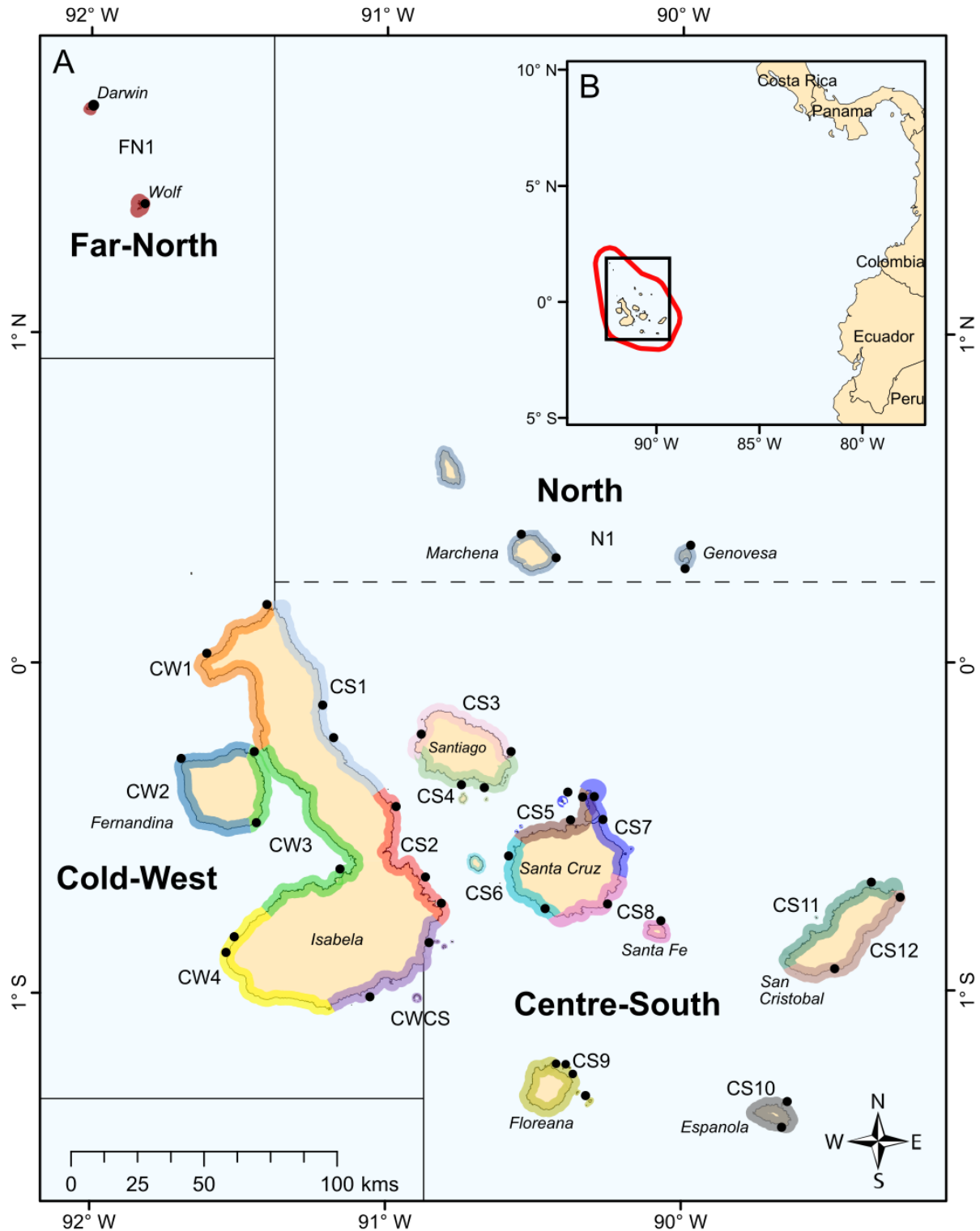


Figure 2.1.A. Location of the 43 sites sampled using stereo-BRUVs in 2015 (black dots). Bold text and lines indicate the four main bioregions – Far-North, North, Centre-South and Cold-West based on reef fish and invertebrate species communities (Edgar et al., 2004a). Capital letter acronyms denote the 19 unique geographic strata marked out along the coastline by different coloured shading. **B.** Location of the Galápagos Archipelago in the Eastern Tropical Pacific (ETP).

2.3.1c Stereo-BRUVs

Stereo-BRUVs are often used in marine research to sample fish assemblages, compare habitat types, and distinguish differences between areas (Langlois et al., 2020). Stereo-

BRUVs have been used to sample reef fish, commonly using metrics relating to abundance, species richness and functional group presence. Despite the introduction of bait-bias, stereo-BRUVs have been shown to sample across trophic levels (Watson et al., 2010; Logan et al., 2017; Harvey et al., 2018). Our survey used a stereo-BRUV design taken from Cappo et al. (2001) and Santana-Garcon et al. (2014) that was adjusted to mitigate entanglement and bait loss. The adjusted stereo-BRUVs were constructed from two GoPro Hero 4 high-definition cameras enclosed in SeaGIS stereo-video waterproof housing, mounted on a stainless-steel frame 70 cm apart with a six degrees converging angle. A rigid PVC pipe protruded in front of the cameras with a bait canister attached at the end. Each bait canister was filled with 800 g of chopped yellow-fin tuna (*Thunnus albacares*). Both benthic and pelagic deployments used similar frame design and were deployed at each respective target depth (i.e. ~25 m for benthic BRUVs and ~ 10 m for pelagic BRUVs) using an anchoring system made of a ballast weight and a set of buoys.

2.3.1d Data collection/video analysis

The software *EventMeasure* was used to analyse each 90-min video (www.seagis.com.au). Bony and cartilaginous fish observed were identified to species-level. Where a fish could not be identified to a species-level with confidence, individuals were pooled to genus or family (i.e. *Apogon* spp., *Mobula* spp., *Myliobatis* spp., *Triakidae* spp.) in the subsequent functional diversity analysis. Fish were quantified using the MaxN index of relative abundance (Ellis and Demartini, 1995; Cappo et al., 2003; Cappo et al., 2001). MaxN is the maximum number of individuals of a particular species in one still video frame across the entire deployment. Each deployment video was analysed and reviewed by three separate analysts for all species identifications and MaxN counts. For each species, presence and absence (coded 1/0) were recorded at each site, and MaxNs summed at the site level across benthic and pelagic deployments for use in further analysis. In total, three hundred and twenty video deployments were analysed (151 pelagic, 169 benthic), with twenty-four deployments removed due to equipment and video failures.

2.3.2 Functional diversity

2.3.2a Functional trait information

A functional trait matrix was compiled for 121 reef fish species sampled relating to life-history, trophic ecology and habitat use (Table 1; Tables S2.1, S2.2 and S2.3 in the Supplement). These elements were selected following the justifications of Mouillot et al. (2014) and analytical strategies laid out in previous studies of reef fish assemblages (D'agata et al., 2016; Richardson et al., 2017; McLean et al., 2019; Quimbayo et al., 2019; Siqueira et al., 2019). While body size and diet alone are considered to greatly represent the functional roles

of reef fishes (Bellwood et al., 2004; Lokrantz et al., 2008), the additional elements further represent biological and environmental interactions, including the influences of species on ecosystem processes and their responses to environmental change (Mouillot et al., 2013a, Mouillot et al., 2013b; Villéger et al., 2017; McLean et al., 2018) (see Table S2.4 in the Supplement for functional trait working definitions and ecological relevance). The matrix was developed following a comprehensive collection and review procedure. Information for the complete species list was initially extracted using the ‘*fishbase*’ package in R with original references reviewed (Boettiger et al., 2012; R Core Team, 2017; Froese and Pauly, 2019). According to data availability and relevance, the functional traits were then defined, aiming to distinguish trait categories and capture functional information. Where information gaps were present (primarily relating to water column position, substrate, and social associations), alternative sources were used, including the “Reef Fish Identification: Galápagos (Humann and DeLoach, 2003) as well as the “Shorefishes of the Tropical Eastern Pacific” online database (Robertson and Allen, 2015), that is considered a complete data source for fishes of the Eastern Tropical Pacific (Olivier et al., 2018). For the species identified as ‘spp’, information was recorded for the closest relatives (i.e. within the same genera) from a similar climate region. The authors also used their own experience and expertise to make informed decisions.

Table 2.1. Functional trait information for the seven functional traits used to assess the functional diversity of 121 reef fish species sampled in the Galápagos Archipelago in 2015.

Functional trait category	Functional Trait	Type	Units/levels
Body size	Maximum total length (cm)	Numeric	cm
Trophic ecology	Trophic level	Numeric	Position in the food chain
Trophic ecology	Diet breadth	Numeric	Trophic level standard error
Trophic ecology	Feeding behaviour	Factor	Variable Hunting Browsing Grazing Selective plankton feeding Filtering plankton
Ecological niche	Water column position	Factor	Pelagic Benthopelagic Benthic Demersal
Within-reef mobility	Substrate preference	Factor	Soft-bottom Rocky Coral reef
Social behaviour	Largest common group size	Ordered factor	Solitary to small groups Schooling

2.3.2b Functional trait space

To objectively build and select a representative functional space for computation of functional indices, the framework proposed by Maire et al. (2015) was used. Distances between species were first calculated using Gower's coefficient, which was chosen to handle different data types, giving them equal weighting (Gower, 1971). The R function, '*qual_funct_space*' was then applied, producing a functional dendrogram using the UPGMA algorithm and multidimensional functional spaces (MDS) for two to 10 dimensions using a principal coordinates analysis (PCoA), with Cailliez correction for negative eigenvalues (Cailliez, 1983). The functional dendrogram was of lowest quality, while functional spaces with five or six axes were the highest (Fig. S2.1 in the Supplement). However, four axes have been shown to effectively capture functional diversity variation in communities while requiring less computation time (Maire et al., 2015). Hence, four axes were used to compute functional diversity indices showing one of the lowest mean squared deviations (MSD = 0.0024) with the resulting Euclidean distances being strongly correlated with the initial Gower's distances ($r = 0.8826$, $p < 0.0001$) (Mantel and Valand, 1970; Legendre and Legendre, 2012; Oksanen et al., 2019). The function, '*qual_funct_space*', uses the '*ape*', '*clue*', '*cluster*', '*geometry*' and '*gtools*' libraries (Habel et al., 2019; Hornik, 2019; Maechler et al., 2019; Paradis and Schliep, 2019; Warnes et al., 2020).

2.3.2c Functional alpha-diversity indices

The three primary components of functional alpha-diversity were represented by the functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve) indices developed by Villéger et al. (2008). The indices were calculated using the R function, '*multidimFD*' that uses the '*ape*' and '*geometry*' libraries (Villéger et al., 2008; Mouillot et al., 2013b; Laliberté et al., 2014; R Core Team, 2017; Habel et al., 2019; Paradis and Schliep, 2019) using the MaxN data for each species. Functional richness is the proportion of total functional space filled by a species assemblage indicating the number of all possible functional trait combinations (herein 'functional roles') present in a community (Mason et al., 2005; Cornwell et al., 2006; Villéger et al., 2008). Functional divergence is the deviation of species abundances from the centre of the functional space indicating the proportion of the total abundance with the most specialised functional roles (Mason et al., 2005; Mouillot et al., 2013b). Functional evenness represents the distribution of species and abundances in the functional trait space, indicating if some functional roles are more dominant than others (Mason et al., 2005; Villéger et al., 2010).

2.3.2d Functional beta-diversity indices

Functional beta-diversity and its two additive components – functional turnover and functional nestedness – were represented by indices analogous to taxonomic beta-diversity (Baselga et al., 2012; Villéger et al., 2013). The indices were calculated using the R function, '*multiFbetaD*' that uses the '*betapart*' and '*geometry*' libraries (Baselga et al., 2018; Habel et al., 2019) and the Jaccard's dissimilarity index on presence and absence data for each species (Baselga et al., 2018). Functional beta-diversity is the total dissimilarity between two sites in the functional space and consists of functional turnover, a measure of the replacement of functional traits, and functional nestedness, a measure of the difference in functional richness (Villéger et al., 2013). Functional diversity index values were considered low when less than 0.5, moderate between 0.5 and 0.75 and high when greater than 0.75 (Mason et al., 2005).

2.3.3 Statistical analysis

To describe the functional diversity of reef fish assemblages, boxplots were created for each functional alpha-diversity and beta-diversity index for the four bioregions (Fig. 2). All plots were created using the '*ggplot2*' package (Wickham et al., 2020). To assess for differences in species richness and functional alpha-diversity, Euclidean distances between sites were computed and then tested using a two-way nested Permutational Multivariate Analysis of Variance (PERMANOVA, $\alpha = 0.05$) with factors 'bioregion' (fixed, four levels) and strata (fixed, 19 levels nested in bioregion). To assess for differences in functional beta-diversity, the pairwise matrices corresponding to the three functional beta-diversity indices were tested using a two-way nested Permutational Multivariate Analysis of Variance (PERMANOVA, $\alpha = 0.05$) with factors 'bioregion' (fixed, four levels) and strata (fixed, 19 levels nested in bioregion). Tests of terms in the full PERMANOVA model were done using Type III SS using 9999 permutations under a reduced model (Freedman and Lane, 1983). Significant PERMANOVA results between bioregions were then further assessed using pairwise *t*-tests with Monte Carlo bootstrapping (Manly, 2006). Any significant results between strata were not further assessed because pairwise tests cannot be conducted on nested factors. A Canonical Analysis of Principal Coordinates (CAP, $\alpha = 0.05$) with leave-one-out allocation was used to distinguish hypothesised groups ('bioregion') according to functional beta-diversity and functional turnover in multivariate space (Anderson and Robinson, 2003; Anderson and Willis, 2003). The PERMANOVA and CAP procedures were performed within the PERMANOVA+ package (Anderson et al., 2008) in PRIMER v7 (Clarke and Gorley, 2015).

2.4 Results

2.4.1 Functional diversity properties

The Galápagos Archipelago's reef fish communities had a low functional richness (<0.47), high functional divergence (>0.83), and moderate level functional evenness (>0.43 , <0.70) (Fig. 2B-D) compared to the published conventions (Mason et al., 2005). The far-north bioregion had the highest average (mean and median) species richness (Fig. 2A). The north bioregion had the highest average functional richness but the lowest average functional divergence (Fig. 2B-C). The north bioregion also had a similar average species richness to the far-north but with more variation (Fig. 2A). The centre-south had the highest average functional evenness and the greatest variation in species richness and functional richness (Fig. 2A, B and D). The cold-west had the lowest average species richness, functional richness and functional evenness but the highest average functional divergence (Fig. 2A-D).

The Galápagos had a moderate functional beta-diversity level between reef fish assemblages on average (mean < 0.48) (Fig. 2E-G) compared to the published conventions (Mason et al., 2005; Villéger et al., 2013). The contribution of its two additive components, functional turnover (<0.27) and functional nestedness (0.21), were low on average (Fig. 2F-G). The average functional beta-diversity in the cold-west and far-north was slightly higher than the centre-south and north bioregions (Fig. 2E). The north, centre-south and cold-west had a large range of functional beta-diversity values (Fig. 2E). The far-north was the only bioregion where functional nestedness contributed more to the overall average functional beta-diversity than functional turnover (Fig. 2F-G). In contrast, the cold-west had a greater contribution of functional turnover than functional nestedness. The north, centre-south and cold-west had a wide range of functional beta-diversity values between its reef fish assemblages, particularly the centre-south (Fig. 2E).

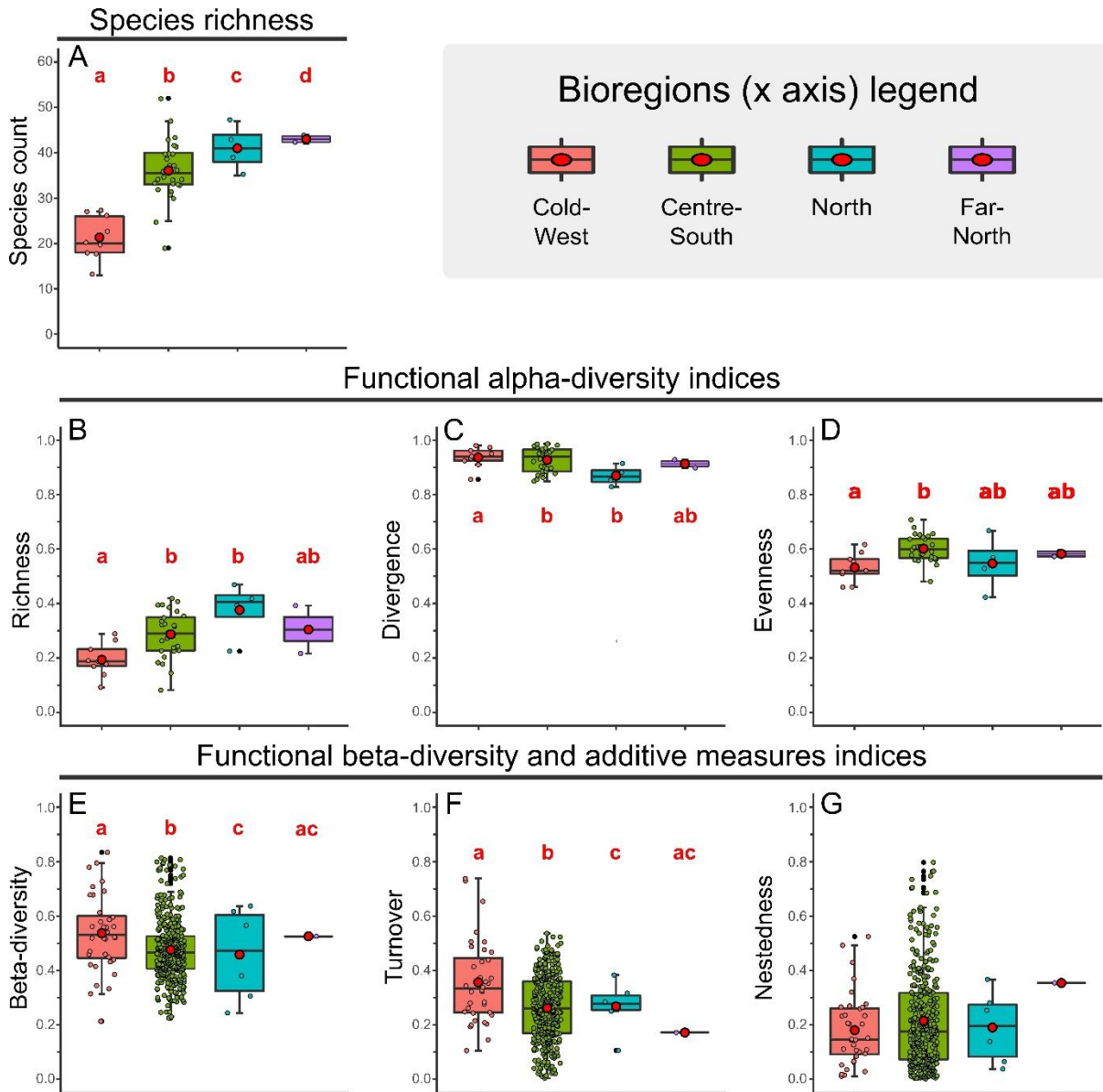


Figure 2.2. Boxplots of reef fish species richness and functional diversity indices for the four Galápagos bioregions. Top row: (A) species richness. Middle row: (B-D) the three components of functional alpha-diversity. Bottom row: (E-G) Functional beta-diversity and its two additive components. Each dot represents a site in the top and middle rows and a pairwise site comparison in the bottom row. The boxplots display medians (black line), upper and lower quartiles (boxes), and minimum and maximum $\pm 1.5 \times$ interquartile range (IQR) (whiskers), the mean (red circle) and outliers (black dots). Letters adjacent to boxes indicate differences between bioregions where bioregions do not share the same letter ($\alpha < 0.05$) based on pairwise *t*-tests in PERMANOVA with Monte Carlo bootstrapping.

2.4.2 Differences in functional diversity

The Galápagos' four bioregions differed significantly according to species richness, functional richness, and functional evenness (Table 2). The geographic strata were not significant for any of these tests (Table 2). The post-hoc pairwise comparisons of the significant PERMANOVA results showed that species richness was significantly different for every bioregion (Fig. 2). The cold-west differed significantly in functional richness and functional divergence to the centre-south and north (Fig. 2). The centre-south and cold-west were the

only significant differences in functional evenness (Fig. 2). The far-north did not differ significantly from any of the bioregions for any of the functional alpha-diversity indices. The bioregions also differed significantly according to functional beta-diversity and functional turnover but not functional nestedness (Table 3). Strata were only significantly different in the one test corresponding to functional beta-diversity (Table 3). The post-hoc pairwise comparisons of the significant PERMANOVA results showed the centre-south to differ from every other bioregion significantly, and the cold-west and north to differ (Fig. 2). However, no significant differences were found between the far-north and north and far-north and cold-west (Fig. 2).

Table 2.2. Two factor nested PERMANOVA for differences in species richness and functional alpha-diversity indices across bioregions and strata. Bioregion and strata are fixed factors with strata nested within bioregion. Bold emphasise significant differences at $\alpha = 0.05$.

Source	DF	Alpha-diversity indices											
		Species richness			Functional richness			Functional divergence			Functional evenness		
		MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Bioregion	3	485.89	15.824	<0.001	0.030	3.949	0.024	0.004	3.044	0.051	0.013	4.283	0.020
Strata(Bioregion)	16	44.725	1.455	0.217	0.006	0.841	0.632	0.002	1.691	0.108	0.003	1.010	0.478
Residuals	23	30.707			0.008			0.001			0.003		
Total	42												

Table 2.3. Two factor nested PERMANOVA for differences in functional beta-diversity and additive indices across bioregions and strata. Bioregion and strata are fixed factors with strata nested within bioregion. Bold emphasise significant differences at $\alpha = 0.05$.

Source	DF	Additive measures								
		Functional beta-diversity			Functional turnover			Functional nestedness		
		MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Bioregion	3	0.415	3.661	<0.001	0.249	6.127	<0.001	0.027	0.770	0.540
Strata(Bioregion)	16	0.146	1.285	0.038	0.057	1.408	0.132	0.035	0.988	0.489
Residuals	23	0.113			0.041			0.035		
Total	42									

The CAP plot for functional beta-diversity showed two main groups: a northern and a centre-south group with a dissimilarity gradient extending away from the main centre-south cluster. All the far-north sites and most north sites were separated from the other bioregions (Fig. 3). The misclassification of a far-north site into the north and a north site into the far-north supported this (Table 4). A north site was misclassified into the centre-south bioregion and vice versa (Table 4). A small group of sites, including a north site and four sites from the

centre-south, were separated from the remaining centre-south sites. The remainder of the centre-south sites were grouped (Fig. 3). A centre-south site was also misclassified into the cold-west and vice versa (Table 4). Sites from the cold-west bioregion were separated from the centre-south; however, some sites were more separated than others (Fig. 3). Enclosures in Fig. 3 highlight the more separated sites.

The CAP plot for functional turnover displayed similarities to the functional beta-diversity CAP plots (Fig. 3 and Fig. 4). The far-north sites and most north sites were still separated from the other sites but with a far-north site comparatively closer to the centre-south (Fig. 4). In contrast, the other far-north site was positioned closer to the north sites, supported by a far-north site's misclassification into the north (Fig. 4, Table 5). A north site was separated from all other sites and bioregions in the plot, while a north site was misclassified into the centre-south (Fig. 4, Table 5). Two sites from the centre-south were misclassified into the north (Table 5). Compared to functional beta-diversity, the centre-south group of sites was less tightly clustered with increased separation between some sites (Fig. 3 and Fig. 4). Some of the cold-west sites remained close to the centre-south sites while others were more separated (Fig. 4). In both CAP plots, sites in the same cold-west strata were more separated from the centre-south region than the other sites in the region (Fig. 3 and Fig. 4). Enclosures in Fig. 4 highlight the more separated sites.

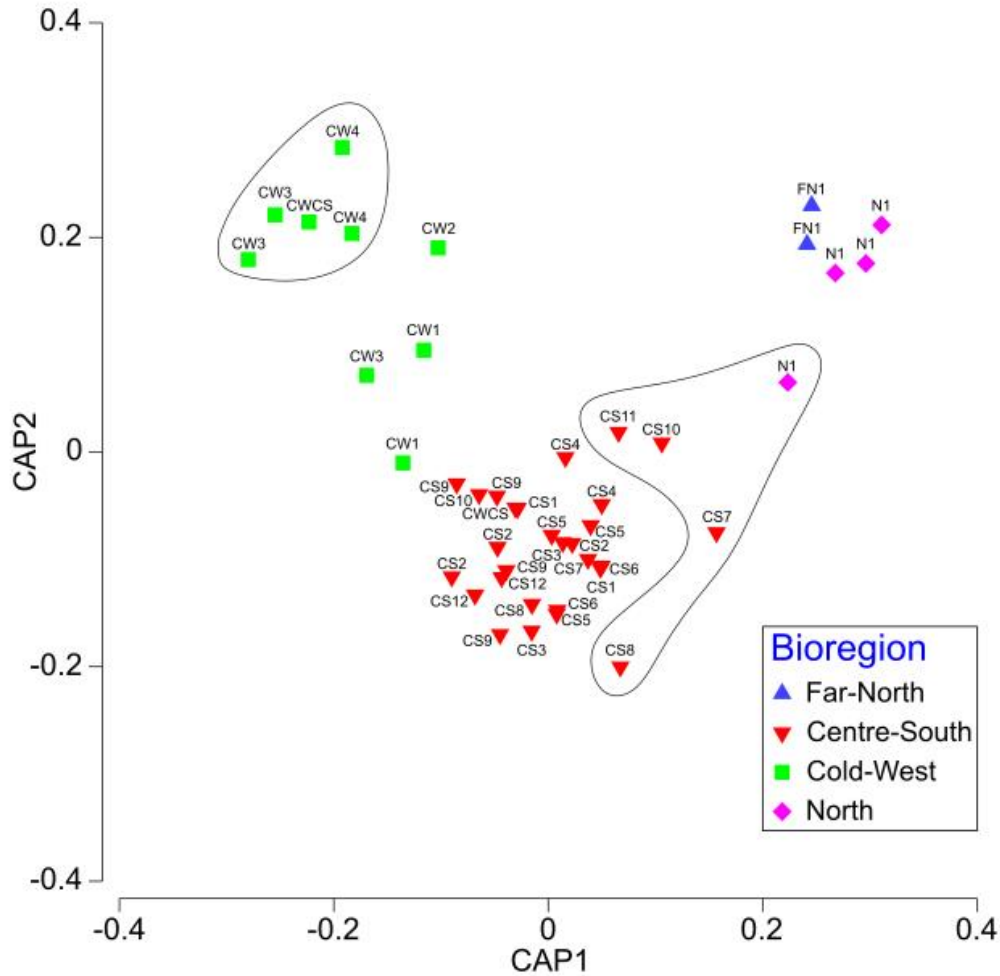


Figure 2.3. Canonical Analysis of Principal Coordinates (CAP) ordination of reef fish assemblages functional beta-diversity index for the four Galápagos bioregions. Coloured symbols are bioregions, and the abbreviated text labels are the geographic strata. Black circles indicate potential sub-groupings.

Table 2.4. Leave-one-out allocation cross-validation of sites to bioregions for functional beta-diversity in the Galápagos Archipelago according to reef fish assemblages sampled in March and April of 2015. The misclassification error was 14%. **Bold** emphasises misclassification.

Original bioregion	Classified bioregion					Total	%Correct
	Far-North	Centre-South	Cold-West	North			
Far-North	1	0	0	1	2	50	
Centre-South	0	26	1	1	28	92.857	
Cold-West	0	1	8	0	9	88.889	
North	1	1	0	2	4	50	

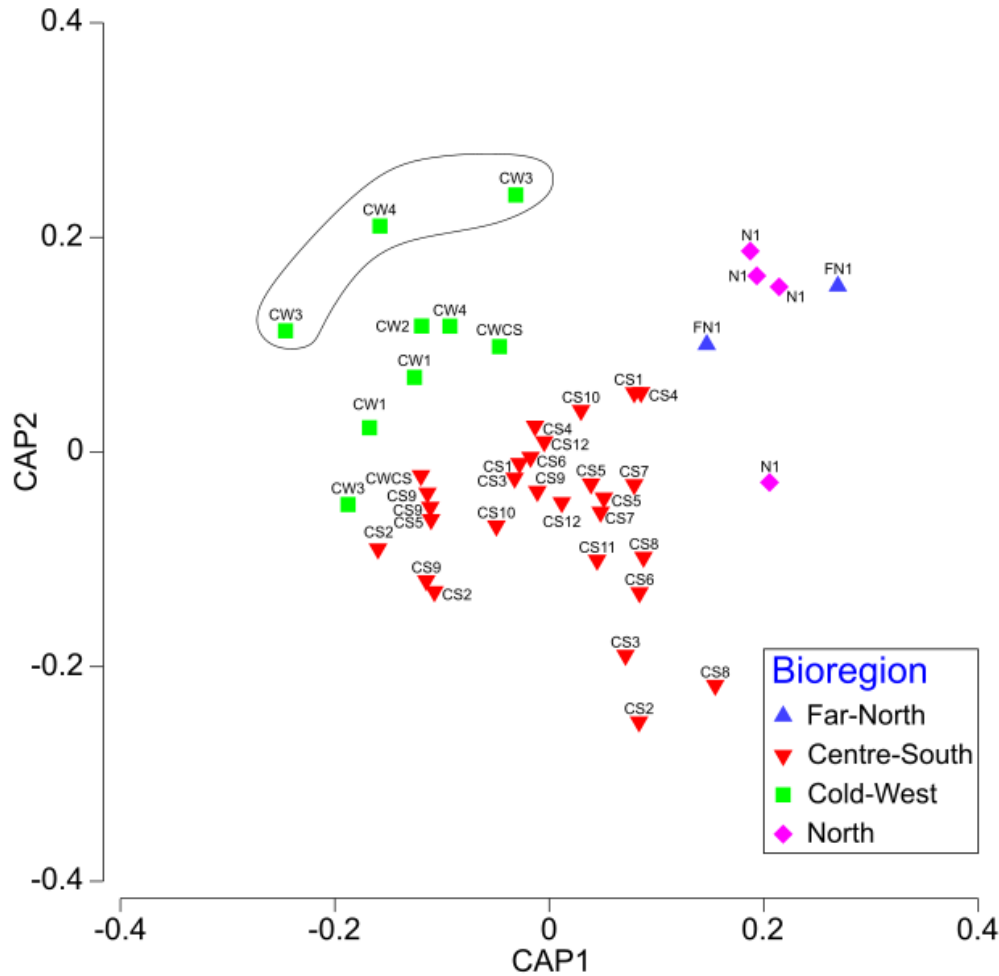


Figure 2.4. Canonical Analysis of Principal Coordinates (CAP) ordination of the reef fish communities functional turnover index for the four Galápagos bioregions. Coloured symbols are bioregions, and the abbreviated text labels are the geographic strata.

Table 2.5. Leave-one-out allocation cross-validation of sites to bioregions for functional turnover in the Galápagos Archipelago according to reef fish assemblages sampled in March and April of 2015. The misclassification error was 19%. **Bold** emphasises misclassification.

Original bioregion	Classified bioregion					Total	%Correct
	Far-North	Centre-South	Cold-West	North			
Far-North	1	0	0	1	2	50	
Centre-South	0	25	1	2	28	89.286	
Cold-West	0	1	7	1	9	77.778	
North	1	1	0	2	4	50	

2.5 Discussion

Each Galápagos bioregion has a small range of functional roles represented within its reef fish assemblages, including a few well represented by abundant species contributing greatly to ecosystem functioning. While there is a low functional alpha-diversity within these assemblages, small scale environmental variability and the presence of species that move between marine habitats have resulted in moderate beta-diversity values between

assemblages and high functional diversity when considered globally (Stuart-Smith et al., 2013). Functional alpha-diversity and beta-diversity indices are often used separately, but in combination, are a powerful tool for understanding ecological patterns in marine communities (Villéger et al., 2011; D'agata et al., 2016). Our use of functional alpha-diversity and beta-diversity indices identified differences at the larger bioregional scale while finding similarities at a finer community (strata) scale. The functional diversity patterns described support the previous bioregionalization patterns based on traditional taxonomic metrics (Edgar et al., 2004a).

2.5.1 Functional diversity properties of the Galápagos Archipelago

Reef fish assemblages in the Galápagos bioregions were characterised by a low functional richness that was supplemented by a moderate functional beta-diversity, a high functional divergence and a moderate functional evenness (sensu Mason et al., 2005; Villéger et al., 2013). The low functional richness within each bioregion suggests that reef fish assemblages' functional roles are a small proportion of the full range of functional trait combinations possible. The low functional richness and moderate functional beta-diversity values indicate that reef fish consistently represent a small range of functional roles in the different bioregions (Mouillot et al., 2014). Such a pattern is evidence that a few very successful combinations of traits are being selected for and the dominance of generalist species within the regional species pool (Villéger et al., 2012). A high proportion of non-specialised species (e.g. carnivores, planktivores and herbivores) have previously been reported in the Galápagos (Edgar et al., 2011). Therefore, reef fish assemblages in the Galápagos may not effectively utilise all available ecosystem resources (Petchey, 2003; Mason et al., 2005). This could reduce ecosystem resilience to niche space invasion (Dukes, 2001) and environmental disturbance (Tilman et al., 1996). The consistently high functional divergence within bioregions suggests that the most abundant species represent a few functional roles that significantly contribute to ecosystem functioning and support a large proportion of the total abundance of these reef fish assemblages (Mason et al., 2005; Devictor et al., 2010a; Mouillot et al., 2013b; Mouillot et al., 2011). Therefore, the dominant functional roles are differentiated from the less represented functional roles, indicating efficient ecosystem resource use and low competition by the most abundant species (Mason et al., 2005; Mouchet et al., 2010). The moderate functional evenness supports the observed patterns in the functional richness and functional divergence, indicating that a few functional roles include larger species abundances, leaving most functions less commonly represented (Mason et al., 2005; Villéger et al., 2010).

Globally, a characteristic of reef fish assemblages is that a few ecosystem functions are represented by multiple species and high abundance, leaving most ecological roles

represented by only one species with low abundance (Mouillot et al., 2014). We found the reef fish assemblages of the Galápagos to be no exception. This community structure implies a redundancy of some functions but a vulnerability of most functions to species loss (Munday, 2004; Mouillot et al., 2014; Mouillot et al., 2013a). While functional redundancy implies a degree of ecosystem resilience as the loss of a species and its functional role is likely to be replaced, functional vulnerability suggests that the loss of a unique and underrepresented function is likely not to be replaced (Munday, 2004). High functional vulnerability is prominent in reef fish assemblages in the Eastern Tropical Pacific (Parravicini et al., 2014). As a result, we suggest that the reef fish assemblages within the Galápagos have some functional resilience with functional redundancy providing insurance to some functional roles. However, we have also identified that some ecosystem niches are filled by only one species with low abundance are inherently vulnerable. These vulnerable niches are likely to be filled by small, habitat-dependent and minimally mobile species (Wilson et al., 2006; Graham et al., 2011; Pratchett et al., 2011). Further research to identify such species is urgently needed to inform management actions and prevent the loss of key ecosystem functions in the Galápagos.

The Galápagos' biodiversity patterns are distinct from global and regional patterns, and its reef fish assemblages have high functional diversity for any given species richness level (Stuart-Smith et al., 2013; Quimbayo et al., 2019). However, our study shows at a smaller spatial scale (within bioregions), a low functional alpha-diversity is characterised by a low richness of functional roles. This pattern is likely due to the Galápagos covering a large area from north to south, with a range of marine habitats and high environmental variation at small spatial scales (Wellington et al., 2001; Palacios, 2004; Edgar et al., 2011). Also, reef fish assemblages of oceanic islands contain high abundances of species with wide geographic ranges and larger body sizes such as sharks and pelagic schooling fish (Luiz et al., 2012; Gove et al., 2016). Combined, the diversity of marine habitats and some species' capacity to move between them results in a gradient of change (functional beta-diversity) in the functional diversity of reef fish in the Galápagos. This pattern has likely led to the comparatively high functional diversity at a global scale that has previously been reported for the region (Stuart-Smith et al., 2013).

Several biogeographical classifications using species compositions have been made for the Eastern Tropical Pacific region (Kulbicki et al., 2013). The Galápagos is either classified into a group with other oceanic islands of the region (i.e. Revillagedo, Cocos and Malpelo Islands) (e.g. Kulbicki et al., 2013; Robertson and Cramer, 2009) or separated into a distinct province (e.g. Briggs, 1974; Hastings, 2000; Spalding et al., 2007). However, there is increasing

evidence that the functional diversity in reef fish assemblages of Eastern Tropical Pacific oceanic islands differs and decreases with latitude and geographic isolation (Bender et al., 2017; Quimbayo et al., 2017b; Ramírez-Ortiz et al., 2017). With low latitude, remoteness and low functional richness within its reef fish assemblages, our study suggests that the Galápagos should indeed be considered functionally separate from the other oceanic islands of the Eastern Tropical Pacific.

2.5.2 Differences in functional diversity across bioregions

The four bioregions of the Galápagos were found to differ according to all functional alpha-diversity indices. These results may be affected by the inherently low number of samples around the small islands in the far-north due to limited available habitat. However, the patterns identified are consistent with previous studies that found differences between different Galápagos regions, including reef fish species compositions (Harris, 1969; Wellington, 1975; Edgar et al., 2004a). Building upon these studies, we linked biogeographical species composition patterns with aspects of functional diversity to demonstrate that the bioregions also differ in the functional diversity of reef fish assemblages, a biodiversity assessment independent of taxonomic structure.

The differences in functional richness within the Galápagos were associated with differences in species richness. Therefore, functional richness changes are attributed to changes in community structure and the influence of assembly rules (Mouchet et al., 2010). The differences in functional richness between bioregions reflect the process of environmental filtering from tropical to temperate reef ecosystems, where certain functional trait combinations are excluded by unsuitable environmental conditions (Cornwell et al., 2006). Sea-surface temperature is a fundamental driver of reef fish speciation processes, influencing biological activity and trophic interactions (Brown et al., 2004; Tittensor et al., 2010). Additionally, more structurally complex coral reef habitats offer more surface area and support more species than less complex reef areas (Bell et al., 2012; Richardson et al., 2017). In the cold-west, average ocean temperatures are the lowest and less complex macroalgae habitats the most dominant (Wellington et al., 2001; Banks, 2002). Such conditions limit the availability of ecological niches and the functional diversity of reef fishes associated with these niches. Furthermore, the eastward Equatorial Undercurrent rises in the cold-west causing frequent sea-surface temperature and primary productivity anomalies (Bustamante et al., 2008). Such unstable conditions are unsuitable for the establishment of species into niches, limiting functional diversity further. Combined, this results in low species and functional richness in the cold-west, the lowest of the main bioregions in the Galápagos.

The differing functional divergence between bioregions showed an inverse association with the differences in functional richness. This finding reiterates the effects of environmental filtering (Cornwell et al., 2006), where a lower richness of functional roles relative to other bioregions results in higher niche specialisation. For example, the cold-west had the lowest functional richness but the highest functional divergence of the Galápagos. This likely reflects the unique environmental conditions compared to the remainder of the Galápagos with persistently high phytoplankton levels, dominant macroalgae habitats and the lowest average water temperatures (Pak and Zaneveld, 1973; Wellington et al., 2001; Edgar et al., 2004a). In contrast, the north bioregion had the highest functional richness and lowest functional divergence. These findings highlight the diversity of marine habitats and therefore ecological functions in reef fish assemblages of the Galápagos and the important connection between species and their environment.

According to functional beta-diversity and functional turnover, the Galápagos' reef fish assemblages were separated into two main groups. There was also evidence of the two subregions previously suggested based upon reef fish species compositions (Edgar et al., 2004a). A northern sample was consistently distinguished from the other northern assemblages, while several centre-south samples were distinct from the centre-south as a whole. The reef fish assemblages distinguished from the remainder of the centre-south correspond to strata that are either exposed to the north (i.e. San Cristóbal north), east (i.e. Santa Cruz east and south) or were found to have similar species compositions to the north (i.e. Española) (Edgar et al., 2004a). The centre-south region is significantly larger in area than the other bioregions, and therefore more sites were sampled. Its marine ecosystems host the largest regional diversity of marine habitats and reef fish species (Witman and Smith, 2003; Edgar et al., 2004a). The large range of species richness and functional diversity values observed in our study further differentiates the region from other regions and indicates a high degree of functional dissimilarity exists between some sites in the bioregion. There was also evidence for the cold-west Bahia Elizabeth/Canal Bolivar subregion (Edgar et al., 2004a). A functional dissimilarity gradient extends away from the main centre-south group. The most functionally dissimilar assemblages corresponded to the strata on the west of Isabela that are sheltered by Fernandina (i.e. Canal Bolivar and Isabela south-west). This bay area is known to harbour unusually high phytoplankton concentrations due to currents and upwelling systems (Pak and Zaneveld, 1973; Banks, 2002). We suggest that the responses to environmental change of reef fish assemblages within these subregions will be different from the Galápagos' current main bioregions. As a result, the current bioregions could be divided and managed as smaller sub-regions.

2.6 Conclusions

Seasonal variation in the strength of major current systems and El Niño significantly affect marine communities of the Galápagos (Chavez et al., 1999; Palacios, 2004). Our study gives a temporal snapshot of functional diversity outside of any El Niño Southern Oscillation events providing a baseline for future functional diversity research.

This study assessed ecological patterns throughout the Galápagos Archipelago by quantifying functional diversity in its reef fish communities. To do so, we used a combination of functional alpha-diversity and beta-diversity indices to assess reef fish assemblages. We suggest low functional alpha-diversity but moderate functional beta-diversity have cumulatively resulted in the high functional diversity distinct from global biodiversity patterns (Stuart-Smith et al., 2013). Galápagos reef fish assemblages have some functional resilience with redundancy providing insurance to a few functional roles. However, there is also evidence that some ecosystem niches are filled by single species with low abundance which makes them vulnerable. Research suggests that El Niño and overfishing have caused extinctions of several Galápagos macroalgae species and the endemic damsel *Azurina eupalama* while threatening many others (Glynn, 1988; Edgar et al., 2010), likely altering marine ecosystem functioning. Therefore, we identify the risk of functional homogenisation and regime shifts occurring in Galápagos reef fish assemblages (Folke et al., 2004; Olden et al., 2004) and raise concerns about the long-term functioning of Galápagos marine ecosystems. It is important to keep studying Galápagos marine communities and functional diversity because climate change is increasing the frequency and intensity of El Niño's and the rate at which such changes will occur (Hoegh-Guldberg et al., 2007; Cai et al., 2014).

Traditionally, marine ecosystem management is prioritised according to species diversity (McGill et al., 2006). This can under-represent functional diversity (Devictor et al., 2010b) and would give a high conservation status to the Galápagos' far-north bioregion but a low conservation status to the cold-west. In terms of functional diversity, each bioregion in the Galápagos is dissimilar and is therefore likely to respond differently to environmental change and biodiversity loss. Functional diversity indices can contribute additional information to supplement traditional taxonomic based diversity metrics and provide an important ecological tool for informing management. Therefore, we suggest combining species compositions and functional diversity metrics in future Galápagos marine management.

CHAPTER 3

Functional vulnerability, redundancy, and biogeographical drivers of reef fish assemblage functions in the Galápagos Archipelago

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3.1 Abstract

The Galápagos archipelago's unique reef biodiversity and distribution patterns are well researched. However, local functional trait structure and the vulnerability of marine ecosystems to losing functional diversity is less well understood. We investigated the functional vulnerability of coastal reef fish communities in the Galápagos using Baited Remote Underwater Stereo-Video systems (stereo-BRUVs). We collected relative abundance data for 41594 individual fish belonging to 121 reef fish species, identified 82 functional entities and estimated functional diversity and vulnerability based on five functional traits. We also assessed the influence of a set of predictor variables on functional entity composition and richness.

We found that Galápagos reef fish communities have a high vulnerability to functional diversity loss following species loss due to the low redundancy and high sensitivity of reef fish functional roles. However, there may be some functional insurance against species loss from species playing ecologically similar functions instead of redundant species filling the same functions. The functional trait structure and vulnerability of Galápagos reef fish assemblages resemble the marine food web. Most functional entities with resilience from redundancy include upper trophic level species with piscivorous diets. Most functional entities that are sensitive and represented by only one species include lower trophic level species. Variables relating to latitudinal environmental variation (from tropical to temperate marine ecosystems) and marine habitat conditions were important predictors of reef fish functional entity distribution. Functional vulnerability may be a particular concern in marine ecosystems where functional diversity is low, including the colder temperate regions, habitats with high macroalgae cover, low bottom incline, or habitats less isolated and exposed to ocean currents. Our study raises concerns about the long-term functioning of Galápagos marine ecosystems under present climate change and human management scenarios. Therefore, we suggest using functional trait analysis and grouping species by ecological functions for consideration in the future marine management of Galápagos marine communities.

Keywords: benthic fish, bioregion, ecosystem, functional diversity, marine reserve, pelagic fish, stereo-BRUVs, redundancy, reef fish, sensitivity, vulnerability

3.2 Introduction

The Galápagos is an oceanic archipelago in the Eastern Tropical Pacific that comprises various sizes of islands and rock formations of volcanic origin (Snell et al., 1996). Straddling the equator 1000km west of Ecuador, the Galápagos is renowned for oceanographic and environmental variability that drives unique regional marine ecology and species distribution patterns (Edgar et al., 2004a). Galápagos marine ecosystems host unique assemblages of marine biodiversity that are characteristic of tropical, temperate and sub-Antarctic environments (Edgar et al., 2004a). Within the shallow-water environments, there is an abundance of reef fish species, with the most recent diversity study documenting ~463 nearshore fish species from four primary sources: the Indo-Pacific, Panamic and mainland Peruvian and Chilean region (McCosker & Rosenblatt, 2010). There are also high degrees of local and regional endemism (Edgar et al., 2004a; McCosker & Rosenblatt, 2010). Reef fishes are key components of reef ecosystems due to their high diversity, wide distribution and the vital roles that they play in ecosystem functioning (Duffy et al., 2016; Stuart-Smith et al., 2013). Galápagos reef fish communities include large biomasses of pelagic-generalist species supported by the high abundance of fish at lower trophic levels (Edgar et al., 2011; Salinas et al., 2016), and the structure of these marine communities varies between different regions (Edgar et al., 2004a). However, there is little research in the Galápagos relating marine species distributions and assemblage composition to ecosystem functioning.

Several factors influence Galápagos reef fish distributions and marine ecosystem functioning. Most significant is the confluence of three major current systems. The Panama current, which supplies warm water from the north-east, the Peru current, which supplies cold water from the south-east, and the Cromwell current, which supplies cold water from the deep (Banks, 2002; Houvenaghel, 1978). The convergence and the resultant mixing of ocean waters create important sea surface temperature gradients from north to south and high environmental variability at small spatial scales (Edgar et al., 2004a; Wellington et al., 2001). Furthermore, an equatorial undercurrent rises in the archipelago's southwest and drives nutrient-rich waters from the deep (Pak & Zaneveld, 1973). Despite the high environmental variation, Galápagos marine habitats are relatively homogenous, primarily being rocky reefs interspersed with sand. However, coral colonies and seaweed patches exist in regions where environmental conditions allow (Bustamante et al., 2002). Several physical and biological parameters help to create what are recognised as between three to five distinct 'bioregions' in the Galápagos, most recently using reef species compositions (Edgar et al., 2004a; Harris, 1969; Wellington, 1975). Based on reef fish species diversity and composition, there are four main Galápagos

bioregions (Edgar et al., 2004a). A tropical far-north, north-south transition zone, mixed centre-south and highly endemic cold-west. These bioregions aided the development of a zoning plan within the large Galápagos Marine Reserve (“GMR”, 138,000km²) that aimed to protect Galápagos marine habitats and biodiversity while sustaining the local fishing industry (Heylings et al., 2002; Moity, 2018). However, there are conflicts regarding the plan’s effectiveness to mitigate human pressures and conserve Galápagos marine biodiversity (Castrejón & Charles, 2013; Edgar et al., 2004b; Moity, 2018). In the Galápagos, anthropogenic impact is increasing with the overfishing of some fish stocks and the introduction of alien species into marine ecosystems (Glynn et al., 2018; Schiller et al., 2015; Toral-Granda et al., 2017). Climate change is expected to increase the average annual sea surface temperatures and the frequency and severity of El Niño events (Cai et al., 2014; Pörtner et al., 2021). As a result, marine habitat degradation and species extinctions have occurred, resulting in permanent changes to Galápagos reef fish populations and marine community structure (Edgar et al., 2010; Glynn, 1988). There has been a call for future marine research in the Galápagos to prioritise assessing ecosystem resilience and vulnerability to environmental disturbance in the Anthropocene (Salinas-de-León et al., 2020).

Increasingly, marine ecological management aims to maintain long-term ecosystem functioning and resilience to environmental disturbance instead of specific taxa or taxonomic groups (Bellwood et al., 2004; Díaz & Cabido, 2001; Naeem et al., 2012). Therefore, the concept of functional diversity has become an important ecological assessment tool which is thought to better inform ecosystem management than traditional species diversity metrics such as species richness and trophic groupings (Bellwood et al., 2004; Cadotte et al., 2011; Mouillot et al., 2011; Tilman et al., 1997). The functional diversity of an assemblage is determined by the unique combinations of functional traits present (Mouillot et al., 2014; Violle et al., 2007). Traits are measurable features of an individual or species linked to or determined by life within an environment (Cadotte et al., 2011; Díaz & Cabido, 2001; Mouillot et al., 2014; Petchey & Gaston, 2006; Violle et al., 2007). Such traits are commonly related to morphology, behaviour, physiology or phenology (Petchey et al., 2009). Functional diversity studies of reef fish have evaluated the resilience of ecosystems to disturbance (Richardson et al., 2018; Villéger et al., 2014), highlighted global marine biodiversity hotspots (Stuart-Smith et al., 2013) and complemented historical biogeographical studies (Olivier et al., 2018; Quimbayo et al., 2019; Ramírez-Ortiz et al., 2017). Furthermore, assessing the distribution of species in a community by their functional traits provides a mechanism to describe and understand marine community structure beyond taxonomy. Understanding reef fish functional trait structure can help predict marine community and ecosystem responses to different environmental disturbances (e.g. climate change, habitat loss and overfishing) through functional redundancy

(Fetzer et al., 2015; Folke et al., 2004; McCann, 2000; McLean et al., 2019; Pratchett et al., 2011; Worm et al., 2006).

Reef fish play vital functional roles in ecosystems, primarily by regulating food webs and recycling nutrients (Holmlund & Hammer, 1999; Stuart-Smith et al., 2013). The likelihood that functional roles are lost following species loss determines their vulnerability (Bellwood et al., 2003; Bihn et al., 2010; Micheli & Halpern, 2005). Functional roles are insured by redundancy when more than one species represents them. However, they are vulnerable when represented by only one species and thus they are less likely to be replaced (Bellwood et al., 2003; Fonseca & Ganade, 2001; Graham et al., 2011; Mouillot et al., 2014). Functional vulnerability assessments use these concepts to estimate the likelihood that changes to functional diversity will occur considering environmental disturbances, ultimately affecting long-term ecosystem functioning (Parravicini et al., 2014). Functional vulnerability assessments of reef fish report a high functional vulnerability globally, and that marine conservation efforts typically do not protect functionally vulnerable areas (D'agata et al., 2016; Mouillot et al., 2013a; Mouillot et al., 2014; Parravicini et al., 2014). The Galápagos is within the Eastern Tropical Pacific region, a reef fish functional sensitivity hotspot with low functional redundancy and species richness compared to other regions globally (Parravicini et al., 2014). However, there is currently no study that examines functional vulnerability of reef fishes within the Galápagos.

This study aimed to describe Galápagos marine fish communities in terms of functional trait structure and vulnerability. To do this, we aimed to:

- I. Describe the functional trait structure of shallow-water reef fish assemblages in the Galápagos bioregions;
- II. Describe Galápagos reef fish assemblages in terms of functional diversity and vulnerability indices; and,
- III. Assess the influence of spatial and environmental variability and human management on Galápagos reef fish functional diversity and vulnerability.

3.3 Methods

3.3.1 Fish community data

3.3.1a Sampling design

We sampled shallow-water reef fish assemblages throughout the Galápagos Archipelago over two months (March-April) in 2015 using Baited Remote Underwater Stereo-Video systems (stereo-BRUVs) along a 20-metre depth contour (Fig. 3.1). We used a spatially stratified

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random sampling design to distinguish sites, as further detailed in Acuña-Marrero et al. (2018) and **Chapter 2**. First, geographic features (i.e. islands, islets and submerged reefs) were distinguished and grouped according to their relative size and distance from each other. These were then further divided into 19 unique geographic strata based on bioregion, orientation, bathymetry gradient, and exposure to predominant south-easterly currents (Banks, 2002). A minimum of 4km always separated sites so that 500m separated stereo-BRUVs alternating between two positions in the water column: benthic, near the sea-bed (~25m) and pelagic, above the sea-bed (~10m below the water surface). Data from three hundred and twenty deployments were collected across the 43 sites within the 19 geographic strata and four bioregions.

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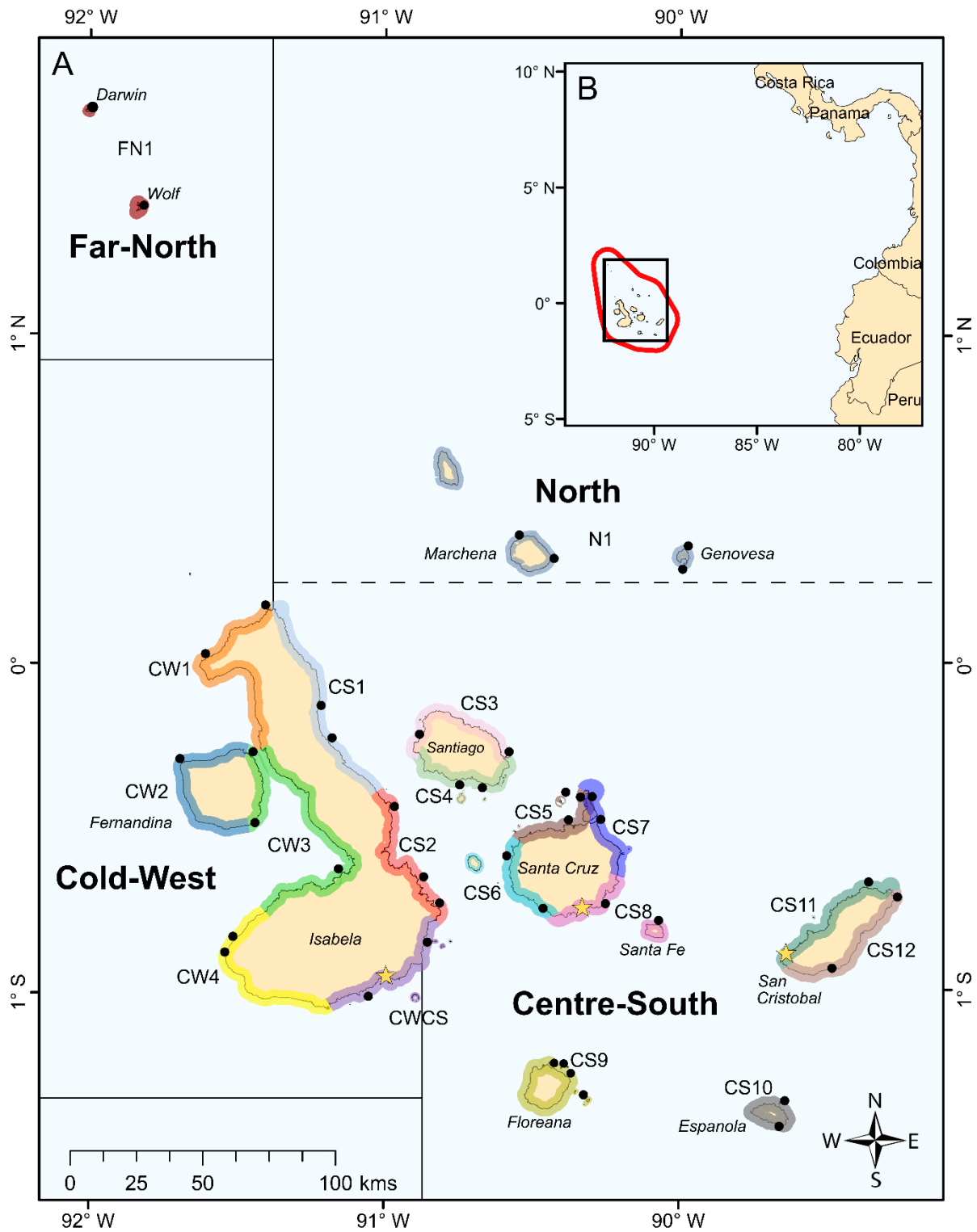


Figure 3.1.A. Location of the 43 sites sampled using stereo-BRUVs in 2015 (black dots). Bold text and lines indicate the four main bioregions – far-north, north, centre-south and cold-west based on reef fish and invertebrate species communities (Edgar et al., 2004a). Capital letter acronyms denote the 19 unique geographic strata marked out along the coastline by different coloured shading. Stars indicate the three main fishing ports. **B.** Location of the Galápagos Archipelago in the Eastern Tropical Pacific (ETP).

3.3.1b Reef fish samples

Our study used both pelagic and benthic stereo-BRUVs to sample fish assemblages. Our stereo-BRUV systems comprised two GoPro Hero 4 high-definition cameras enclosed in SeaGIS stereo-video waterproof housing and mounted on a stainless-steel frame 70cm apart converged at six degrees. A rigid PVC pipe extended in front of the cameras with a mounted bait canister filled with 800g of chopped yellow-fin tuna (*Thunnus albacares*). The setups were the same for both benthic and pelagic deployments, with an anchoring system made of a ballast weight and a set of buoys used to position them at the desired depths (i.e. benthic and pelagic). Using the SeaGIS software, *EventMeasure* (www.seagis.com.au), analysts reviewed the 90-minute deployments videos and all bony and cartilaginous fish observed were identified to species level and quantified using the MaxN index of relative abundance. The MaxN index of relative abundance is the maximum number of individuals of a particular species counted in one still video frame across the video length (Cappo et al., 2003b; Cappo et al., 2001; Ellis & Demartini, 1995). Three hundred and twenty video deployments were analysed (151 pelagic, 169 benthic). We summed the MaxNs of each species to the site level combining benthic and pelagic deployments and converted them to presence and absence (coded 1/0).

3.3.2 Functional traits and entities

Using a comprehensive collection and review procedure, we compiled a functional trait matrix for the 121 reef fish species sampled (Table 3.1; Table S3.1, Table S3.2 and Table S3.3 in the Supplement). We initially extracted ecological information from Fishbase using the 'rfishbase' package in R (Boettiger et al., 2012; Froese & Pauly, 2019) before defining five functional trait categories and reviewing the original publications for relevant information. To finalise the matrix and fill uncertainties in the information, we considered comprehensive sources of information for reef fish in the Galápagos including, the 'Reef Fish Identification: Galápagos' book and the Shorefishes of the Tropical Eastern Pacific database (Humann & DeLoach, 2003; Robertson & Allen, 2015). The five trait categories describe most of the significant biological and ecological interactions of reef fish and have been used in previous studies with similar analytical strategies (e.g. D'agata et al., 2016; Mouillot et al., 2014; Parravicini et al., 2014) and included 1. Body size, 2. Diet, 3. Ecological niche, 4. Within-reef mobility, and 5. Social behaviour. See Table S3.4 in the Supplement for a description of the five functional trait categories, our working definitions, and their ecological relevance.

We assigned each species to a body size category based on maximum total length measurements from FishBase using five ordered categories: 0-20cm, 20.01-50cm, 50.01-100cm, 100.01-200cm, and >200.01cm. We assigned each species to a trophic ecology category based on trophic level and feeding method (i.e. grazing, browsing, hunting, filtering plankton) (herein, 'feeding habit') from Fishbase using six categories: herbivore (consumes

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detritus and algae), invertivore (consumes invertebrates), planktivore (consumes planktonic organisms), piscivore (consumes fish and cephalopods), omnivore (consuming a variety of all categories) and filter-feeder (filters plankton using cephalic fins). We assigned each species to an ecological niche category based on water column position, habitat associations and biological descriptions from Fishbase using four categories: demersal (lives on the substrate), benthic (lives near the substrate), benthopelagic (lives between the substrate and water column) and pelagic (lives in the water column). We assigned each species to a within-reef mobility category based on substrate preference, habitat associations and biological descriptions from Fishbase and the dominant marine habitat types in the Galápagos using four categories: soft substrates (predominantly prefers sandy bottoms), hard substrates (predominantly found on rocky or coral reefs), both soft and hard substrates (found across substrate types) and open-water (predominantly not found near reef substrates). We assigned each species to a social behaviour category based on largest common group size using observations of social behaviour from FishBase, the MaxNs in our data and the literature using three categories: solitary to pairing (mostly observed singly or in pairs), small groups (mostly observed in aggregations of up to 20 individuals) and large groups (mostly observed schooling with more than 20 individuals). Using all of these categories we then determined the 'functional role' of reef fish in the Galápagos using 'functional entities' (FEs). Functional entities are all the unique combinations of functional traits within an assemblage computed using the R function '*species_to_FE*' (Mouillot et al., 2014; Parravicini et al., 2014). There were eighty-two FEs for the 121 reef fish species.

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Table 3.1. Functional trait information for the five functional traits used to identify functional entities and assess the functional diversity and vulnerability of 121 reef fish species sampled in the Galápagos Archipelago in 2015.

Trait category	Functional trait/s	Type	Trait category levels
Body size	Maximum total length	Ordinal	0-20cm 20.01-50cm 50.01-100cm 100-200cm >200.01cm
Trophic ecology	Feeding habits	Categorical	Herbivore Invertivore Planktivore Piscivore Omnivore Filter-feeder
Ecological niche	Water column position	Categorical	Demersal Benthic Bentho-pelagic Pelagic
Within-reef mobility	Substrate preference	Categorical	Soft substrates Hard substrates Both hard and soft substrates Open-water
Social behaviour	Largest common group size	Ordinal	Solitary to pairing Small groups Large groups (schooling)

3.3.3 Functional vulnerability and diversity indices

We obtained the presence and absence of the 82 FEs at each site and then applied the R function, 'FE_metrics', to calculate the three complementary components proposed by (Mouillot et al. (2014) and Parravicini et al. (2014) that determine functional vulnerability. Reef fish functional vulnerability was therefore described using the three indices of functional redundancy – the mean species richness per FE, functional over-redundancy – the proportion of FEs at a site with more species than the functional redundancy of that site and, functional sensitivity – the proportion of FEs having only one species (i.e. no redundancy) (Parravicini et al., 2014) The three indices are calculated using the following formulas:

$$\begin{aligned}\text{Functional redundancy (Fred)} &= \frac{S}{FE} \\ \text{Functional over - redundancy} &= \frac{\sum_{i=1}^{FE} \min [\max(n_i, \text{Fred})] - \text{Fred}, 1]}{FE} \\ \text{Functional sensitivity} &= \frac{FE - \sum_{i=1}^{FE} \min (n_i - 1, 1)}{FE}\end{aligned}$$

Where S is the species richness and n_i is the number of species represented in the i_{th} FE.

Functional sensitivity ranges between 0 when all FEs are redundant and 1 when there is no redundancy. Functional redundancy ranges between 1, when all FEs have no redundancy, and S (number of species), when one FE includes all species within an assemblage. Finally, functional over-redundancy is greater than 0 when there is an uneven distribution of species within the FEs.

We also used the number of FEs at each site to describe functional diversity and calculated functional originality to consider the similarity between FEs not considered by the functional redundancy index. To calculate functional originality, we first produced a representative functional space following Maire et al's. (2015) framework. We calculated pairwise functional trait dissimilarity between FEs using Gower's coefficient to handle categorical data while giving them equal weighting (Gower, 1971). We then projected the FEs into a multidimensional space using a principal coordinate analysis (PcoA). We selected the principal coordinate space with four axes because the resulting Euclidean distances strongly correlated with the Gower's distances ($r = 0.77$, $p < 0.001$) and there were low mean squared deviations from the original data (MSD = 0.0257; Figure S3.1 in the Supplement). Functional originality was then calculated as the mean Euclidean distance between each FE and its nearest neighbour in the functional space by the R function '*multidimFD*' (Mouillot et al., 2013b). We considered functional originality values to be low when less than 0.5, moderate between 0.5 and 0.75, and high when greater than 0.75 (Mason et al., 2005). Functional originality is low when FEs at a site are, on average, functionally close and there is possible redundancy and high when FEs are, on average, functionally distinct (Mouillot et al., 2013b). The PcoA was conducted in R using the functions '*qual_funct_space*' and '*plot_funct_space*' that use the '*ape*', '*clue*', '*cluster*', '*geometry*' and '*gtools*' libraries (Habel et al., 2019; Hornik, 2019; Maechler et al., 2019; Paradis & Schliep, 2019; R Core Team, 2017; Warnes et al., 2020).

3.3.4 Environmental and human variables for modelling

We collated available data relating to the geography, environment, habitat type, and human activity to investigate their influence on Galápagos reef fish communities' functional diversity (Table 3.2). The geographic variables included latitude, longitude and mean fetch. Latitude and longitude were recorded *in situ* for each deployment. Mean fetch was calculated as the average distance of each deployment to land in all directions using the R package 'waver' (Marchand & Gill, 2018). Mean fetch is a proxy for exposure to oceanographic conditions such as waves and currents (Smith et al., 2013). The means of the geographic variables were calculated across stereo-BRUVs deployments for each site. The environmental variables included sea surface temperature (SST) and chlorophyll-a concentrations (chlo-a, mg m⁻³). SST was collected *in situ* during sampling, and monthly daytime chlo-a concentrations were obtained from remote-sensing data at a 4km spatial resolution (<https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua>). The means of the environmental variables were calculated across stereo-BRUVs deployments for each site. Several habitat variables were included to describe different aspects of habitat type and distance-based connectivity between them. We used a fine-scale habitat analysis to characterise the seabed composition for each benthic stereo-BRUVs deployment following Acuña-Marrero et al. (2018). For each benthic deployment, the full 90 minutes of video was visually analysed with the seabed first characterised according to its percentage cover of rock and sand. Then its finer composition was estimated using an ordinal value from 0 to 3 (0 = nil, 1 = low, 2 = medium, 3 = high) for the presence of corals, macroalgae, rubble and its bottom incline. Each habitat variable was averaged across the stereo-BRUVs deployments for each site. The standard deviation of sand and rock cover across site deployments was also calculated to account for habitat variation. Around each site, a 30km radius buffer was computed, and the number of larger islands within it visually counted in the ArcGIS v10 software. This distanced-based connectivity measure can be considered a reliable proxy for ecological connectivity (Mellin et al., 2010). The human use variables included proxies for distance to the protected area and fishing effort for each site. The degree of protection was estimated based upon the average distance of the stereo-BRUVs deployments to the nearest no-take zone using data from Moity (2018) in ArcGIS v10. Two proxies for fishing effort were estimated based upon the distance to fishing ports. Distance to fishing ports is a suitable proxy for fishing effort in the Galápagos as fishing effort is associated with the willingness of the owner of a fishing boat to travel, considering income and travel costs (Castrejón & Charles, 2014, 2020). The first measure, the sum of the distance to fishing ports, was the sum of each site's distances to Galápagos' three main fishing ports (i.e. Puerto Ayora, Baquerizo Moreno and Puerto Villamil). The second was the mean distance of deployments at each site to the nearest fishing port. We measured the most direct route

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from each site to each fishing port around islands using a series of straight lines with the distance measurement tool.

Table 3.2. Summary of the variables used to model the variation in the number of FEs of 121 reef fish species sampled in the Galápagos in 2015. Every variable used in the DistLM is presented with the variables used in the GLMs highlighted in **bold and italics**.

Category	Predictor	Data type	Observed range	Observed mean \pm SD
Spatial	<i>Latitude</i>	Continuous	-1.409 to 1.678	-0.451 \pm 0.633
Spatial	<i>Longitude</i>	Continuous	-91.995 to -89.242	-90.635 \pm 0.664
Spatial	<i>Mean fetch (m)</i>	Continuous	10640.548 to 36291.990	23447.932 \pm 5754.312
Environmental	Chlorophyll concentration (mg m ⁻³) ^a	Continuous	0.158 to 1.431	0.5601 \pm 0.344
Environmental	<i>Sea surface temperature (SST) (°C)</i>	Continuous	19.250 to 29.800	26.196 \pm 2.577
Habitat	Rock and sand cover (%)	Ordinal	12.500 to 98.750	59.758 \pm 23.215
Habitat	Hard coral cover	Ordinal	0 to 1.250	0.046 \pm 0.204
Habitat	Soft coral cover	Ordinal	0 to 2.750	0.814 \pm 0.701
Habitat	<i>Macroalgae cover</i>	Ordinal	0 to 3	0.901 \pm 0.945
Habitat	Rubble cover	Ordinal	0 to 2	0.116 \pm 0.375
Habitat	Habitat variation	Continuous	2.500 to 57.735	31.320 \pm 14.944
Habitat	<i>Bottom incline</i>	Ordinal	1 to 3	1.488 \pm 0.511
Habitat	<i>Number of islands within 30km</i>	Ordinal	1 to 6	2.163 \pm 1.627
Human management	Distance to nearest no-take zone (m)	Continuous	0 to 23456.224	4852.423 \pm 6427.855
Human management	<i>Sum of the distance to fishing ports (m)</i>	Continuous	168.150 1142.631	386.507 \pm 203.439
Human management	Distance to nearest fishing port (m)	Continuous	9.250 to 355.664	89.574 \pm 69.252

3.3.5 Statistical analysis

3.3.5a Functional trait structure, vulnerability and diversity

To illustrate the functional trait structure of Galápagos reef fish assemblages, a series of barplots were created for the five functional traits used to distinguish the FEs according to the number of species sampled in the four bioregions. To distinguish the FEs and describe their functional vulnerability, the first two axes of a principal coordinate analysis (PcoA) were plotted using the R function '*plot_funct_space*' that uses the '*geometry*' library (Villéger et al., 2008). To illustrate the changes in functional vulnerability and diversity of reef fish assemblages between the four bioregions boxplots were created. The barplots and boxplots plots were

created using the 'ggplot2' package in R (Wickham et al., 2020). All functional vulnerability and diversity indices were then assessed for differences between factors 'bioregion' (fixed, four levels) and strata (fixed, 19 levels nested in bioregion) using a two-way nested Permutational Multivariate Analysis of Variance (PERMANOVA, $\alpha=0.05$) based on a Euclidean distance similarity matrix. Tests of terms in the full PERMANOVA model used Type III SS and 9999 permutations under a reduced model (Freedman & Lane, 1983). Any significant PERMANOVA results between bioregions were also further assessed using pairwise t-tests with Monte Carlo bootstrapping (Manly, 2006). Any significant PERMANOVA results between geographic strata were not further assessed because pairwise tests cannot be conducted on nested factors. The PERMANOVA procedures were conducted within the PERMANOVA+ (Anderson et al., 2008) add-in for PRIMER v7 (Clarke & Gorley, 2015).

3.3.5b Multivariate ordination and selection of environmental variables for models

To examine the role of the predictor variables influencing the number of individuals within each FE at each site, we conducted a distance-based linear model (DistLM) using the PERMANOVA+ (Anderson et al., 2008) in PRIMER v7 (Clarke & Gorley, 2015). We also used the DistLM analysis to select a subset of all the potential predictor variables that best explain the variation in FE distribution for use in the subsequent univariate modelling of the functional indices. Predictor variables were not transformed. However, we did exclude distance to the nearest fishing port because it was strongly correlated with latitude and the sum of the distance to fishing ports (+80%). A similarity matrix between sites was calculated on square-root transformed FE abundances using the Bray-Curtis coefficient, which reliably analyses multivariate assemblage data (Clarke, 1993; Clarke et al., 2006). We performed the DistLM using the best selection procedure with the 15 explanatory variables available for selection (Table 3.2). We examined the models according to corrected AIC selection criteria (AICc), the proportion of the variance explained, and model fit (residual sum of squares, RSS) (Table 3.3). We chose AICc because it improves model selection with smaller sample sizes (Hurvich et al., 1990; Hurvich & Tsai, 1989). We also assessed the explanatory power of individual variables using marginal tests. We plotted the variables selected in the most parsimonious model using distance-based redundancy analysis (dbRDA) and the Pearson correlations of each functional entity's abundances to the dbRDA axes. The subset of eight variables selected for the generalised linear models (GLMs) were all those within the three best performing models as judged by the AICc (highlighted in bold in Table 3.2).

3.3.5c Generalised linear models (GLMs)

To investigate the relationship of Galápagos reef fish assemblage functional diversity with the chosen explanatory variables, we constructed generalised linear models (GLMs) using the

number of FEs at each site (Zuur et al., 2009). We fit the models using the *glm()* function in R with a Poisson distribution (R Core Team, 2017). We selected the model with the lowest AIC from both the forwards and backwards selection procedures, beginning with the eight available explanatory variables. We plotted the relationships between the number of FEs and each of the explanatory variables from this most parsimonious model using data predicted from the model. We also recorded any models within two AIC units of the selected model. Throughout the analysis, we explored the distribution of the residuals to assess model fit and select the appropriate distribution (Zuur et al., 2009). We also tested models against the functional vulnerability indices. However, as there was no change in these indices across the Galápagos bioregions, there was no value in creating models for these indices (Table 3.2).

3.4 Results

3.4.1 Functional trait structure

There were some functional traits that were common across the Galápagos reef fish assemblages. Generally, species had body sizes between 20-50cm or 50-100cm in each bioregion-(Fig. 3.2A). Most Galápagos reef fish were piscivores (Fig 3.2B). A smaller number were invertivores or omnivores and even fewer were herbivores, planktivores or filter-feeders. A larger number of species were benthic or benthic-pelagic than demersal or pelagic (Fig 3.2C). Most reef fish species preferred hard substrates or both soft and hard substrates compared to soft substrates or open-water (Fig 3.2D). A large number of species were solitary or pairing compared to a smaller number that occur in large groups and even fewer in small groups (Fig. 3.2E). This functional trait structure was mostly consistent across the Galápagos bioregions. However, a greater number of reef fish species were sampled in the larger centre-south bioregion than the other smaller bioregions.

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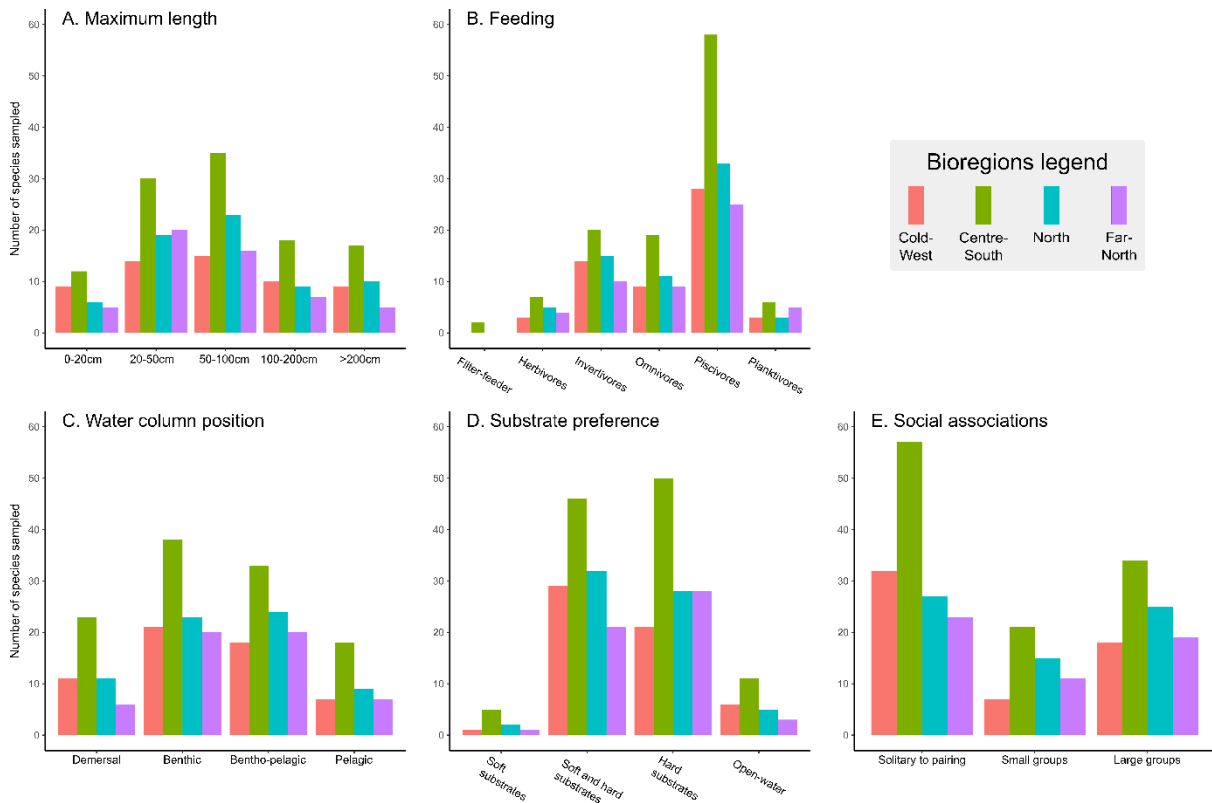


Figure 3.2. Barplots of the five functional traits (A-E) used to distinguish FEs according to the number of reef fish species sampled in the four Galápagos bioregions in 2015.

3.4.2 Functional vulnerability of functional entities

The 121 observed reef fish species were categorised into 82 FEs (Table S3.1 in the Supplement). Across the Galápagos, the distribution of species into the FEs was uneven, with 55 FEs having only one species. There were 27 FEs with redundancy (i.e. more than one species represents them), including one with five species, one with four species, seven with three species and 18 with two species (Table S3.1 in the Supplement). Within each of the four main Galápagos bioregions, the distribution of species into FEs was also uneven, and as a result, only a few FEs had redundancy (11 FEs in the Cold-west, 24 in Centre-south, 11 in North and 8 in Far-north), while a high number were sensitive (33 FEs in Cold-west, 55 in Centre-south, 41 in North and 36 in Far-north) (Fig. 3.3). In each Galápagos bioregion, most of the FEs with redundancy included piscivorous species (Fig. 3.3). However, there were also many sensitive piscivorous FEs. In the far-north, north and centre-south bioregions, the piscivorous FEs were distributed throughout most of the functional space and close to other piscivorous FEs, reflecting high functional trait diversity for piscivorous species (Fig. 3.3). In the cold-west bioregion, the piscivorous FEs were distributed through approximately half of the functional space but were still close to other piscivorous FEs (Fig. 3.3). The distribution and sensitivity of the other feeding habit groups varied among the bioregions (Fig. 3.3). In the far-north, there were several invertivorous and omnivorous FEs distributed through similar areas of the functional space (Fig. 3.3). These FEs were mainly close to other FEs of the same

feeding habit group. Two pairs of planktivorous FEs and an herbivorous FE were separated from FEs of the same feeding habit group. In the north, there were also several invertivorous and omnivorous FEs (Fig. 3.3). However, some of the omnivorous FEs were more separated from other omnivorous FEs. The planktivorous and herbivorous FEs were all separated from other FEs of the same feeding habit group. In the centre-south, like the piscivorous FEs, the omnivorous FEs were distributed throughout most of the functional space and close to other omnivorous FEs, reflecting functional trait diversity for omnivorous species (Fig. 3.3). The invertivorous FEs were all located close to another invertivorous FE. However, the herbivorous and planktivorous FEs were separated from other FEs of the same feeding habit group. In the cold-west, the non-piscivorous diet groups occupied the remaining half of the functional space (Fig. 3.3). The omnivorous and invertivorous FEs were again more widely distributed and close to other FEs of the same feeding habit group, and the two planktivorous FEs were located close to each other. However, the herbivorous FEs were again separated in the functional space.

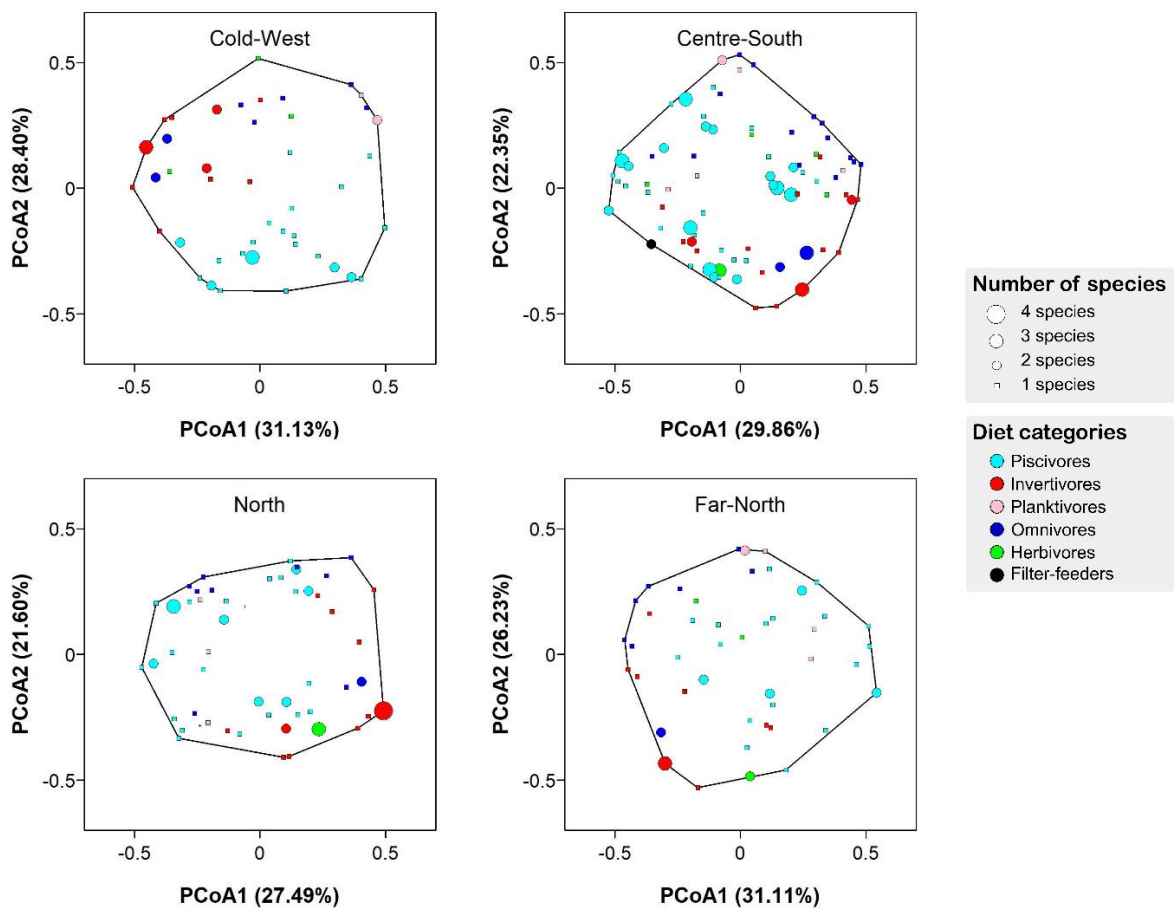


Figure 3.3. First two axes of a principal coordinate analysis (PcoA) of the reef fish assemblages in each of the four Galápagos bioregions using five functional traits. Inside the convex-hull, circles of different sizes colour-coded to the six diet groups represent the redundant FEs with more than one species. The coloured squares represent sensitive single species FEs.

3.4.3 Functional vulnerability and diversity indices

The reef fish assemblages of the Galápagos had a low functional redundancy (<1.308), high functional sensitivity (>0.731) and low functional over-redundancy (<0.172) (Fig. 3.4C-E). There was some variation in these indices between sites in the north, centre-south and cold-west bioregions (Fig. 3.4C-E). None of the functional vulnerability indices differed significantly between the bioregions or strata for any tests (Table 3.3). The number of FEs was, on average (mean and median), highest in the far-north and lowest in the cold-west (Fig. 3.4A). The north, centre-south and cold-west had some variation in the number of FEs between sites (Fig. 3.4A). The number of FEs differed significantly between bioregions, but not between strata (Table 3.4). The post-hoc pairwise comparisons of the number of FEs between bioregions showed that the cold-west differed significantly to every other bioregion. The centre-south, north and far-north did not differ significantly from each other. Functional originality was low in all the Galápagos bioregions on average (mean<0.496) (Fig. 3.4). The north, centre-south and cold-west regions had some variation in functional originality between sites. Functional originality differed significantly for both bioregions and strata (Table. 3.4). The post-hoc pairwise comparisons of functional originality between bioregions showed that the cold-west differed significantly to the centre-south and north. The centre-south also differed significantly to the north. The far-north did not differ significantly in functional originality to any other bioregion.

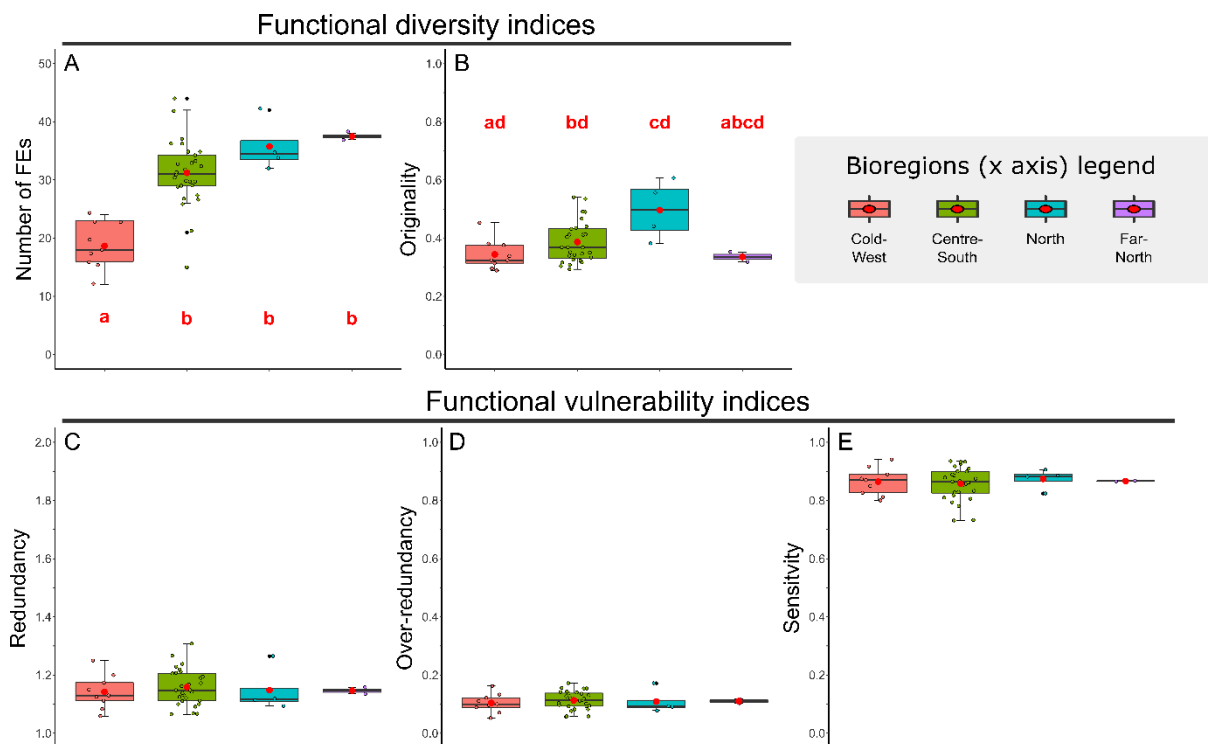


Figure 3.4. Boxplots of functional diversity (top row) and functional vulnerability (bottom row) indices for reef fish assemblages in the four Galápagos bioregions. Each dot represents a site. The boxplots display medians (black line), upper and lower quartiles (boxes), and minimum and maximum $\pm 1.5 \times$ interquartile range (IQR) (whiskers), the mean (red circle) and outliers (black dots).

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Table 3.3. Two factor nested PERMANOVA for differences in the functional vulnerability indices across the bioregions and strata. Bioregion and strata are fixed factors with strata nested in bioregion. **Bold** emphasises significant differences at $\alpha = 0.05$.

Source	DF	Functional redundancy indices								
		Functional redundancy			Functional over-redundancy			Functional sensitivity		
		MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Bioregion	3	0.001	0.120	0.945	0.002	0.151	0.932	0.001	0.059	0.978
Strata(Bioregion)	16	0.003	0.682	0.781	0.001	0.794	0.680	0.002	0.744	0.725
Residuals	23	0.004			0.001			0.003		
Total	42									

Table 3.4. Two factor nested PERMANOVA for differences in the functional diversity indices across the bioregions and strata. Bioregion and strata are fixed factors with strata nested in bioregion. **Bold** emphasises significant differences at $\alpha = 0.05$.

Source	DF	Functional diversity indices					
		Number of FEs			Functional originality		
		MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Bioregion	3	360.98	13.822	<0.001	0.214	6.747	0.006
Strata(Bioregion)	16	29.206	1.118	0.404	0.007	2.278	0.036
Residuals	23	26.116			0.003		
Total	42						

3.4.4 Multivariate ordination and selection of explanatory variables for generalised linear models

The distance-based linear models (DistLM) used to examine the explanatory variables' influence on the multivariate FE assemblages across the Galápagos, produced three best models. These were essentially identical in terms of their AICc and explained a moderate proportion (35-39%) of the variation in the composition of FEs (Table 3.5). Galápagos These models used either four or five explanatory variables, and all included bottom incline and latitude. All included a spatial component, but these varied between these top models (Table 3.5). Models 2 and 3 included SST, and model 3 included the number of Islands within 30km, an estimate of ecological connectivity. The single variable with the greatest explanatory power was SST (17%), followed by macroalgae cover (14%), bottom Incline (10%), and longitude (10%, Table 3.5). Alternative models for each number of variables within two AICc units of these best models are presented in Table S3.5 in the Supplement. The first two dbRDA axes accounted for 51.1% and 31.7% of the fitted model variation respectively, and together 32.4% of the total variation in the functional entity compositions (Fig. 3.5). Latitude was negatively correlated to the first dbRDA axis. Macroalgae cover was positively correlated to the first dbRDA axis and in the direction of the cold-west bioregion. Bottom incline and the sum of the

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distance to fishing ports were negatively correlated to the second dbRDA axis. Mean fetch was not correlated to either the first or second dbRDA axis.

Table 3.5. Summary of the top three distance-based linear models (DistLMs) used to model the abundance of FEs using environmental variables, the best selection procedure and AICc selection criteria. The Pseudo-F statistic, P-value and Proportion of variation explained by each explanatory variable in each model are also presented.

Model number, number of variables	R ²	RSS	AICc	Variables	Pseudo-F	P-value	Proportion explained (%)
1, 5	0.391	35971	303.69	Latitude Mean fetch Macroalgae cover Bottom Incline Distance to ports	3.462 2.513 6.785 4.655 3.838	0.001 0.001 <0.001 <0.001 <0.001	7.78 5.77 14.20 10.20 8.56
2, 4	0.351	38321	303.7	Latitude Longitude SST Bottom Incline	3.462 4.658 8.326 4.655	0.001 <0.001 <0.001 <0.001	7.78 10.20 16.88 10.20
3, 5	0.391	35980	303.7	Latitude Longitude SST Bottom Incline No. islands within 30km	3.462 4.658 8.326 4.655 3.109	0.001 <0.001 <0.001 <0.001 0.003	7.78 10.20 16.88 10.20 7.05

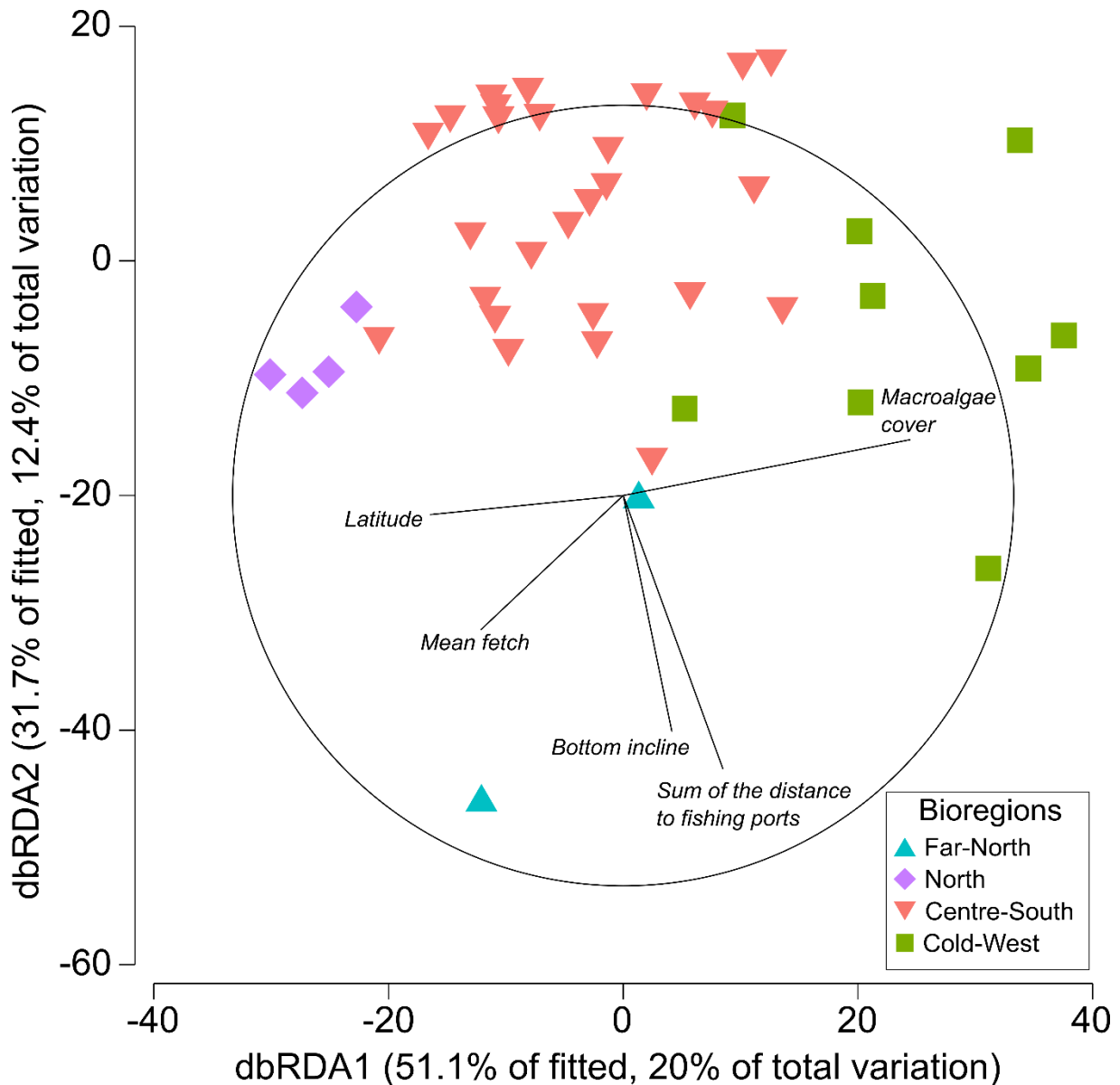


Figure 3.5. Distance-based redundancy analysis (dbRDA) plot. Vectors show strength and direction of multiple partial correlations of the environmental variables to the first and second fitted RDA axes. Coloured symbols are the four main bioregions.

3.4.5 Generalised linear models explaining number of functional entities

The most parsimonious generalised linear model explaining variation in the number of FEs included sea surface temperature, macroalgae cover, mean fetch and bottom incline (Table 3.6). The model explained 65% of the variation in the number of FEs (explained deviance = 0.649, AIC = 264.84, Table 3.6). Every variable explained a statistically significant proportion of the variation (Table 3.6). Alternate models within two AIC units are presented in Table 3.6. The number of FEs had a positive relationship with SST, bottom incline and mean fetch, and a negative relationship with macroalgae cover (Fig. 3.6).

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Table 3.6. Summary of the generalised linear models fitted to model the number of FEs.

Dependent variable and model selected	Explained deviance	AIC	Explanatory variables	Z-value	P-value	Alternate models (within two AIC units)
Number of FEs	0.649	264.84	Sea-surface temperature Macroalgae cover Mean fetch Bottom incline	3.489 -2.857 2.431 2.085	0.0004 0.004 0.015 0.037	Alt. 1 = Best Model. + number of islands within 30km (AIC = 266.17) Alt. 2 = Best Model. + sum of the distance to fishing ports (AIC = 266.66) Alt. 3 = Best Model + latitude (AIC = 266.74) Alt. 4 = Best Model. + longitude (AIC = 266.79)
$E\{\text{Number of } FEs_i\} = e^{(1.550 + (0.0547 \times \text{Sea Surface Temperature}_i) - (0.115 \times \text{Macroalgae Cover}_i) + (1.1241 \times 10^{-5} \times \text{Mean Fetch}_i) + (0.123 \times \text{Bottom Incline}_i))} + \varepsilon$ <p>Where <i>Number of FEs_i</i> (Poisson)</p>						

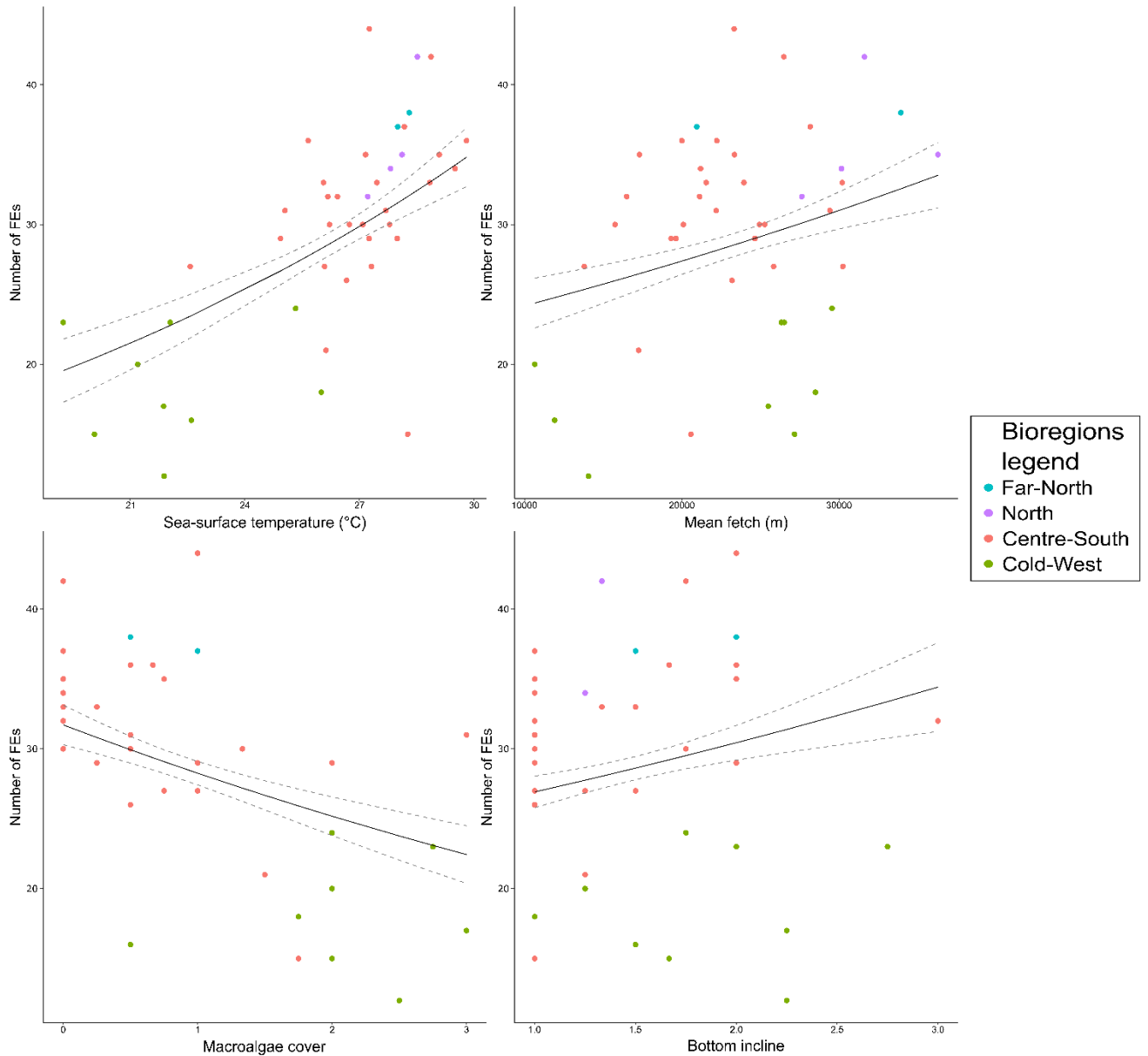


Figure 3.6. The relationships between the number of FEs at each site and the four environmental variables from the most parsimonious model (Table 3.6). Dashed lines illustrate 95% confidence intervals.

3.5 Discussion

This study highlights that reef fish assemblages within each Galápagos bioregion have a low redundancy and high sensitivity of functional roles and are therefore highly vulnerable to functional diversity loss following species loss. Most reef fish functional roles with resilience to species loss from redundancy include piscivores, leaving functions of the lower trophic levels with increased sensitivity. We also identified that variables relating to latitudinal environmental variability and marine habitat conditions are important drivers of functional entity distribution throughout the archipelago. Assessment of the vulnerability of marine ecosystems and functional trait structure of their marine communities are important to understand the response of ecosystems to environmental disturbance (Fetzer et al., 2015; Folke et al., 2004; McCann,

2000; McLean et al., 2019; Pratchett et al., 2011; Worm et al., 2006). However, vulnerability assessments are often conducted at large spatial scales (see Mouillot et al., 2014; Parravicini et al., 2014). Our use of a functional vulnerability assessment at a smaller spatial scale agreed with these studies, identifying a high vulnerability of most reef fish functional roles within the Galápagos.

3.5.1 Functional vulnerability and redundancy

Galápagos reef fish assemblages had a low functional redundancy and high functional sensitivity, despite differing numbers of functional entities between bioregions. There was also a low functional over-redundancy and functional originality. Galápagos reef fish assemblages had a low redundancy within functional roles and most of the functional roles were represented by a single species (i.e. high sensitivity) (Mouillot et al., 2014). More than one species is needed to represent a functional role to insure it is not lost following the loss of a species (Lawton & Brown, 1994). The low functional redundancy and high sensitivity in Galápagos reef fish assemblages means they are highly vulnerable to functional diversity loss following species loss (Bellwood et al., 2003; Bihn et al., 2010; Micheli & Halpern, 2005). Low functional redundancy can also indicate that reef fish functional roles fill all available reef ecosystem niches (Gajdzik et al., 2018). The low functional over-redundancy supports this, indicating that Galápagos reef fish species over-represent functional roles less commonly than reef fish faunas globally (Mouillot et al., 2014). As a result, there is less functional redundancy in communities but there are more ecologically distinct species and ecosystem niches filled. High ecosystem niche differentiation and functional complementarity make Galápagos reef fish assemblages distinct from other reef fish faunas globally (Stuart-Smith et al., 2013). Combined, the low functional redundancy and over-redundancy suggest that reef fish communities of ecologically different species are efficiently using ecosystem resources with low competition (Hooper et al., 2012; Loreau et al., 2001). However, this increases the vulnerability of the whole reef ecosystem because more ecosystem niches are vulnerable to species loss. Conversely, the low functional originality suggests that some reef fish functional roles are functionally close, indicating possible functional redundancy between similar roles (Brandl et al., 2016; Mouillot et al., 2013b). We suggest that functional resilience of Galápagos reef fish assemblages against biodiversity loss may come from a lost species being replaced by a species that plays similar ecological functions instead of from redundant species that fulfil the same functions (Thibaut et al., 2012). Currently, Galápagos reef fish communities may be functionally stable with high functional complementarity between species, but they are likely to be at risk of losing reef fish functional roles in the future due to low redundancy of species within functional roles.

Galápagos reef fish assemblages have a high functional vulnerability to biodiversity loss due to low functional redundancy and high functional sensitivity. These results are consistent with previous studies that found a high vulnerability in global and regional reef fish assemblages (Mouillot et al., 2014; Parravicini et al., 2014). Globally, reef fish assemblages have a low functional redundancy. However, it is lowest in the ETP region – a functional sensitivity hotspot (i.e. an average of 2.8 species per FE compared to 7.9 species per FE in the Indo-Pacific) (Parravicini et al., 2014). Building upon these studies, we found that in the Galápagos, an oceanic archipelago within the ETP, reef fish assemblages have exceptionally low functional redundancy and high functional sensitivity. Reef fish assemblages of oceanic islands in the Indo-Pacific also have a high functional vulnerability due to low redundancy (D'agata et al., 2016). Geographic isolation limits species diversity on oceanic islands (Bellwood et al., 2002). Fine-scale environmental variation and biotic processes (e.g. predation, competition and recruitment) limit it further (Mellin et al., 2010). Lower reef fish species richness means that fewer species are available to fill ecosystem niches, resulting in more unique functional roles and higher ecological niche differentiation than in species-rich faunas (Parravicini et al., 2014; Stuart-Smith et al., 2013). Marine ecosystems of oceanic islands globally may be hotspots of functional vulnerability to species loss. In particular, reef fish functional vulnerability is a concern in the oceanic islands of the ETP because species richness is already low (Parravicini et al., 2014), and anthropogenic pressure strongly affects reef fish communities in these islands (Quimbayo et al., 2019).

In the Galápagos, most reef fish functional roles are represented by only a single species and are sensitive to being lost from marine ecosystems following species loss. In isolated islands and marine ecosystems, the loss of a unique species and function can have a more immediate impact on ecosystem functioning (Fetzer et al., 2015) and is more likely to be permanent because colonisation and replacement are less likely (Bender et al., 2017; Quimbayo et al., 2017b, 2019). As an example, the large benthic invertivore, *Bodianus diplotaenia* (Mexican hogfish) represents a unique FE, whose removal from some Galápagos marine ecosystems may explain the overgrazing caused by increased densities of the herbivorous sea urchin, *Eucidaris thouarsii* (Glynn et al., 1979; Okey et al., 2004; Wellington, 1975). Other functionally unique species are keystone species in the Galápagos (Okey et al., 2004), having a high functional impact compared to the total reef fish abundance (Power et al., 1996). Our study highlights the piscivorous species, *Mycteroperca olfax* (Bacalao), represents a unique FE. This species has been overfished to the degree that it is hypothesised to be 'functionally extinct' in some marine ecosystems (Coello & Grimm, 1993; Okey et al., 2004; Reck, 1986). Unique reef fish functional roles have already been removed from some marine ecosystems in the Galápagos, impacting ecosystem functioning and resilience. The loss of additional unique

functional roles is possible under the present fishing and climate change scenarios. The removal of reef fish functional roles due to environmental disturbance and species loss causes functional diversity loss that can result in functional homogenisation (Olden et al., 2004), regime shifts (Folke et al., 2004), trophic cascades (Boyce et al., 2015), and severely impact reef fish biomass production (Duffy et al., 2016). Therefore, we highlight the necessity of considering functional diversity and entities in the marine management of the Galápagos. It is important to preserve reef fish functional roles that contribute unique and important functions to marine ecosystems and to protect species that are functionally irreplaceable, regardless of taxonomy.

The functional trait structure and vulnerability of Galápagos reef fish assemblages resemble the marine food web that is characterised by a diversity of piscivores supported by the high abundance of fish at lower trophic levels (Okey et al., 2004; Salinas et al., 2016). Most FEs with resilience from redundancy include top trophic level species with piscivorous diets, including sharks, jacks, groupers and snappers. Many piscivores are already important to marine ecosystem functioning in the Galápagos as keystone species (Okey et al., 2004). Our study further highlights the functional importance of piscivorous reef fish species, which contribute more to ecosystem resilience through redundancy than the lower trophic levels species. However, fishing and ecosystem degradation generally impact piscivores first (Pauly et al., 1998), and some are already depleted in the Galápagos (Okey et al., 2004). Overfishing of redundant piscivorous species weakens the functional impact and top-down control these species exert resulting in trophic cascades (Heithaus et al., 2008). Additionally, fishers increasingly fish down the food web targeting lower trophic level species that we have found are mostly functionally unique and sensitive in the Galápagos (i.e. invertivores, planktivores, omnivores and herbivores) (Pauly et al., 1998). Marine ecosystem functioning has already been altered in the Galápagos by overfishing compounding upon El Niño disturbances to cause trophic cascades and changes to the marine food web (Edgar et al., 2010; Sonnenholzner et al., 2009). Our research identifies an important link between trophic diversity of reef fish and ecosystem functioning and resilience in the Galápagos. We highlight that fisheries management in the Galápagos needs to consider this important link in the future and the impacts of fishing different trophic levels on marine ecosystem functioning and resilience.

3.5.2 Predictive models

The distribution of reef fish functional entities in the Galápagos were mainly explained by variables relating to geographical position (SST and mean fetch) and habitat type (bottom incline and macroalgae cover). Sea-surface temperature was important with increasing numbers of reef fish functional entities as temperatures increased. In the Galápagos, sea-

surface temperatures increase with latitude from warm and tropical in the north to cold and temperate in the south (Wellington et al., 2001). Sea-surface temperature is a fundamental driver of reef fish speciation processes, influencing morphology, biological activity, and trophic interactions (Brown et al., 2004; Tittensor et al., 2010). Sea-surface temperature then acts as an environmental filter for reef fish functional diversity, excluding certain functional trait combinations as temperatures decrease and limiting the number of reef fish functional roles (Cornwell et al., 2006). Mean fetch and other variables relating to geographical isolation were also significant with increasing numbers of reef fish functional roles as isolation and exposure to oceanographic conditions increased. Isolation can reduce reef fish diversity, limiting speciation and colonisation rates (Losos & Schluter, 2000; MacArthur & Wilson, 2001; Pinheiro et al., 2017). However, this was not the case in our study. The Galápagos sits at the convergence of three major current systems that create latitudinal environmental variation and influence local oceanic processes (Palacios, 2004; G. Wellington et al., 2001). These currents first collide with the outer islands separate from the Galápagos' central islands in the far-north, north and south (Banks, 2002; Edgar et al., 2004a; Houvenaghel, 1978). Reef fish assemblages around exposed oceanic islands generally contain both species with larger body sizes and wide geographic ranges that are suited to living in high wave energy benthic-pelagic environments, and smaller resident species that are protected from this wave energy by remaining in close association the benthic habitat (Gove et al., 2016; Kulbicki et al., 2015; Luiz et al., 2012; Quimbayo et al., 2017a). Because marine ecosystem niches are more diverse in both the water column and around the substrate, there are increased numbers of reef fish functional roles. Isolated island habitats and reef fish communities are also less likely to be influenced by human disturbances, possibly increasing species and functional diversity in these assemblages further (Cinner et al., 2016; Maire et al., 2016). Variation in habitat composition, including topographic relief and benthic cover, are important in structuring reef fish communities (Jones & Syms, 1998; Komyakova et al., 2013; Luckhurst & Luckhurst, 1978; Roberts & Ormond, 1987). In our study, bottom incline was important for increasing numbers of reef fish functional roles as the bottom incline increased. Complex benthic habitat with high relief increases the numbers of less mobile demersal and benthic species offering caves and ledges to shelter (Beukers & Jones, 1998; Walsh, 1983). Prey availability then increases trophic and functional diversity due to attracting larger predatory species (Beukers & Jones, 1998; Gratwicke & Speight, 2005; Walsh, 1983). In contrast, flatter marine habitats are less complex and offer less protection but allow macroalgae assemblages to establish (Harman et al., 2003). Macroalgae is the primary source of food and production for reef fish in temperate marine ecosystems (Harman et al., 2003; Klumpp & McKinnon, 1989). Temperate reef ecosystem conditions limit marine ecological niches primarily to macroalgae associated species (e.g. herbivores) and their predators, decreasing the number of functional roles in

these reef fish assemblages. Instead of pelagic productivity, benthic productivity may represent a more important energy source in these marine ecosystems (Klumpp & McKinnon, 1989).

Overall, most of the explanatory variables were consistent with other Galápagos studies describing the latitudinal environmental variation, from tropical to temperate marine ecosystems, that influences reef species compositions and distinguishes bioregions (Edgar et al., 2004a; Harris, 1969; Wellington, 1975). Increased isolation and exposure to high energy oceanographic conditions, and habitat bottom incline were interesting additions, possibly explaining the increased functional diversity in some reef fish assemblages of the southern Galápagos islands where ocean temperatures are cooler.

3.6 Conclusions

We assessed the vulnerability of marine ecosystems in the Galápagos by describing the functional trait structure, redundancy and vulnerability of its reef fish communities. To do so, we described Galápagos reef fish using functional entities and a combination of functional diversity and vulnerability indices. We then assessed the influence of a set of predictor variables on functional entity composition. We suggest that Galápagos reef fish communities are currently functionally stable consisting of ecologically dissimilar reef fishes that efficiently use ecosystem resources. This conclusion is drawn from the low redundancy of species within functional roles. While this low redundancy might leave some functional roles vulnerable, we suggest that there may be some functional insurance against species loss which would come from species playing ecologically similar functions instead of redundant species filling the same functions. However, this means that Galápagos reef fish communities are still highly vulnerable to loss of specific functional roles and therefore functional diversity loss following loss of species. Therefore, we also identify the risk of functional homogenisation, regime shifts and trophic cascades occurring in Galápagos reef fish assemblages (Boyce et al., 2015; Folke et al., 2004; Olden et al., 2004) and raise concerns about the long-term functioning of Galápagos marine ecosystems. El Niño and overfishing have already caused extinctions of several Galápagos macroalgae species and the endemic damselfish *Azurina eupalama* while threatening many others (Edgar et al., 2010; Glynn, 1988; Lamb et al., 2018), and possibly altering marine ecosystem functioning. Future research should continue to monitor reef fish functional diversity, entities and vulnerability because El Niño's are increasing in frequency and intensity, and local human populations are growing (Cai et al., 2014; Hoegh-Guldberg et al., 2007).

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Traditionally, marine management prioritises conservation according to species diversity or specific taxonomic groups (Naeem et al., 2012). This has resulted in functionally vulnerable areas not being protected globally (D'agata et al., 2016; Mouillot et al., 2013a; Mouillot et al., 2014; Parravicini et al., 2014). Galápagos marine communities are vulnerable to functional diversity loss independent of species diversity and taxonomic structure across bioregions. Furthermore, the low redundancy indicates that most reef fish functional roles are unique and not likely to be replaced, giving every species a high conservation significance. Functional vulnerability assessments highlight the importance of all species to ecosystem functioning and provide an important ecological tool for informing marine management independent of taxonomic structure. We suggest considering reef fish species by ecological functions in future Galápagos marine research and management.

CHAPTER 4

General discussion

4.1 Messages across chapters

I used a combination of functional alpha-diversity, beta-diversity, and vulnerability analysis methods to describe reef fish assemblages of the Galápagos (**Chapter 2 and 3**). Across the Galápagos, reef fish functional diversity was variable (**Chapter 2**). However, there were also consistent functional diversity properties (i.e. functional alpha-diversity) and functional trait structure (**Chapter 2 and 3**), highlighting the bioregionalization and different environmental conditions that have created recognised marine bioregions in the Galápagos archipelago (Edgar et al., 2004a; Harris, 1969; Wellington, 1975). Some reef fish assemblages within the current bioregions are functionally dissimilar, and likely to respond differently to environmental change (**Chapter 2**). Sub-dividing the current large bioregions and managing them as smaller sub-regions would more accurately capture marine community variation and functional diversity (Fig. 4.1). There was a low richness of functional roles within communities, in which reef fish species and abundances are mostly distributed evenly (**Chapter 2 and 3**). Some species in high abundance represent a few distinct and supportive functional roles in marine ecosystems and these are likely functionally resilient because of redundancy (**Chapter 2**). Redundant functional roles are mostly represented by upper trophic level piscivorous species (**Chapter 3**). In comparison, most reef fish functional roles are represented by only a single species and low abundance (**Chapter 2 and 3**), a characteristic of reef fish assemblages globally that makes marine ecosystems vulnerable to losing functional diversity (Mouillot et al., 2014; Parravicini et al., 2014). These vulnerable functional roles are mainly represented by the lower trophic level species such as invertivores, herbivores and planktivores that are food for the abundant apex predators (i.e. piscivores) (**Chapter 3**). The functional vulnerability of reef fish assemblages highlights an important link between functional and trophic diversity, reflecting the marine food web that supports large abundances of apex predators. Functional diversity assessments integrate key aspects of ecosystem functioning into marine biodiversity studies to supplement traditional taxonomic based metrics and inform marine management. Continued investigation of functional diversity in the Galápagos is important to preserve reef fish functional diversity, which is critical to maintaining long-term marine community and ecosystem functioning and services to humans in a biological age of extinction (Fig. 4.1).

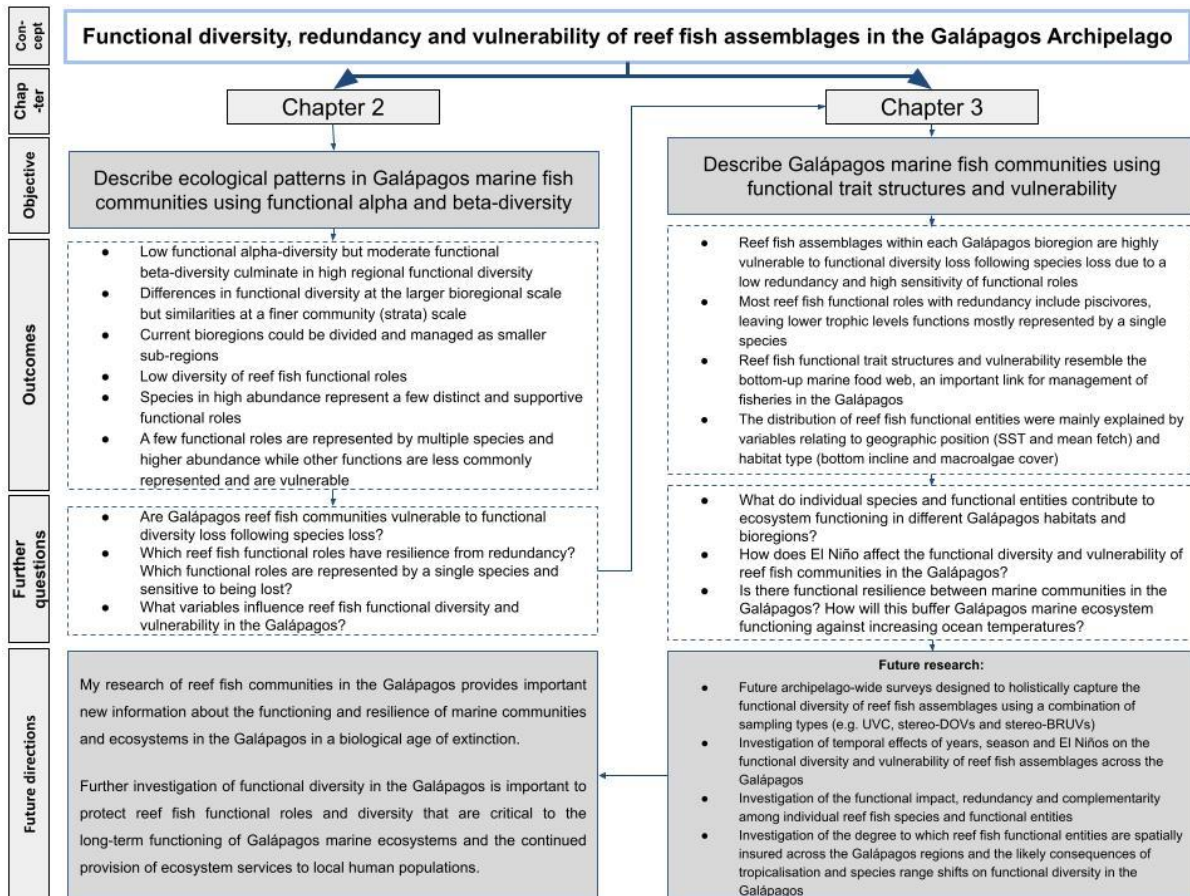


Figure 4.1. Conceptual diagram outlining the outcomes and opportunities for future research generated from this thesis.

4.2 New perspectives

4.2.1 Advantages of local functional diversity assessments

My research on reef fish assemblages within the Galápagos has resulted in a finer resolution investigation of the functional diversity and vulnerability patterns than described in the larger studies undertaken at global and regional scales (Mouillot et al., 2014; Parravicini et al., 2013; Stuart-Smith et al., 2013). Compared to other regions globally, the functional diversity of Galápagos reef fish assemblages is the highest in the world and distinct from global biodiversity patterns (Stuart-Smith et al., 2013). In contrast, my study shows that within each of the recognised bioregions (Edgar et al., 2004a) the functional diversity of Galápagos reef fish communities is actually very low (**Chapter 2**). However, combining reef fish assemblages across tropical and temperate reef ecosystems results in high functional diversity for the Galápagos on a global scale.

The Galápagos is located within the Eastern Tropical Pacific region, a functional vulnerability hotspot (Parravicini et al., 2014). My research provides important new information about that the functional vulnerability of Galápagos reef fish, highlighting increased functional sensitivity and decreased redundancy at a smaller spatial scale (**Chapter 3**).

4.2.2 Galápagos marine ecosystem functioning

Community functional diversity is a measure of ecosystem functioning and resilience (Hooper & Vitousek, 1997; Reich et al., 2004; Tilman et al., 1997). My study suggests that Galápagos marine ecosystem functioning is low but its reef fish assemblages are currently functionally stable (**Chapter 2 and 3**). Low functional diversity (i.e. functional richness) and low redundancy across the Galápagos suggests ecosystem niches and resources are limited, but that they are being effectively used by communities of ecologically distinct reef fishes (**Chapter 3**) (Loreau et al., 2001). It is also therefore likely that ecological functions that can endure environmental disturbances or assist ecosystem recovery are missing or underrepresented (Brandl et al., 2019; Elmqvist et al., 2003; Holling, 1996; Holling, 1973). This highlights that ecosystem resilience is reduced. Functional diversity assessments provide a mechanism to investigate marine ecosystem functioning and resilience through the study of marine biodiversity. My functional diversity study in the Galápagos suggests marine ecosystem functioning and resilience to environmental disturbance are low and likely to be reduced further because of the possibility of losing reef fish functional roles in the future (**Chapter 2 and 3**).

4.3 Galápagos marine management

4.3.1 Species-specific management

My assessment of the functional diversity of reef fish assemblages highlights that all reef fish species play a significant role in the functioning of the Galápagos marine ecosystems. A few species in high abundance represent a few specialised functional roles and have a high functional impact (**Chapter 2**). At the same time, most reef fish species represent unique functional roles that are vulnerable to being lost from Galápagos marine ecosystems (**Chapter 2 and 3**). Globally, marine species conservation tends to prioritise a small number of species that are generally more abundant or have larger body sizes (Palacios-Salgado et al., 2019). In the Galápagos, species of economic significance to tourism and fisheries are most commonly protected (Edgar et al., 2004b), leaving most reef fish species under-represented in marine management and conservation strategies. However, my study highlights that all reef fish species are significant to ecosystem functioning, contributing functional roles to community functional diversity, and should be considered individually in Galápagos marine management and spatial planning.

4.3.2 Spatial management

Historically, between three and five main biogeographical regions have been proposed for the Galápagos using different physical and biological parameters (Edgar et al., 2004a; Harris,

1969; Jennings et al., 1994; Wellington, 1975). However, to aid in developing future zoning plans for the Galápagos Marine Reserve to protect marine biodiversity and ecosystem functioning more effectively, the number of regions and their boundaries could be further refined (**Chapter 2 and 3**). This is because of the environmental gradients within the centre-south and cold-west bioregions which create variation in ecological niches and functions. As a result, some reef fish assemblages are functionally dissimilar within the current bioregions according to reef fish functional beta-diversity (**Chapter 2 and 3**). Therefore, it is likely that marine ecosystem functioning and responses to environmental disturbance are also dissimilar within the current bioregions. Sub-dividing the centre-south and cold-west bioregions and managing them as smaller sub-regions would more accurately capture reef fish functional diversity in the Galápagos. Managing at a smaller spatial scale will incorporate fine-scale environmental variation to manage ecosystems according to changes in functioning and resilience.

4.3.3 Fishery management

The assessment of reef fish functional trait structure indicate that reef fish functional diversity and trophic diversity are related, an important link for future fisheries management in the Galápagos (**Chapter 3**). Historically, fishing has depleted some reef fish species to the degree that the ecological consequences of overfishing on trophic diversity and ecosystem functioning are already evident in some areas of the archipelago (Coello & Grimm, 1993; Glynn et al., 1979; Okey et al., 2004; Reck, 1986; Wellington, 1975) (**Chapter 3**). Fishing lower trophic level species is more likely to remove unique functional roles and impact ecosystem functioning sooner because my research has identified that these roles are functionally vulnerable (**Chapter 3**). However, some lower trophic level species may intrinsically be less impacted by fishing, which may partially mitigate this risk. For example, untargeted herbivorous damselfish or 'r' selected species such as sardines, herring, and anchovies (Adams, 1980; Edwards et al., 2014). In comparison, fishing upper trophic level piscivorous species is less likely to remove a functional role because my research has identified that most of these roles are functionally redundant (**Chapter 3**). However, these species are generally more vulnerable to fishing due to large size, slow growth, and low reproductive output (for example 'k' selected shark species (Pauly et al., 2002). Overfishing these species would reduce this redundancy and impact the functional redundancy of Galápagos reef fish assemblages. Furthermore, overfishing piscivorous species may weaken their top-down control of lower trophic level species and significantly impact ecosystem resilience because many have been shown to be keystone species (Heithaus et al., 2008; Okey et al., 2004; Pauly et al., 1998). The consideration of abundances is also important for redundancy because a higher number of individuals in the same functional role can buffer against anthropogenic or

environmental disturbance (D'agata et al., 2016; de Bello et al., 2007). However, my study did not incorporate abundance into redundancy analyses. Applying a functional redundancy index that includes abundances of individuals would better inform fisheries management practices (see McLean et al., 2019; Ricotta et al., 2016) where the aim is to maintain species diversity and abundances across trophic levels that are important to both ecosystem functioning and fisheries.

4.4 Limitations and future opportunities

4.4.1 Sampling methods and design

My study used reef fish diversity and abundance data collected from benthic and pelagic habitats using stereo-BRUVs. Stereo-BRUVs have been demonstrated to be an effective tool to sample a broad group of fishes across a number of trophic levels (Cappo et al., 2003a; Harvey et al., 2007; Langlois et al., 2020). Consequently, I believe that the stereo-BRUVs data I used created a meaningful assessment of reef fish functional diversity in the Galápagos archipelago (**Chapter 2 and 3**). I note one of the limitations of using stereo-BRUVs is that cryptic and rare fish species are likely to be observed less frequently than more mobile fishes (Harvey et al., 2007). Ninety-eight percent of reef fish functional specialists in diverse ecosystems are rare and occur in low abundance (Mouillot et al., 2013a). Therefore, it is possible that by using only stereo-BRUVs data my study did not elucidate some important reef fish functional roles. Several different non-extractive fish survey techniques exist that effectively sample different metrics of reef fish assemblages (Goetze et al., 2015). Diver Operated stereo-Video (stereo-DOV) surveys can more effectively survey cryptic species than stereo-BRUVs (Watson et al., 2005, 2010), and in comparison to these stereo-video methods, underwater visual censuses (UVC) can more effectively survey and identify cryptic fish species because the human eye can search complex reef habitats (Colton & Swearer, 2010; Holmes et al., 2013; Lowry et al., 2012). More recently environmental DNA has been shown to be an effective and complementary tool to visual sampling (Cole et al., 2021; Stat et al., 2019; Valdivia-Carrillo et al., 2021), but cannot be used to estimate abundances. Extractive sampling methods, including the use of ichthyocides can improve estimates of small and cryptic taxa (e.g. gobies and blennies) (Ackerman & Bellwood, 2000; Willis & Anderson, 2003). Using a combination of complementary techniques which effectively sample different parts of reef fish assemblages would generate a more comprehensive survey of whole reef fish communities (Goetze et al., 2015; Shedrawi et al., 2014; Watson et al., 2010). Despite this, I feel the patterns observed in this study using stereo-BRUVs would be representative of the functional roles and diversity of reef fish communities in the Galápagos as a whole.

4.5 Future opportunities for functional diversity research

There are several opportunities for future research that build upon the community-scale reef fish functional diversity assessment of this thesis:

4.5.1 Temporal comparisons

In the Galápagos, El Niño periodically impacts reef fish populations (Edgar et al., 2010; Glynn, 1988), and has likely already altered marine ecosystem functioning in the different bioregions. I acknowledge that the data used in this study is a snapshot and suggest that incorporating a temporal component that includes years and seasons will offer insights into ecosystem functioning and recovery following environmental fluctuations and disturbance. A functional diversity approach is advantageous over taxonomic diversity for temporal studies because it can reveal the impacts of environmental disturbance sooner (Mouillot et al., 2013b). This approach would be useful because the impacts of El Niño's are vitally important for the Galápagos marine ecosystem and globally relevant because the regular El Niño's in the Galápagos are comparable to the recent marine heatwaves exacerbated by climate change that impact ecosystems in other regions (Frölicher & Laufkötter, 2018).

4.5.2 Functional impact of species and functional entities

Detailed knowledge of the functional roles of individual species and functional entities gives an understanding of whole ecosystem processes and identifies species groups most important to conservation (Brandl & Bellwood, 2014). Brandl & Bellwood (2014) propose a multidimensional framework that investigates ecosystem niche occupation and redundancy of a select group of species. This analytical strategy has been applied to key functional groups such as herbivorous fishes on coral reefs and has identified reef fish functional roles that are critical to marine ecosystem recovery, but were previously not a priority for marine management (Bellwood et al., 2006; Bonaldo et al., 2014; Fox & Bellwood, 2008). Applying individual-based functional analyses across trophic levels in the different Galápagos regions would give an understanding of the functional contribution of reef fish species and may identify important functional roles to prioritise for conservation.

4.5.3 Spatial functional insurance of species and functional entities

While the functional redundancy of reef fish communities is increasingly being investigated (Mouillot et al., 2014; Parravicini et al., 2014) the spatial functional insurance and the likelihood that neighbouring communities could replace lost functional roles are less well understood. Functional nestedness indicates whether similar functional roles are present across communities despite differences in functional richness (Bender et al., 2017). However,

assessing species functional rarity or commonness (Grenié et al., 2018; Violle et al., 2017), could be a better mechanism for understanding functional redundancy across geographic areas while identifying functionally rare species that need protection. Similar analytical strategies have also simulated the impact of local and regional species extinctions on the functional structure of reef fish communities using functional diversity indices (Leitão et al., 2016). Functional rarity assessments determine the uniqueness or commonness of species functional roles locally and across regions (Grenié et al., 2018). Such an assessment could have application as an indicator of functional redundancy spatially across regions while prioritising the protection of functionally rare species that are restricted to specific communities and habitats. This approach would be useful to investigate the possible replacement of functional diversity in reef fish assemblages across the Galápagos as ocean warming pushes warm-water species distributions towards temperate regions, causing shifts in the functionally dominant species within marine ecosystems (Graham et al., 2014; Vergés et al., 2014).

4.6 Overall thesis conclusion

My research has demonstrated that although the Galápagos is overall highly functionally diverse in its reef fish assemblages compared to other regions globally, within bioregions it is not. While within bioregions functional diversity is low, the functional diversity of reef fish assemblages differs between bioregions, leading to the high functional diversity of the Galápagos as a whole. Within reef fish assemblages, there is a low diversity of functions that is supplemented by a few species in high abundance representing highly specialised functional roles and strong ecosystem support. Such functional roles are resilient due to redundancy; however, most functional roles are unique to a single species making them vulnerable to being permanently lost from Galápagos marine ecosystems. Lower trophic levels functions are most vulnerable, while there is more functional redundancy at the highest trophic levels which reflects the marine food web that supports large abundances of apex predators.

My research extends understanding of marine biodiversity beyond the traditional taxonomic structure, highlighting that all reef fish species and the current trophic structure are critical to marine ecosystem functioning and resilience in the Galápagos. These findings feed important information into marine spatial, conservation and fisheries management. The unusual geographic and oceanographic setting that drives reef fish species composition patterns, also makes the Galápagos functionally distinct because of the characteristic functional diversity of each different bioregion. The Galápagos is a region of high functional diversity that is globally significant and deserves continued investigation.

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APPENDIX A: Copyright statements

CHAPTER 2

Functional diversity of reef fish assemblages in the Galápagos Archipelago

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To whom it may concern, I, Simon McKinley, contributed to the design of this study, analysed the data, and wrote and edited the following manuscript:

McKinley, S.J., Saunders, B. J., Rastoin-Laplane, E., Salinas-de-León, P., Harvey, E. S.
Functional diversity of reef fish assemblages in the Galápagos Archipelago.

I, as a co-author, endorse that the level of contribution by the candidate stated above is appropriate.

Signed:

Dr. Benjamin Saunders

Signed:

Etienne Rastoin-Laplane

Signed:

Pelayo Salinas-de-León

Signed:

Prof. Euan Harvey

CHAPTER 3

Functional vulnerability, redundancy, and biogeographical drivers of reef fish assemblage functions in the Galápagos Archipelago

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To whom it may concern, I, Simon McKinley, contributed to the design of this study, analysed the data, and wrote and edited the following manuscript:

McKinley, S.J., Saunders, B. J., Rastoin-Laplane, E., Salinas-de-León, P., Harvey, E. S. Functional vulnerability, redundancy, and biogeographical drivers of reef fish assemblage functions in the Galápagos Archipelago.

I, as a co-author, endorse that the level of contribution by the candidate stated above is appropriate.

Signed:

Dr. Benjamin Saunders

Signed:

Etienne Rastoin-Laplane

Signed:

Pelayo Salinas-de-León

Signed:

Prof. Euan Harvey

SUPPLEMENTARY INFORMATION

CHAPTER 2

Table S2.1. Functional trait matrix for the seven functional traits used to assess the functional diversity of 121 reef fish species sampled in the Galápagos Archipelago in 2015. Corresponding FishBase references numbers and references for each species functional traits are below in Table S2.2 and S2.3.

Functional trait category		Body size	Trophic ecology								Ecological niche				Within-reef mobility			Social behaviour		
Functional trait		Maximum total length (cm)	Trophic level	Diet breadth	Feeding behaviour						Water column position				Substrate preference			Largest common group size		
genus species	gen sp				Variable	Hunting	Browsing	Grazing	Selective Plankton Feeding	Filtering Plankton	Pelagic	Benthopelagic	Benthic	Demersal	Soft Bottom	Rocky	Coral Reef	Solitary /small group	Schooling	
<i>Abudefduf troschelii</i>	Abud tro	20	2.95	0.32	1	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1
<i>Acanthocybium solandri</i>	Acan sol	250	4.42	0.9249	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0
<i>Acanthurus nigricans</i>	Acan nig	21.3	2	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0
<i>Acanthurus xanthopterus</i>	Acan xan	70	2.87	0.36	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0
<i>Aetobatus narinari</i>	Aeto nari	330	3.32	0.43	0	1	0	0	0	0	0	1	0	1	1	0	1	1	1	0
<i>Alectis ciliaris</i>	Alec ciliar	150	4	0.7	0	1	0	0	0	0	0	1	0	0	1	0	1	1	1	0
<i>Aluterus monoceros</i>	Alut monoc	76.2	3.49	0.4	0	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1
<i>Aluterus scriptus</i>	Alut scrip	110	3.02	0.19	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0
<i>Anisotremus interruptus</i>	Anis in	51	3.5	0.37	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1	1
<i>Anisotremus scapularis</i>	Anis sc	40	3.27	0.47	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
<i>Apogon spp</i>	Apog spp	10	3.4	0.45	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	0
<i>Archosargus pourtalesii</i>	Arch po	35.6	2.94	0.32	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0
<i>Arothron hispidus</i>	Arot hispi	50	3.1	0.3797	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0
<i>Arothron meleagris</i>	Arot melea	50	3.06	0.32	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0
<i>Aulostomus chinensis</i>	Aulo chi	80	4.24	0.74	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0
<i>Balistes polylepis</i>	Bali polyl	76	3.34	0.37	0	1	0	0	0	0	0	1	0	0	1	1	1	1	1	0
<i>Bodianus diplotaenia</i>	Bodi diplo	76	3.44	0.46	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1	0
<i>Bodianus eclancheri</i>	Bodi eclan	61	2.7	0.24	0	0	0	1	0	0	0	0	1	0	0	1	0	1	1	1
<i>Bothus leopardinus</i>	Both leopard	23.5	3.65	0.52	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	0
<i>Calamus taurinus</i>	Cala taurin	40	3.34	0.52	0	1	0	0	0	0	0	0	1	0	1	0	0	1	1	0

Supplementary information

genus species	gen sp	Maximum total length (cm)	Trophic level	Diet breadth	Variable	Hunting	Browsing	Grazing	Selective Plankton Feeding	Filtering Plankton	Pelagic	Bentho-pelagic	Benthic	Demersal	Soft Bottom	Rocky	Coral Reef	Solitary /small group	Schooling
<i>Canthidermis maculata</i>	Cant mac	50	3.47	0.45	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0
<i>Caranx caballus</i>	Cara caballu	61.05	4.05	0.54	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1
<i>Caranx caninus</i>	Cara caninus	112.11	3.9	0.61	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0
<i>Caranx lugubris</i>	Cara lugubri	100	4	0.6519	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1
<i>Caranx melampygus</i>	Cara melampy	129.87	4.28	0.83	0	1	0	0	0	0	1	0	0	0	0	1	1	1	1
<i>Caranx sexfasciatus</i>	Cara sexfasc	120	3.58	0.49	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1
<i>Carcharhinus falciformis</i>	Carc fal	350	4.4	0.73	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0
<i>Carcharhinus galapagensis</i>	Carc gal	370	4.34	0.77	0	1	0	0	0	0	1	1	0	0	0	1	1	1	0
<i>Carcharhinus limbatus</i>	Carc lim	275	4.46	0.77	0	1	0	0	0	0	0	1	0	0	1	1	1	1	0
<i>Caulolatilus princeps</i>	Caul prin	102	3.9	0.53	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0
<i>Cephalopholis panamensis</i>	Ceph pan	39	4.15	0.71	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0
<i>Chaetodon humeralis</i>	Chae hume	25.4	2.72	0.24	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1
<i>Chanos chanos</i>	Chan chan	219.6	2.4	0.2	0	0	0	1	0	0	0	1	0	0	1	0	1	1	1
<i>Chilomycterus reticulatus</i>	Chil ret	29.78	3.45	0.41	1	0	0	0	0	0	0	0	1	0	1	1	1	1	0
<i>Chromis alta</i>	Chro alta	15.86	3.4	0.45	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1
<i>Chromis atrilobata</i>	Chro atrilo	13.4	3.4	0.45	0	0	0	0	1	0	0	1	0	0	0	1	1	0	1
<i>Cirrhitichthys oxycephalus</i>	Cirr oxyce	10	4.01	0.66	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0
<i>Cratinus agassizii</i>	Crat agass	60	4.2	0.73	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0
<i>Dasyatis brevis</i>	Dasy brevi	187	3.84	0.6	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0
<i>Dasyatis longus</i>	Dasy longu	260	3.5	0.37	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0
<i>Dermatolepis dermatolepis</i>	Derm derm	100	4.5	0.8	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0
<i>Elagatis bipinnulata</i>	Elag bipin	180	3.59	0.49	0	1	0	0	0	0	1	0	0	0	0	1	1	1	1
<i>Enchelycore lichenosa</i>	Ench li	90	4.5	0.8	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0
<i>Epinephelus labriformis</i>	Epin la	60	4	0.66	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0
<i>Euthynnus lineatus</i>	Euth line	93.24	3.83	0.6	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1
<i>Fistularia commersonii</i>	Fist com	160	4.28	0.78	0	1	0	0	0	0	0	1	0	0	1	1	1	1	0
<i>Galeocerdo cuvier</i>	Gale cuv	750	4.42	0.91	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0
<i>Girella freminvillei</i>	Gire fremin	45	2	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1

Supplementary information

genus species	gen sp	Maximum total length (cm)	Trophic level	Diet breadth	Variable	Hunting	Browsing	Grazing	Selective Plankton Feeding	Filtering Plankton	Pelagic	Bentho-pelagic	Benthic	Demersal	Soft Bottom	Rocky	Coral Reef	Solitary /small group	Schooling
<i>Gobioclinus dendriticus</i>	Gobio den	13	3.98	0.66	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0
<i>Gymnothorax dovii</i>	Gymn do	170	4.25	0.68	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0
<i>Gymnothorax flavimarginatus</i>	Gymn fl	240	4.16	0.72	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0
<i>Haemulon scudderii</i>	Haem scudd	35	4.2	0.73	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1
<i>Halichoeres dispilus</i>	Hali disp	25	3.85	0.57	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1
<i>Halichoeres nicholsi</i>	Hali nich	38	4	0.61	0	1	0	0	0	0	0	0	1	0	1	1	1	1	0
<i>Halichoeres notospilus</i>	Hali noto	25.4	3.52	0.43	0	1	0	0	0	0	0	0	1	0	1	1	1	1	0
<i>Hemilutjanus macrophthalmos</i>	Hemi mac	61	3.98	0.58	0	1	0	0	0	0	1	0	1	0	0	1	0	1	0
<i>Heteroconger klausewitzii</i>	Hete klau	70	3.4	0.45	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1
<i>Heterodontus quoyi</i>	Hete quoy	130.54	3.54	0.5	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0
<i>Holacanthus passer</i>	Hola pass	35.6	2.61	0.33	1	0	0	0	0	0	0	1	0	0	0	1	1	1	0
<i>Hoplopagrus guentherii</i>	Hopl guen	92	3.85	0.6	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0
<i>Johnrandallia nigrirostris</i>	John nig	20	2.97	0.44	1	0	0	0	0	0	0	1	0	0	0	1	1	1	0
<i>Kyphosus analogus</i>	Kyph analo	70	2.83	0.34	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1
<i>Kyphosus elegans</i>	Kyph elag	53	2.94	0.32	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1
<i>Kyphosus ocyurus</i>	Kyph ocyur	59	3.5	0.37	0	1	0	0	0	0	1	0	0	0	0	1	1	1	1
<i>Lutjanus aratus</i>	Lutj aratu	100	4.09	0.65	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0
<i>Lutjanus argentiventris</i>	Lutj argen	71	4.04	0.6338	0	1	0	0	0	0	0	1	0	0	0	1	1	1	1
<i>Lutjanus guttatus</i>	Lutj gutta	80	3.83	0.66	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0
<i>Lutjanus novemfasciatus</i>	Lutj novem	170	4.1	0.72	0	1	0	0	0	0	0	1	0	0	0	1	1	1	1
<i>Lutjanus viridis</i>	Lutj virid	30	4.16	0.74	0	1	0	0	0	0	0	1	0	0	0	1	1	1	1
<i>Melichthys niger</i>	Meli nig	50	2.73	0.3	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0
<i>Mobula birostris</i>	Mobu biros	910	3.46	0.4965	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0
<i>Mobula spp</i>	Mobu spp	520	3.71	0.53	0	1	0	0	0	0	1	0	0	0	0	1	1	1	0
<i>Mola ramsayi</i>	Mola ram	300	3.8	0.6	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0
<i>Mugil galapagensis</i>	Mugi galapa	40	2.46	0.2367	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1
<i>Mulloidichthys dentatus</i>	Mull dent	31	3.69	0.55	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1
<i>Muraena argus</i>	Mura arg	120	4.02	0.62	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0

Supplementary information

genus species	gen sp	Maximum total length (cm)	Trophic level	Diet breadth	Variable	Hunting	Browsing	Grazing	Selective Plankton Feeding	Filtering Plankton	Pelagic	Bentho-pelagic	Benthic	Demersal	Soft Bottom	Rocky	Coral Reef	Solitary /small group	Schooling
<i>Muraena clepsydra</i>	Mura clepsy	120	4.03	0.62	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0
<i>Muraena lentiginosa</i>	Mura lentig	61	3.94	0.61	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0
<i>Mycteroperca olfax</i>	Myct olf	120	4.5	0.8	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0
<i>Myliobatis spp</i>	Mylio spp	180	3.5	0.37	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0
<i>Ogcocephalus darwini</i>	Ogco darw	24.77	3.44	0.59	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0
<i>Ophioblennius steindachneri</i>	Ophi stein	21.96	2.74	0.25	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0
<i>Oplegnathus insignis</i>	Ople insig	66	3.12	0.43	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0
<i>Orthopristis forbesi</i>	Orth forb	37.21	3.51	0.32	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1
<i>Paralabrax albomaculatus</i>	Para albo	61.98	4.5	0.8	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0
<i>Paranthias colonus</i>	Para col	35.6	3.76	0.59	0	0	0	0	1	0	0	1	0	0	0	1	1	1	1
<i>Plagiotremus azaleus</i>	Plag aza	10	4.42	0.78	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1
<i>Prionurus laticlavus</i>	Prio lati	60	2.72	0.31	0	0	1	0	0	0	0	0	1	0	0	1	1	1	1
<i>Prognathodes carlhubbsi</i>	Prog carl	15	3.31	0.34	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0
<i>Remora remora</i>	Remo remo	86.4	3	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0
<i>Rhinoptera steindachneri</i>	Rhin stein	90	3.55	0.5	0	1	0	0	0	0	0	1	0	0	1	1	1	0	1
<i>Rypticus bicolor</i>	Rypt bicol	28	3.96	0.67	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0
<i>Sarda orientalis</i>	Sard orient	113.22	4.21	0.6859	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Scarus compressus</i>	Scar comp	68	2	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	0
<i>Scarus ghobban</i>	Scar ghob	75	2	0	0	0	1	0	0	0	0	0	1	0	1	1	1	1	1
<i>Scarus perrico</i>	Scar perr	76	2	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	0
<i>Scarus rubroviolaceus</i>	Scar rubro	70	2	0	0	0	0	1	0	0	0	1	1	0	1	1	1	1	0
<i>Scomberomorus sierra</i>	Scom sier	109.89	4.21	0.73	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0
<i>Scorpaena plumieri</i>	Scor plum	45	4.04	0.61	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0
<i>Semicossyphus darwini</i>	Semi darw	70	3.37	0.55	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0
<i>Seriola lalandi</i>	Seri lalan	250	3.85	0.49	0	1	0	0	0	0	0	1	0	0	0	1	1	1	1
<i>Seriola rivoliana</i>	Seri rivo	177.6	4.5	0.78	0	1	0	0	0	0	0	1	0	1	0	1	1	1	1
<i>Serranus psittacinus</i>	Serr psit	18	3.53	0.37	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0
<i>Sphoeroides angusteiceps</i>	Spho angu	25	3.47	0.38	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0

Supplementary information

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<i>Sphoeroides annulatus</i>	Spho anna	44	3.07	0.44	1	0	0	0	0	0	0	1	0	0	1	1	1	1	0
<i>Sphyrna idiaestes</i>	Sphy idia	91	4.5	0.8	0	1	0	0	0	0	0	1	0	0	0	1	1	1	1
<i>Sphyrna lewini</i>	Sphy lewi	430	4.21	0.6833	0	1	0	0	0	0	1	1	0	0	0	1	1	1	1
<i>Stegastes leucorus</i>	Steg leuc	17.08	3	0.44	0	0	0	1	0	0	0	0	1	0	0	1	1	1	0
<i>Sufflamen verres</i>	Suff verr	40	3.27	0.35	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0
<i>Taeniurops meyeri</i>	Taen mey	330	4.2	0.69	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0
<i>Thalassoma grammaticum</i>	Thal gra	32	3.5	0.37	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0
<i>Thalassoma lucasanum</i>	Thal luc	15	3.45	0.41	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1
<i>Thunnus albacares</i>	Thun alba	265.29	4.48	0.93	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1
<i>Trachinotus stilbe</i>	Trac stil	37.74	3.59	0.56	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Trachurus murphyi</i>	Trac symm	81	3.82	0.52	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Triaenodon obesus</i>	Tria obe	213	4.36	0.75	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0
<i>Triakidae spp</i>	Tria spp	180	3.5	0.37	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0
<i>Umbrina galapagorum</i>	Umbr gala	45	3.4	0.5	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0
<i>Uraspis helvola</i>	Uras helv	50	4	0.52	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1
<i>Xanthichthys mento</i>	Xant ment	27.76	4	0.28	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0
<i>Zanclus cornutus</i>	Zanc cornut	23	2.49	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0

Table S2.2. FishBase references numbers for the functional traits and categories used to assess the functional diversity of 121 each reef fish species sampled in the Galápagos Archipelago in 2015. Corresponding references are below in Table S2.3.

genus species	gen sp	Body size	Trophic ecology					Ecological niche and within-reef mobility references							Social behaviour references			
<i>Abudefduf troschelii</i>	Abud tro	55763	69278		5592	57615			5592	28023	9334	57615					28023	57615
<i>Acanthocybium solandri</i>	Acan sol	30573	69278	168	6769				51243	168	53568						168	6769
<i>Acanthurus nigricans</i>	Acan nig	2334	69278	57615	57615				1602	275	57615	58302	58652	58534			275	90102
<i>Acanthurus xanthopterus</i>	Acan xan	4795	69278	3921	1602	48637	5543		9267	1920	48637	57615	1602	48673	58302		1920	1602
<i>Aetobatus narinari</i>	Aeto nari	58048	33	33	9862				51243	33	58534	58302	6871	9862			33	7251
<i>Alectis ciliaris</i>	Alec ciliar	30573	69278	9137	9283				37816	5217	58302	58534					5217	
<i>Aluterus monoceros</i>	Alut monoc	26340	46593	30573	30573				90102	3592	53568	58534	58302	9318	48637		3592	9318

Supplementary information

genus species	gen sp	Body size	Trophic ecology						Ecological niche and within-reef mobility references							Social behaviour references		
<i>Aluterus scriptus</i>	Alut scrip	9710	33	33	26165				36484	33	53568	58534	57616				33	
<i>Anisotremus interruptus</i>	Anis in	55763	69278	57615	9114				5227	9114	57615	A1					9114	205
<i>Anisotremus scapularis</i>	Anis sc	11482	53696		28023				5227	28023							28023	5227
<i>Apogon spp</i>	Apog spp	11482	69278	57615					5227	28023	57615						28023	
<i>Archosargus pourtalesii</i>	Arch po	5590	69278		28023				5227	28023	A2						28023	
<i>Arothron hispidus</i>	Arot hispi	30874	55797	1602	11889				90102	1602	57615	11889					1602	11889
<i>Arothron meleagris</i>	Arot melea	9710	3921	3921	57615				89467	3921	53568	57615	58302	A1			3921	90102
<i>Aulostomus chinensis</i>	Aulo chi	2334	69278	3921	9275				1602	3921	53568	57615	58472	58302			3921	48635
<i>Balistes polylepis</i>	Bali polyl	2850	69278		5227				91172	28023	2850	57615	28023				28023	
<i>Bodianus diplotaenia</i>	Bodi diplo	5592	69278	57615	57615				9311	9823	57615						9823	9311
<i>Bodianus eclancheri</i>	Bodi eclan	5592	69278		28023				5227	28023	A2						28023	205
<i>Bothus leopardinus</i>	Both leopard	911972	69278		28023				9281	28023	5227						28023	
<i>Calamus taurinus</i>	Cala taurin	11482	69278		28023				5227	28023	11482						28023	
<i>Canthidermis maculata</i>	Cant mac	9276	69278		88972				9710	13385	43538	37816	1602	7251	44187		13385	205
<i>Caranx caballus</i>	Cara caballu	estimate*	69278	9283	9283	57615			9283	57615							9283	
<i>Caranx caninus</i>	Cara caninus	estimate*	69278		28023	9283			51243	28023	9283						28023	9283
<i>Caranx lugubris</i>	Cara lugubri	7251	33	4887	4887	5213	57615		51243	7300	57615	9283	26938				7300	9283
<i>Caranx melampygus</i>	Cara melampy	estimate*	6057	6057	6057	9283	9710		9710	6057	53568	57615	58302	7300	9283		6057	90102
<i>Caranx sexfasciatus</i>	Cara sexfasc	9987	6932	6932	6932	90102			57178	4887	57615	44894	9283	58534			4887	90102
<i>Carcharhinus falciformis</i>	Carc fal	9997	37512	244	37816	37816			51243	244	58302						244	26340
<i>Carcharhinus galapagensis</i>	Carc gal	1602	33559	26464	26464	244	28023		58302	26464	12400	244					26464	244
<i>Carcharhinus limbatus</i>	Carc lim	27169	33559		11889	5578	37816	5485	51243	11889	26970	244	58302				11889	
<i>Caulolatilus princeps</i>	Caul prin	2850	69278		5227				5227	9119	9952						9119	5227
<i>Cephalopholis panamensis</i>	Ceph pan	89707	69278	57615	57615	89707			55763	5222	57615	A1					5222	
<i>Chaetodon humeralis</i>	Chae hume	5592	69278		28023	57615			37955	28023	4858	57615	A1				28023	9286
<i>Chanos chanos</i>	Chan chan	estimate*	12509	49	49	11889			51243	49	119549						49	12868
<i>Chilomycterus reticulatus</i>	Chil ret	estimate*	69278	9680	9680				9680	53568	30573	9680	A1				9680	30573
<i>Chromis alta</i>	Chro alta	estimate*	69278		9334				9334				A1				9334	
<i>Chromis atrilobata</i>	Chro atrilo	59088	69278	57615	57615				9334	28023	57615	28023	A1				28023	205

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genus species	gen sp	Body size	Trophic ecology						Ecological niche and within-reef mobility references								Social behaviour references	
<i>Cirrhitichthys oxycephalus</i>	Cirr oxyce	9289	69278	57615		37955			9710	58534	37955						58534	
<i>Cratinus agassizii</i>	Crat agass	55763	69278			28023			55763	28023	5227						28023	
<i>Dasyatis brevis</i>	Dasy brevi	40637	69278	7445		37955			37955	7445	12591	5227					7445	
<i>Dasyatis longus</i>	Dasy longu	9254	69278	12951	57615	114953			117334	57615	12951						117334	
<i>Dermatolepis dermatolepis</i>	Derm derm	5222	69278	57615		28023			5222	28023	57615	A1					28023	
<i>Elagatis bipinnulata</i>	Elag bipin	26340	69278	275	57615	9283	26145		9710	275	53568	57615	58534	9283	48635	90102	275	48635
<i>Enchelycore lichenosa</i>	Ench li	11114	69278	9137	9137				5227	9137	28023						9137	
<i>Epinephelus labriformis</i>	Epin la	11035	69278	5222	5592	57615			89707	5222	57615	11035					5222	5592
<i>Euthynnus lineatus</i>	Euth line	estimate*	69278	168	168				51243	168	11035						168	168
<i>Fistularia commersonii</i>	Fist com	9301	26908	26908	36710	36327	37816	57615	58302	26908	53568	57615	58472	36710	41878	A1	26908	9710
<i>Galeocerdo cuvier</i>	Gale cuv	58784	37512	33	33	9997	37816		51243	4805	2683	9137					4805	
<i>Girella freminvillei</i>	Gire fremin	11482	69278			28023			11482	28023	A1						28023	5227
<i>Gobioclinus dendriticus</i>	Gobio den	11482	69278	28023					5227	28023	A1						9313	
<i>Gymnothorax dovii</i>	Gymn do	5227	69278						5227									
<i>Gymnothorax flavimarginatus</i>	Gymn fl	48635	69278	3921	3921	30573	89972		1602	57615	58302	48635					1602	90102
<i>Haemulon scudderii</i>	Haem scudd	9114	69278	57615	57615				5227								5227	205
<i>Halichoeres dispilus</i>	Hali disp	9311	69278			28023	9311		9311	28023	57615	A1					28023	5227
<i>Halichoeres nicholsi</i>	Hali nich	9311	69278	57615	57615	28023			9311	28023	57615	A1					9311	205
<i>Halichoeres notospilus</i>	Hali noto	5592	69278	57615	57615				9311	57615	A1						28023	205
<i>Hemilutjanus macrophthalmos</i>	Hemi mac	28023	53696			53696	28023		104864	28023							28023	
<i>Heteroconger klausewitzii</i>	Hete klau	11482	69278			28023			11482	28023							247	28023
<i>Heterodontus quoyi</i>	Hete quoy	5227	69278	28023	28023				5227	247	A1						28023	5227
<i>Holacanthus passer</i>	Hola pass	5592	69278			28023	57615	38503	5227	28023	57615	A1	A2				28023	9333
<i>Hoplopagrus guentherii</i>	Hopl guen	9313	46593	46593	46593	9313			55763	28023	57615	9313	A1				9286	
<i>Johnrandallia nigristrostris</i>	John nig	9286	69278	57615	57615	9286			9286	57615	5227	205	A1				28015	205
<i>Kyphosus analogus</i>	Kyph analo	559	28015	559					51243	28015	53568	58652	559				28023	28023
<i>Kyphosus elegans</i>	Kyph elag	55763	69278			28023			55763	28023	57615	A1					5227	95491
<i>Kyphosus ocyurus</i>	Kyph ocyur	38398	69278	57615	57615	95491			89972	5227	57615	58302	95491				28023	559
<i>Lutjanus aratus</i>	Lutj aratu	55763	69278	9313	9313				55763	9313	A1						55	9313

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genus species	gen sp	Body size	Trophic ecology						Ecological niche and within-reef mobility references							Social behaviour references		
<i>Lutjanus argentiventris</i>	Lutj argen	40637	69278	55	9313				9313	55	57615						55	9313
<i>Lutjanus guttatus</i>	Lutj gutta	9313	37029	9313	9313	57615			91172	55	57615	9313					28023	9313
<i>Lutjanus novemfasciatus</i>	Lutj novem	9313	69278	57615	57615	9313			9313	28023	57615	A1					28023	
<i>Lutjanus viridis</i>	Lutj virid	55	69278	57615	57615				5227	28023	57615	A1					33	9313
<i>Melichthys niger</i>	Meli nig	5217	33	33	1602	48637	33499	5213	9710	33	41878	9276	48637				275	33
<i>Mobula birostris</i>	Mobu biros	58048	69278	9137	9137	9911			51243	275	9137	9911	58302	12951			117334	12951
<i>Mobula spp</i>	Mobu spp	4442	69278		6679				51243	4442								
<i>Mola ramsayi</i>	Mola ram	4424	69278		4925	48637			86942	117334							28023	
<i>Mugil galapagensis</i>	Mugi galapa	11482	69278		28023	11482			11482	28023	A1						205	
<i>Mulloidichthys dentatus</i>	Mull dent	2850	69278	57615	57615				5227	4930	9322	57615	A1				2850	5227
<i>Muraena argus</i>	Mura arg	57763	69278		57615	6852	A1		5227								28023	
<i>Muraena clepsydra</i>	Mura clepsy	57763	69278		57615	6852	A1		57763								6930	
<i>Muraena lentiginosa</i>	Mura lentig	5590	69278	57615	57615	6852			9324	28023	57615						9257	
<i>Mycteroperca olfax</i>	Myct olf	5222	69278	6930	6930	11295			11295	6930	5222						3921	
<i>Myliobatis spp</i>	Mylio spp	2850	69278	6253		9257			96339	9257	2850						28023	2334
<i>Ogcocephalus darwini</i>	Ogco darw	estimate*	69278		28023				5227	28023	40824						28023	205
<i>Ophioblennius steindachneri</i>	Ophi stein	28023	69278	57615	57615	28023			5227	28023	57615						5227	5590
<i>Oplegnathus insignis</i>	Ople insig	55763	53696			28023			55763	28023	5227	A1					3921	205
<i>Orthopristis forbesi</i>	Orth forb	estimate*	69278		25	9626	A1		5227	A1							33482	52884
<i>Paralabrax albomaculatus</i>	Para albo	estimate*	69278		33482				33482	11295	A2	A1					28023	57615
<i>Paranthias colonus</i>	Para col	5592	69278	57615	57615				5222	28023	57615	A2					78172	205
<i>Plagiotremus azaleus</i>	Plag aza	11482	69278	57615	57615	5227	28023		5227	28023	57615						27115	
<i>Prionurus laticlavus</i>	Prio lati	55763	69278	57615					5227	27115	55763	57615	28023	9267	A1		4858	
<i>Prognathodes carlhubbsi</i>	Prog carl	9286	69278	4930					4858	5227							9263	
<i>Remora remora</i>	Remo remo	26340	33	33	33	35388			86942	33	41878	58302	33				12951	
<i>Rhinoptera steindachneri</i>	Rhin stein	28023	69278	9263					51243	9263	12951						168	12951
<i>Rypticus bicolor</i>	Rypt bicol	5227	69278		57615	5227			5227	57615	11482						5227	
<i>Sarda orientalis</i>	Sard orient	estimate*	69278	168	168				51243	168	A2						6110	9340
<i>Scarus compressus</i>	Scar comp	55763	69278	57615	57615				5227	57615	A1						28023	205

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genus species	gen sp	Body size	Trophic ecology							Ecological niche and within-reef mobility references								Social behaviour references	
<i>Scarus ghobban</i>	Scar ghob	90102	69278	6110	6110	5227	43650	57615	89642	6110	58652	58534	5490	1602	4821	48636	26993	48636	
<i>Scarus perrico</i>	Scar perr	5592	69278	57615	57615				5227	28023	57615	A1					168	205	
<i>Scarus rubroviolaceus</i>	Scar rubro	2334	69278	26993	26993	30573	57615		5227	26993	43539	58534	26993	48636			33	48636	
<i>Scomberomorus sierra</i>	Scom sier	estimate*	46593	168	168				51243	168	11035						42311	11035	
<i>Scorpaena plumieri</i>	Scor plum	5288	33	33	33				5228	33	42268	9710					9654		
<i>Semicossyphus darwini</i>	Semi darw	11295	53696		42311	11295			11295	42311	A1						205		
<i>Seriola lalandi</i>	Seri lalan	27865	69278	9654	9654	27121			4517	9654	53568	2850	9563	6390			4887	27865	
<i>Seriola rivoliana</i>	Seri rivo	estimate*	50226	4887	4887	57615			90102	4887	9283	57615	58534	26235			58302	4887	
<i>Serranus psittacinus</i>	Serr psit	9342	69278		57615				5227	57615	9342						28023	9342	
<i>Sphoeroides angusticeps</i>	Spho angu	9349	69278			A1			5227	9349									
<i>Sphoeroides annulatus</i>	Spho anna	9349	69278	75737	75737				91172	28023	9349						28023		
<i>Sphyraena idiastes</i>	Sphy idia	5590	69278		28023				5227	28023	A1						13562	58784	
<i>Sphyrna lewini</i>	Sphy lewi	26938	33559	568	568	6871	37816	30573	51243	568	58302	11230	244				12400	205	
<i>Stegastes leucurus</i>	Steg leuc	estimate*	69278	28023	9334				9334	7247							9311		
<i>Sufflamen verres</i>	Suff verr	9276	69278	28023	28023	5227	57615		5227	28023	57615	9276					28023		
<i>Taeniurops meyeri</i>	Taen mey	30573	69278	9137	9137	5578			37816	12400	75154	9137	1602						
<i>Thalassoma grammaticum</i>	Thal gra	9311	69278	9311	9311	57615			9311	57615							9311	5227	
<i>Thalassoma lucasanum</i>	Thal luc	9311	69278	57615	57615	9311			9311	28023	A1						9311		
<i>Thunnus albacares</i>	Thun alba	estimate*	27003	168	168				51243	168	6390	48637					568	9283	
<i>Trachinotus stilbe</i>	Trac stil	estimate*	69278		A1				5227								244	2850	
<i>Trachurus murphyi</i>	Trac symm	2850	40330	6262	6262	9283			51243	6262							2850		
<i>Triacodon obesus</i>	Tria obe	244	33559	568	568	244			244	568	9137	6871	37816	58302					
<i>Triakidae spp</i>	Tria spp	244	69278	28023					244	6252									
<i>Umbrina galapagorum</i>	Umbr gala	9118	120179	A1					9118										
<i>Uraspis helvola</i>	Uras helv	7251	69278		4887				51243	2850	A2						30573		
<i>Xanthichthys mento</i>	Xant ment	estimate*	69278		1602	89972			89972	1602	A2						2850	9710	
<i>Zanclus cornutus</i>	Zanc cornut	6113	6110	6110	6110	6113	59308	57615	9710	53568	58534	6110	1602	48637			9267	48637	
		*total length estimated from models by Fishbase																	

Supplementary information

Table S2.3. FishBase references corresponding to the reference numbers in Table S2.2.

FishBase reference number	Author	Year	Title	Source
25	Darcy, G.H.	1983	Synopsis of biological data on the pigfish, <i>Orthopristis chrysoptera</i> (Pisces: Haemulidae).	FAO Fish. Synop. (134); NOAA Tech. Rep. NMFS Circ. (449).
33	Randall, J.E.	1967	Food habits of reef fishes of the West Indies.	Stud. Trop. Oceanogr. Miami 5:665-847.
55	Allen, G.R.	1985	FAO Species Catalogue. Vol. 6. Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date.	FAO Fish. Synop. 125(6):208 p. Rome: FAO.
168	Collette, B.B. and C.E. Nauen	1983	FAO Species Catalogue. Vol. 2. Scombrids of the world. An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date.	Rome: FAO. FAO Fish. Synop. 125(2):137 p.
205	Breder, C.M. and D.E. Rosen	1966	Modes of reproduction in fishes.	T.F.H. Publications, Neptune City, New Jersey. 941 p.
244	Compagno, L.J.V.	1984	FAO Species Catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2 - Carcharhiniformes.	FAO Fish. Synop. 125(4 2):251-655. Rome: FAO.
275	Hiatt, R.W. and D.W. Strasburg	1960	Ecological relationships of the fish fauna on coral reefs of the Marshall Islands.	Ecol. Monogr. 30(1):65-127.
559	Masuda, H., K. Amaoka, C. Araga, T. Uyeno and T. Yoshino	1984	The fishes of the Japanese Archipelago. Vol. 1.	Tokai University Press, Tokyo, Japan. 437 p. (text).
568	Wetherbee, B.M., S.H. Gruber and E. Cortes	1990	Diet, feeding habits, digestion, and consumption in sharks, with special reference to the lemon shark, <i>Negaprion brevirostris</i> .	p. 29-47. In H.L. Pratt, Jr., S.H. Gruber and T. Taniuchi (eds.) Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Tech. Rep. NMFS 90, 517 p.
1602	Myers, R.F.	1991	Micronesian reef fishes.	Second Ed. Coral Graphics, Barrigada, Guam. 298 p.
1920	Randall, J.E.	1956	A revision of the surgeonfish genus, <i>Acanthurus</i> .	Pac. Sci. 10(2):159-235.
2334	Randall, J.E., G.R. Allen and R.C. Steene	1990	Fishes of the Great Barrier Reef and Coral Sea.	University of Hawaii Press, Honolulu, Hawaii. 506 p.
2683	Schneider, W.	1990	FAO species identification sheets for fishery purposes. Field guide to the commercial marine resources of the Gulf of Guinea. Prepared and published with the support of the FAO Regional Office for Africa.	Rome: FAO. 268 p.
2850	Eschmeyer, W.N., E.S. Herald and H. Hammann	1983	A field guide to Pacific coast fishes of North America.	Boston (MA, USA): Houghton Mifflin Company. xii+336 p.
3592	Harmelin-Vivien, M.L. and J.C. Quero	1990	Monacanthidae.	p. 1061-1066. In J.C. Quero, J.C. Hureau, C. Karrer, A. Post and L. Saldanha (eds.) Check-list of the fishes of the eastern tropical Atlantic (CLOFETA). JNICT, Lisbon; SEI, Paris; and UNESCO, Paris. Vol. 2.
3798	Courtenay, W.R. and H.F. Sahlman	1978	Pomadasyidae.	In W. Fischer (ed.) FAO species identification sheets for fishery purposes. Western Central Atlantic (Fishing Area 31), Volume 4. FAO, Rome.
3921	Randall, J.E.	1985	Guide to Hawaiian reef fishes.	Harrowood Books, Newtown Square, PA 19073, USA. 74 p.
3978	Cohen, D.M.	1986	Argentinidae.	p. 215-216. In M.M. Smith and P.C. Heemstra (eds.) Smiths' sea fishes. Springer-Verlag, Berlin.
4424	Heemstra, P.C.	1986	Molidae.	p. 907-908. In M.M. Smith and P.C. Heemstra (eds.) Smiths' sea fishes. Springer-Verlag, Berlin.
4442	McEachran, J.D. and B. Seibert	1990	Mobulidae.	p. 73-76. In J.C. Quero, J.C. Hureau, C. Karrer, A. Post and L. Saldanha (eds.) Check-list of the fishes of the eastern tropical Atlantic (CLOFETA). JNICT, Lisbon; SEI, Paris; and UNESCO, Paris. Vol. 1.
4517	Hureau, J.C.	1991	La base de données GICIM : Gestion informatisée des collections ichthyologiques du Muséum.	p. 225-227. In Atlas Préliminaire des Poissons d'Eau Douce de France. Conseil Supérieur de la Pêche, Ministère de l'Environnement, CEMAGREF et Muséum national d'Histoire naturelle, Paris.
4805	Randall, J.E.	1992	Review of the biology of the tiger shark (<i>Galeocerdo cuvier</i>).	Aust. J. Mar. Freshwat. Res. 43(1):21-31.
4821	Bagnis, R., P. Mazellier, J. Bennett and E. Christian	1972	Fishes of Polynesia.	Les Editions du Pacifique, Tahiti. 368 p.

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FishBase reference number	Author	Year	Title	Source
4858	Allen, G.R.	1985	Butterfly and angelfishes of the world. Vol. 2.	3rd edit. in English. Mergus Publishers, Melle, Germany.
4887	Honebrink, R.	1990	Fishing in Hawaii: a student manual.	Education Program, Division of Aquatic Resources, Honolulu, Hawaii. 79 p.
4925	Clemens, W.A. and G.V. Wilby	1961	Fishes of the Pacific coast of Canada.	2nd ed. Fish. Res. Bd. Canada Bull. (68):443 p.
5213	Fischer, W., I. Sousa, C. Silva, A. de Freitas, J.M. Poutiers, W. Schneider, T.C. Borges, J.P. Feral and A. Massinga	1990	Fichas FAO de identificação de espécies para actividades de pesca. Guia de campo das espécies comerciais marinhas e de águas salobras de Moçambique.	Publicação preparada em colaboração com o Instituto de Investigação Pesqueira de Moçambique, com financiamento do Projecto PNUD/FAO MOZ/86/030 e de NORAD. Roma, FAO. 1990. 424 p.
5217	Cervigon, F., R. Cipriani, W. Fischer, L. Garibaldi, M. Hendrickx, A.J. Lemus, R. Merquez, J.M. Poutiers, G. Robaina and B. Rodriguez	1992	FAO species identification sheets for the purposes of fishing. Field guide to commercial marine and brackish aquatic species on the northern coast of South America.	FAO, Rome. 513 p. Prepared with financing from the Commission of the European Communities and NORAD.
5222	Heemstra, P.C. and J.E. Randall	1993	FAO Species Catalogue. Vol. 16. Groupers of the world (family Serranidae, subfamily Epinephelinae). An annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper and lyretail species known to date.	Rome: FAO. FAO Fish. Synop. 125(16):382 p.
5227	Humann, P. and N. Deloach	1993	Reef fish identification. Galápagos.	New World Publications, Inc., Florida. 267 p.
5228	Smith, D.G.	1990	Derichthyidae.	p. 193-194. In J.C. Quero, J.C. Hureau, C. Karrer, A. Post and L. Saldanha (eds.) Check-list of the fishes of the eastern tropical Atlantic (CLOFETA). JNICT, Lisbon; SEI, Paris; and UNESCO, Paris. Vol. 1.
5288	Edwards, A.	1990	Fish and fisheries of Saint Helena Island.	Centre for Tropical Coastal Management Studies, University of Newcastle upon Tyne, England.
5485	Bass, A.J., P.C. Heemstra and L.J.V. Compagno	1986	Carcharhinidae.	p. 67-87. In M.M. Smith and P.C. Heemstra (eds.) Smiths' sea fishes. Springer-Verlag, Berlin.
5490	Randall, J.E.	1986	Scaridae.	p. 706-714. In M.M. Smith and P.C. Heemstra (eds.) Smiths' sea fishes. Springer-Verlag, Berlin.
5543	Dalzell, P.	1989	The biology of surgeon fishes with particular emphasis on <i>Acanthurus nigricauda</i> and <i>A. xanthopterus</i> from northern Papua New Guinea.	University of Newcastle Upon Tyne, England. 285 p. M.S. thesis.
5578	Compagno, L.J.V., D.A. Ebert and M.J. Smale	1989	Guide to the sharks and rays of southern Africa.	New Holland (Publ.) Ltd., London. 158 p.
5590	Merlen, G.	1988	A field guide to the fishes of Galápagos.	Wilmot Books, London, England 60 p.
6057	Sudekum, A.E., J.D. Parrish, R.L. Radtke and S. Ralston	1991	Life history and ecology of large jacks in undisturbed, shallow, oceanic communities.	Fish. Bull. 89:493-513.
6110	Sano, M., M. Shimizu and Y. Nose	1984	Food habits of teleostean reef fishes in Okinawa Island, southern Japan.	University of Tokyo Bulletin, no. 25. v,128p. University of Tokyo Press, Tokyo, Japan. 128 p.
6113	Anderson, C. and A. Hafiz	1987	Common reef fishes of the Maldives. Part 1.	Novelty Press, Republic of Maldives. 83 p.
6252	Talent, L.G.	1976	Food habits of the leopard shark, <i>Triakis semifasciata</i> , in Elkhorn Slough, Monterey Bay, California.	Calif. Fish Game 62(4):286-298.
6253	Talent, L.G.	1982	Food habits of the gray smoothhound, <i>Mustelus californicus</i> , the brown smoothhound, <i>Mustelus henlei</i> , the shovelnose guitarfish, <i>Rhinobatos productus</i> , and the bat ray, <i>Myliobatis californica</i> , in Elkhorn Slough, California.	Calif. Fish Game 68(4):224-234.
6262	Konchina, Y.V.	1983	The feeding niche of the hake, <i>Merluccius gayi</i> (Merlucciidae), and the jack mackerel, <i>Trachurus symmetricus</i> (Carangidae), in the trophic system of the Peruvian coastal upwelling.	J. Ichthyol. 23(2):87-98.
6390	Kailola, P.J., M.J. Williams, P.C. Stewart, R.E. Reichelt, A. McNee and C. Grieve	1993	Australian fisheries resources.	Bureau of Resource Sciences, Canberra, Australia. 422 p.
6679	McEachran, J.D. and C. Capape	1984	Mobulidae.	p. 210-211. In P.J.P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (eds.) Fishes of the north-eastern Atlantic and the Mediterranean. UNESCO, Paris. Vol. 1.
6769	Collette, B.B.	1986	Scombridae (including Thunnidae, Scomberomoridae, Gasterochismatidae and Sardidae).	p. 981-997. In P.J.P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (eds.) Fishes of the north-eastern Atlantic and the Mediterranean, Volume 2. Unesco, Paris.
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FishBase reference number	Author	Year	Title	Source
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91172	Nieto-Navarro, J.T., M. Zetina-Rejon and F. Arreguin-Sanchez	2010	Length-weight relationship of demersal fish from the eastern coast of the mouth of the gulf of California.	J. Fish. Aquat. Sci. 5(6):494-502.
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114953	Last, P.R., W.T. White, M.R. de Carvalho, B. Seret, M.F.W. Stehmann and G.J.P. Naylor	2016	Rays of the world.	CSIRO Publishing, Comstock Publishing Associates. i-ix + 1-790.
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FishBase reference number	Author	Year	Title	Source
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120179	Froese, R., N. Demirel, G. Coro, K.M. Kleisner and H. Winker	2017	Estimating fisheries reference points from catch and resilience	Fish and Fisheries 18(3):506-526
AlternativeRefs				
A1	Robertson, D. R. and G. R. Allen	2015	Shorefishes of the Tropical Eastern Pacific: online information system	https://biogeodb.stri.si.edu/sfstep/en/findafish
A2	Humann, P. and N. Deloach	2003	Reef Fish Identification: Galápagos	New World Publications, Inc., Florida. 240p.

Table S2.4. Working definitions and ecosystem effects of the seven functional traits used to assess the functional diversity of 121 reef fish species sampled in the Galápagos Archipelago in 2015.

Functional trait category	Functional trait	Source	Working definitions	Ecosystem effects
Body size	Maximum total length (cm)	Estimated using maximum total length measurements from FishBase.	The greatest length of the whole body between the most anterior point of the body and the most posterior point, in a straight line, not over the curve of the body.	Body size is a primary indicator of reef fish ecological niche (Fisher, Frank, & Leggett, 2010; Lokrantz, Nyström, Thyresson, & Johansson, 2008; Wilson, 1975). Body size indicates resource depletion through energy requirements in relation to body mass (Munday & Jones, 1998), growth rates (Brown, Gillooly, Allen, Savage, & West, 2004) and mortality rates (Munday & Jones, 1998). Body size also indicates resource contributions through secondary production (Woodward et al., 2005).
Trophic ecology	Trophic level	Estimated by FishBase from a number of food items and a randomised resampling routine, the size and trophs of closest relatives or from 1+ troph of a single food item.	Position in the food chain determined by the number of energy-transfer steps to that level from 2 (herbivore) to 4.5 (piscivore).	Diet is the other primary indicator of reef fish ecological niche (Bellwood, Wainwright, Fulton, & Hoey, 2006; Burkepile & Hay, 2008). Diet indicates resource depletion and addition through trophic interactions, predator-prey relationships and nutrient recycling (Burkepile et al., 2013; Vanni, 2002). Diet also indicates resource availability and habitat requirements because some resources are only available at particular habitats (Brandl & Bellwood, 2013).
Trophic ecology	Diet breadth	Estimated using the standard error derived from trophic level estimates by FishBase.	Estimate of the range of diet items consumed from 0 (no variation, strict diet) to 0.93 (variation, broad diet).	
Trophic ecology	Feeding behaviour	Estimated using feeding habit that integrates main food type and feeding method by FishBase.	Variable: Diet is variable and includes a range of food items and feeding methods. Hunting: Hunts on fish and invertebrates (e.g. crustaceans and bivalves). Browsing: Moves along the substrate digging or scraping for invertebrates and algae. Grazing: Moves vertically in the water-column grazing on algae, plankton and/or detritus. Selective plankton feeding:	

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Functional trait category	Functional trait	Source	Working definitions	Ecosystem effects
			Picks suspended planktonic organisms from the water-column. Filtering plankton: Filtering suspended food particles from a water current by means of gill rakers, or similar organs.	
Ecological niche	Water column position	Estimated using distribution information and biological descriptions relating to feeding and mobility from FishBase.	Preferred vertical position in the water column for living and feeding. Pelagic: Living and free swimming within the middle depths or near the surface not in association with the bottom eeding in the open sea; associated with the surface or middle depths of a body of water; free swimming in the seas, oceans or open waters; not in association with the bottom Benthopelagic: Living near the bottom as well as in midwaters or near the surface and feeding on benthic as well as free swimming organisms. Benthic: Living near and relating to, the bottom of a body of water feeding on benthic organisms Demersal: Living on or in the bottom substrate and feeding on benthic organisms	Water column position in reef fish indicates ecological connectivity and nutrient cycling both within-reef through benthic-pelagic coupling (Schaus & Vanni, 2000) and, between-reefs through home-ranges (Rijnsdorp, Peck, Engelhard, Möllmann, & Pinnegar, 2009) and prey availability (Bellwood et al., 2006). Water column position also indicates resource depletion because pelagic species are likely to be more mobile than demersal species, thereby having more significant energy needs (Norman & Jones, 1984).
Within-reef mobility	Substrate preference	Estimated using substrate and habitat associations and biological descriptions relating to feeding and mobility from FishBase.	Preferred substrate for living and feeding including soft bottom habitats such as sand and mud and, hard bottom habitats such as rocky or coral reefs.	Substrate preference in reef fishes indicates within-reef mobility, resource depletion and nutrient transfer and recycling (Meyer & Schultz, 1985; Nagelkerkenlv, Dorenbosch, de la Moriniere, & Van der Velde 2000). Within-reef mobility also indicates a habitats resources and prey availability.
Social behaviour	Largest common group size	Estimated using association information and biological descriptions in FishBase.	Predominant social behaviour with regards to other similar individuals and fish species. Solitary to small group: Mostly occur alone or in pairs for living and feeding but can also aggregate into small groups for a time. Schooling: Behaviourally group together with other individuals and species, living and moving together as a group and acting as a school.	Social behaviour in reef fishes indicates resource depletion because larger groups instigate rapid nutrient cycling and also, resource addition because larger groups indicate an abundance of prey (Foster, 1985; Meyer & Schultz, 1985). Social behaviour can also indicate prey vulnerability and avoidance (Hoare, Krause, Peuhkuri, & Godin, 2000; Stier, Geange, & Bolker, 2013).

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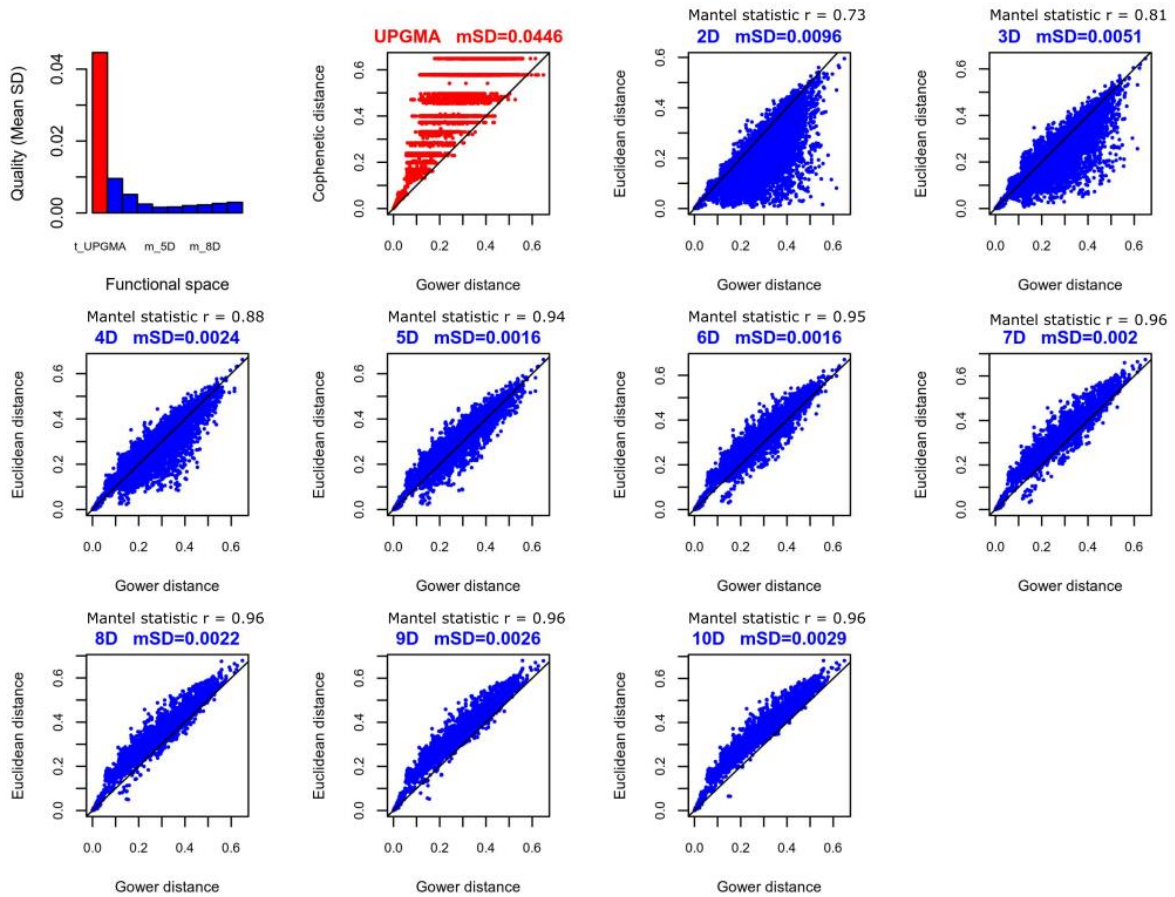


Figure S2.1. The quality of functional spaces used to compute functional diversity indices for Galápagos reef fish assemblages sampled in 2015. The top-left panel shows the mean squared deviation for the ten functional spaces. The remaining ten panels show the correlation between the initial Gower's distances and the standardised distances in each of the ten functional spaces including a functional dendrogram built from the unweighted pair group method with arithmetic mean (UPGMA) clustering algorithm and 2D-10D multidimensional spaces built using principal coordinates analysis (PCoA) for two to 10 axes. Mantel tests between the original Gowers matrix and resulting specie positions are also included. Each point represents a species.

CHAPTER 3

Table S3.1. Functional trait matrix for the five functional traits used to identify 82 functional entities and assess the functional vulnerability of 121 reef fish species sampled in the Galápagos Archipelago in 2015. Corresponding FishBase references numbers and references for each species functional traits are below in Table S3.2 and S3.3

Functional entity	Functional trait category		Body size	Trophic ecology	Ecological niche	Within-reef mobility	Social behaviour
	Functional trait		Maximum total length (cm)	Diet	Water column position	Substrate preference	Largest common group size
	genus_species	gen_sp					
MLvs_Dlom_WCbp_SPha_SAso	<i>Abudefduf troschelii</i>	Abud_tro	very-small	omnivorous	bentho-pelagic	hard	solitary or pairing
MLvl_Dlpi_WCpe_SPPx_SAsg	<i>Acanthocybium solandri</i>	Acan_sol	very-large	piscivorous	pelagic	open-water	small-group
MLsm_Dlhe_WCbp_SPha_SAsg	<i>Acanthurus nigricans</i>	Acan_nig	small	herbivorous	bentho-pelagic	hard	small-group
MLme_Dlhe_WCbp_SPhs_SAlg	<i>Acanthurus xanthopterus</i>	Acan_xan	medium	herbivorous	bentho-pelagic	rd and soft	large-group
MLvl_Dlpi_WCbp_SPhs_SAlg	<i>Aetobatus narinari</i>	Aeto_nari	very-large	piscivorous	bentho-pelagic	hard and soft	large-group
MLla_Dlin_WCbp_SPhs_SAsg	<i>Alectis ciliaris</i>	Alec_ciliar	large	invertivorous	bentho-pelagic	hard and soft	small-group
MLme_Dlin_WCbp_SPhs_SAsg	<i>Aluterus monoceros</i>	Alut_monoc	medium	invertivorous	bentho-pelagic	hard and soft	small-group
MLla_Dlom_WCbp_SPha_SAso	<i>Aluterus scriptus</i>	Alut_scrip	large	omnivorous	bentho-pelagic	hard	solitary or pairing
MLme_Dlin_WCbe_SPha_SAsg	<i>Anisotremus interruptus</i>	Anis_in	medium	invertivorous	benthic	hard	small-group
MLsm_Dlom_WCbp_SPha_SAlg	<i>Anisotremus scapularis</i>	Anis_sc	small	omnivorous	bentho-pelagic	hard	large-group
MLvs_Dlpi_WCbe_SPha_SAso	<i>Apogon spp</i>	Apog_spp	very-small	planktivorous	benthic	hard	solitary or pairing
MLsm_Dlom_WCbp_SPso_SAso	<i>Archosargus pourtalesii</i>	Arch_po	small	omnivorous	bentho-pelagic	soft	solitary or pairing
MLsm_Dlom_WCbe_SPhs_SAso	<i>Arothron hispidus</i>	Arot_hispi	small	omnivorous	benthic	hard and soft	solitary or pairing
MLsm_Dlom_WCbe_SPha_SAso	<i>Arothron meleagris</i>	Arot_melea	small	omnivorous	benthic	hard	solitary or pairing
MLme_Dlpi_WCbe_SPhs_SAsg	<i>Aulostomus chinensis</i>	Aulo_chi	medium	piscivorous	benthic	hard and soft	small-group
MLme_Dlin_WCbp_SPhs_SAsg	<i>Balistes polylepis</i>	Bali_polyl	medium	invertivorous	bentho-pelagic	hard and soft	small-group
MLme_Dlin_WCbe_SPhs_SAso	<i>Bodianus diplotaenia</i>	Bodi_diplo	medium	invertivorous	benthic	hard and soft	solitary or pairing
MLme_Dlom_WCbe_SPhs_SAso	<i>Bodianus eclancheri</i>	Bodi_eclan	medium	omnivorous	benthic	hard and soft	solitary or pairing
MLsm_Dlpi_WCde_SPhs_SAso	<i>Bothus leopardinus</i>	Both_leopard	small	piscivorous	demersal	hard and soft	solitary or pairing
MLsm_Dlin_WCbe_SPso_SAso	<i>Calamus taurinus</i>	Cala_taurin	small	invertivorous	benthic	soft	solitary or pairing
MLsm_Dlpi_WCpe_SPhs_SAlg	<i>Canthidemis maculata</i>	Cant_mac	small	planktivorous	pelagic	hard and soft	large-group
MLme_Dlpi_WCbp_SPha_SAlg	<i>Caranx caballus</i>	Cara_caballu	medium	piscivorous	bentho-pelagic	hard	large-group
MLla_Dlpi_WCpe_SPPx_SAlg	<i>Caranx caninus</i>	Cara_caninus	large	piscivorous	pelagic	open-water	large-group

Supplementary information

Functional entity	Genus_species	Gen_sp	Maximum total length (cm)	Diet	Water column position	Substrate preference	Largest common group size
MLme_Dlpi_WCbp_SPha_SAlq	<i>Caranx lugubris</i>	Cara_lugubri	medium	piscivorous	bentho-pelagic	hard	large-group
MLla_Dlpi_WCpe_SPhs_SAlq	<i>Caranx melampygus</i>	Cara_melampy	large	piscivorous	pelagic	hard and soft	large-group
MLla_Dlpi_WCbp_SPhs_SAlq	<i>Caranx sexfasciatus</i>	Cara_sexfasc	large	piscivorous	bentho-pelagic	hard and soft	large-group
MLvl_Dlpi_WCpe_SPPx_SAso	<i>Carcharhinus falciformis</i>	Carc_fal	very-large	piscivorous	pelagic	open-water	solitary or pairing
MLvl_Dlpi_WCbp_SPhs_SAso	<i>Carcharhinus galapagensis</i>	Carc_gal	very-large	piscivorous	bentho-pelagic	hard and soft	solitary or pairing
MLvl_Dlpi_WCbp_SPhs_SAso	<i>Carcharhinus limbatus</i>	Carc_lim	very-large	piscivorous	bentho-pelagic	hard and soft	solitary or pairing
MLme_Dlpi_WCbe_SPhs_SAso	<i>Caulolatilus princeps</i>	Caul_prin	medium	piscivorous	benthic	hard and soft	solitary or pairing
MLsm_Dlpi_WCde_SPha_SAso	<i>Cephalopholis panamensis</i>	Ceph_pan	small	piscivorous	demersal	hard	solitary or pairing
MLsm_Dlom_WCbe_SPha_SAsq	<i>Chaetodon humeralis</i>	Chae_hume	small	omnivorous	benthic	hard	small-group
MLvl_Dlom_WCbp_SPhs_SAlq	<i>Chanos chanos</i>	Chan_chan	very-large	omnivorous	bentho-pelagic	hard and soft	large-group
MLsm_Dlin_WCbe_SPhs_SAso	<i>Chilomycterus reticulatus</i>	Chil_ret	small	invertivorous	benthic	hard and soft	solitary or pairing
MLvs_Dlpi_WCbp_SPha_SAlq	<i>Chromis alta</i>	Chro_alta	very-small	planktivorous	bentho-pelagic	hard	large-group
MLvs_Dlpi_WCbp_SPha_SAlq	<i>Chromis atrilobata</i>	Chro_atrilo	very-small	planktivorous	bentho-pelagic	hard	large-group
MLvs_Dlpi_WCde_SPha_SAso	<i>Cirrhichthys oxycephalus</i>	Cirr_oxyce	very-small	piscivorous	demersal	hard	solitary or pairing
MLme_Dlpi_WCde_SPhs_SAso	<i>Cratinus agassizii</i>	Crat_agass	medium	piscivorous	demersal	hard and soft	solitary or pairing
MLla_Dlpi_WCde_SPhs_SAso	<i>Dasyatis brevis</i>	Dasy_brevi	large	piscivorous	demersal	hard and soft	solitary or pairing
MLvl_Dlpi_WCde_SPhs_SAso	<i>Dasyatis longus</i>	Dasy_longu	very-large	piscivorous	demersal	hard and soft	solitary or pairing
MLme_Dlpi_WCbe_SPha_SAso	<i>Dermatolepis dermatolepis</i>	Derm_derm	medium	piscivorous	benthic	hard	solitary or pairing
MLla_Dlpi_WCpe_SPhs_SAlq	<i>Elagatis bipinnulata</i>	Elag_bipin	large	piscivorous	pelagic	hard and soft	large-group
MLme_Dlpi_WCde_SPha_SAso	<i>Enchelycore lichenosa</i>	Ench_li	medium	piscivorous	demersal	hard	solitary or pairing
MLme_Dlpi_WCde_SPha_SAso	<i>Epinephelus labriformis</i>	Epin_la	medium	piscivorous	demersal	hard	solitary or pairing
MLme_Dlpi_WCpe_SPPx_SAlq	<i>Euthynnus lineatus</i>	Euth_line	medium	piscivorous	pelagic	open-water	large-group
MLla_Dlpi_WCbe_SPhs_SAlq	<i>Fistularia commersonii</i>	Fist_com	large	piscivorous	benthic	hard and soft	large-group
MLvl_Dlpi_WCbp_SPhs_SAso	<i>Galeocerdo cuvier</i>	Gale_cuv	very-large	piscivorous	bentho-pelagic	hard and soft	solitary or pairing
MLsm_Dlthe_WCbe_SPha_SAsq	<i>Girella freminvillei</i>	Gire_fremin	small	herbivorous	benthic	hard	small-group
MLvs_Dlpi_WCde_SPha_SAso	<i>Gobioclinus dendriticus</i>	Gobio_den	very-small	piscivorous	demersal	hard	solitary or pairing
MLvl_Dlpi_WCde_SPha_SAso	<i>Gymnothorax dovii</i>	Gymn_do	very-large	piscivorous	demersal	hard	solitary or pairing
MLvl_Dlpi_WCde_SPha_SAso	<i>Gymnothorax flavimarginatus</i>	Gymn_fl	very-large	piscivorous	demersal	hard	solitary or pairing
MLsm_Dlpi_WCbe_SPha_SAlq	<i>Haemulon scudderii</i>	Haem_scudd	small	piscivorous	benthic	hard	large-group

Supplementary information

Functional entity	Genus_species	Gen_sp	Maximum total length (cm)	Diet	Water column position	Substrate preference	Largest common group size
MLsm_Dlin_WCbe_SPhs_SAsO	<i>Halichoeres dispilus</i>	Hali_disp	small	invertivorous	benthic	hard and soft	solitary or pairing
MLsm_Dlin_WCbe_SPhs_SAsO	<i>Halichoeres nicholsi</i>	Hali_nich	small	invertivorous	benthic	hard and soft	solitary or pairing
MLsm_Dlin_WCbe_SPhs_SAsO	<i>Halichoeres notospilus</i>	Hali_noto	small	invertivorous	benthic	hard and soft	solitary or pairing
MLme_Dlpi_WCbe_SPha_SAsO	<i>Hemilutjanus macrophthalmos</i>	Hemi_mac	medium	piscivorous	benthic	hard	solitary or pairing
MLme_Dlpi_WCde_SPso_SAlq	<i>Heteroconger klausewitzii</i>	Hete_klau	medium	planktivorous	demersal	soft	large-group
MLla_Dlin_WCde_SPhs_SAsO	<i>Heterodontus quoyi</i>	Hete_quoy	large	invertivorous	demersal	hard and soft	solitary or pairing
MLsm_Dlom_WCbp_SPha_SAsO	<i>Holacanthus passer</i>	Hola_pass	small	omnivorous	bentho-pelagic	hard	solitary or pairing
MLme_Dlpi_WCbe_SPha_SAsO	<i>Hoplopagrus guentherii</i>	Hopl_guen	medium	piscivorous	benthic	hard	solitary or pairing
MLvs_Dlom_WCbp_SPha_SAlq	<i>Johnrandallia nigrirostris</i>	John_nig	very-small	omnivorous	bentho-pelagic	hard	large-group
MLme_Dlpi_WCbp_SPha_SAlq	<i>Kyphosus analogus</i>	Kyph_analo	medium	piscivorous	bentho-pelagic	hard	large-group
MLme_Dlom_WCbp_SPha_SAlq	<i>Kyphosus elegans</i>	Kyph_elag	medium	omnivorous	bentho-pelagic	hard	large-group
MLme_Dlom_WCpe_SPha_SAlq	<i>Kyphosus ocyurus</i>	Kyph_ocyur	medium	omnivorous	pelagic	hard	large-group
MLme_Dlpi_WCbp_SPha_SAlq	<i>Lutjanus aratus</i>	Lutj_aratu	medium	piscivorous	bentho-pelagic	hard	large-group
MLme_Dlpi_WCbp_SPha_SASg	<i>Lutjanus argentiventris</i>	Lutj_argen	medium	piscivorous	bentho-pelagic	hard	small-group
MLme_Dlpi_WCbp_SPha_SASg	<i>Lutjanus guttatus</i>	Lutj_gutta	medium	piscivorous	bentho-pelagic	hard	small-group
MLla_Dlpi_WCbp_SPha_SASg	<i>Lutjanus novemfasciatus</i>	Lutj_novem	large	piscivorous	bentho-pelagic	hard	small-group
MLsm_Dlpi_WCbp_SPha_SAlq	<i>Lutjanus viridis</i>	Lutj_virid	small	piscivorous	bentho-pelagic	hard	large-group
MLsm_Dlom_WCbp_SPha_SASg	<i>Melichthys niger</i>	Meli_nig	small	omnivorous	bentho-pelagic	hard	small-group
MLvi_Dlfi_WCpe_SPhs_SASg	<i>Mobula birostris</i>	Mobu_biros	very-large	filterfeeding	pelagic	hard and soft	small-group
MLvi_Dlfi_WCpe_SPhs_SASg	<i>Mobula spp</i>	Mobu_spp	very-large	filterfeeding	pelagic	hard and soft	small-group
MLvi_Dlpi_WCpe_SPhs_SAsO	<i>Mola ramsayi</i>	Mola_ram	very-large	piscivorous	pelagic	open-water	solitary or pairing
MLsm_Dlom_WCbp_SPhs_SAlq	<i>Mugil galapagensis</i>	Mugi_galapa	small	omnivorous	bentho-pelagic	hard and soft	large-group
MLsm_Dlpi_WCbe_SPhs_SASg	<i>Mulloidichthys dentatus</i>	Mull_dent	small	piscivorous	benthic	hard and soft	small-group
MLla_Dlpi_WCde_SPha_SAsO	<i>Muraena argus</i>	Mura_arg	large	piscivorous	demersal	hard	solitary or pairing
MLla_Dlpi_WCde_SPha_SAsO	<i>Muraena clepsydra</i>	Mura_clepsy	large	piscivorous	demersal	hard	solitary or pairing
MLme_Dlpi_WCde_SPha_SAsO	<i>Muraena lentiginosa</i>	Mura_lentig	medium	piscivorous	demersal	hard	solitary or pairing
MLla_Dlpi_WCbp_SPhs_SAsO	<i>Mycteroperca olfax</i>	Myct_olf	large	piscivorous	bentho-pelagic	hard and soft	solitary or pairing
MLla_Dlin_WCbe_SPhs_SAlq	<i>Myliobatis spp</i>	Mylio_spp	large	invertivorous	benthic	hard and soft	large-group
MLsm_Dlin_WCde_SPso_SAsO	<i>Ogcocephalus darwini</i>	Ogco_darw	small	invertivorous	demersal	soft	solitary or pairing

Supplementary information

Functional entity	Genus_species	Gen_sp	Maximum total length (cm)	Diet	Water column position	Substrate preference	Largest common group size
MLsm_Dlom_WCde_SPha_SAso	<i>Ophioblennius steindachneri</i>	Ophi_stein	small	omnivorous	demersal	hard	solitary or pairing
MLme_Dlom_WCbe_SPha_SAso	<i>Oplegnathus insignis</i>	Ople_insig	medium	omnivorous	benthic	hard	solitary or pairing
MLsm_Dlin_WCbe_SPhs_SAsq	<i>Orthopristis forbesi</i>	Orth_forb	small	invertivorous	benthic	hard and soft	small-group
MLme_Dlpi_WCbe_SPhs_SAso	<i>Paralabrax albomaculatus</i>	Para_albo	medium	piscivorous	benthic	hard and soft	solitary or pairing
MLsm_Dlpi_WCbp_SPha_SAlq	<i>Paranthias colonus</i>	Para_col	small	planktivorous	bentho-pelagic	hard	large-group
MLvs_Dlpi_WCbe_SPha_SAsq	<i>Plagiotremus azaleus</i>	Plag_aza	very-small	piscivorous	benthic	hard	small-group
MLme_Dlhe_WCbe_SPha_SAlq	<i>Prionurus laticlavus</i>	Prio_lati	medium	herbivorous	benthic	hard	large-group
MLvs_Dlin_WCbe_SPha_SAso	<i>Prognathodes carlhubbsi</i>	Prog_carl	very-small	invertivorous	benthic	hard	solitary or pairing
MLme_Dlin_WCpe_SPpx_SAso	<i>Remora remora</i>	Remo_remo	medium	invertivorous	pelagic	open-water	solitary or pairing
MLme_Dlin_WCbp_SPhs_SAlq	<i>Rhinoptera steindachneri</i>	Rhin_stein	medium	invertivorous	bentho-pelagic	hard and soft	large-group
MLsm_Dlpi_WCbe_SPha_SAso	<i>Rypticus bicolor</i>	Rypt_bicol	small	piscivorous	benthic	hard	solitary or pairing
MLla_Dlpi_WCpe_SPpx_SAlq	<i>Sarda orientalis</i>	Sard_orient	large	piscivorous	pelagic	open-water	large-group
MLme_Dlhe_WCbe_SPha_SAso	<i>Scarus compressus</i>	Scar_comp	medium	herbivorous	benthic	hard	solitary or pairing
MLme_Dlhe_WCbe_SPhs_SAsq	<i>Scarus ghobban</i>	Scar_ghob	medium	herbivorous	benthic	hard and soft	small-group
MLme_Dlhe_WCbe_SPhs_SAsq	<i>Scarus perrico</i>	Scar_perr	medium	herbivorous	benthic	hard and soft	small-group
MLme_Dlhe_WCbe_SPhs_SAsq	<i>Scarus rubroviolaceus</i>	Scar_rubro	medium	herbivorous	benthic	hard and soft	small-group
MLla_Dlpi_WCpe_SPpx_SAlq	<i>Scomberomorus sierra</i>	Scom_sier	large	piscivorous	pelagic	open-water	large-group
MLsm_Dlpi_WCde_SPha_SAso	<i>Scorpaena plumieri</i>	Scor_plum	small	piscivorous	demersal	hard	solitary or pairing
MLme_Dlom_WCbe_SPhs_SAso	<i>Semicossyphus darwini</i>	Semi_darw	medium	omnivorous	benthic	hard and soft	solitary or pairing
MLvl_Dlpi_WCbp_SPha_SAsq	<i>Seriola lalandi</i>	Seri_lalan	very-large	piscivorous	bentho-pelagic	hard	small-group
MLla_Dlpi_WCbp_SPha_SAsq	<i>Seriola rivoliana</i>	Seri_rivo	large	piscivorous	bentho-pelagic	hard	small-group
MLvs_Dlpi_WCde_SPhs_SAso	<i>Serranus psittacinus</i>	Serr_psit	very-small	piscivorous	demersal	hard and soft	solitary or pairing
MLsm_Dlom_WCbe_SPhs_SAso	<i>Sphoeroides angusteceps</i>	Spho_angu	small	omnivorous	benthic	hard and soft	solitary or pairing
MLsm_Dlom_WCbe_SPhs_SAso	<i>Sphoeroides annulatus</i>	Spho_anna	small	omnivorous	benthic	hard and soft	solitary or pairing
MLme_Dlpi_WCbp_SPhs_SAlq	<i>Sphyraena idiastes</i>	Sphy_idia	medium	piscivorous	bentho-pelagic	hard and soft	large-group
MLvl_Dlpi_WCpe_SPha_SAlq	<i>Sphyma lewini</i>	Sphy_lewi	very-large	piscivorous	pelagic	hard	large-group
MLvs_Dlom_WCbe_SPha_SAso	<i>Stegastes leucorus</i>	Steg_leuc	very-small	omnivorous	benthic	hard	solitary or pairing
MLsm_Dlin_WCbp_SPha_SAso	<i>Sufflamen verres</i>	Suff_verr	small	invertivorous	bentho-pelagic	hard	solitary or pairing
MLvl_Dlpi_WCde_SPhs_SAso	<i>Taeniurops meyeri</i>	Taen_mey	very-large	piscivorous	demersal	hard and soft	solitary or pairing

Supplementary information

Functional entity	Genus_species	Gen_sp	Maximum total length (cm)	Diet	Water column position	Substrate preference	Largest common group size
MLsm_Dlin_WCbe_SPha_SAso	<i>Thalassoma grammaticum</i>	Thal_gra	small	invertivorous	benthic	hard	solitary or pairing
MLvs_Dlin_WCbe_SPha_SAso	<i>Thalassoma lucasanum</i>	Thal_luc	very-small	invertivorous	benthic	hard	solitary or pairing
MLvl_Dlpi_WCpe_SPPx_SAlg	<i>Thunnus albacares</i>	Thun_alba	very-large	piscivorous	pelagic	open-water	large-group
MLsm_Dlpi_WCpe_SPPx_SAlg	<i>Trachinotus stilbe</i>	Trac_stil	small	piscivorous	pelagic	open-water	large-group
MLme_Dlpi_WCpe_SPPx_SAlg	<i>Trachurus murphyi</i>	Trac_symm	medium	piscivorous	pelagic	open-water	large-group
MLvl_Dlpi_WCde_SPhs_SAso	<i>Triaenodon obesus</i>	Tria_obe	very-large	piscivorous	demersal	hard and soft	solitary or pairing
MLla_Dlpi_WCde_SPhs_SAso	<i>Triakidae</i> spp	Tria_spp	large	piscivorous	demersal	hard and soft	solitary or pairing
MLsm_Dlin_WCde_SPha_SAso	<i>Umbrina galapagorum</i>	Umbr_gala	small	invertivorous	demersal	hard	solitary or pairing
MLsm_Dlpi_WCpe_SPPx_SAlg	<i>Uraspis helvola</i>	Uras_helv	small	piscivorous	pelagic	open-water	large-group
MLsm_Dlpi_WCbp_SPha_SAlg	<i>Xanthichthys mento</i>	Xant_ment	small	planktivorous	benthopelagic	hard	large-group
MLsm_Dlin_WCbe_SPhs_SAso	<i>Zanclus cornutus</i>	Zanc_cornut	small	invertivorous	benthic	hard and soft	solitary or pairing

Table S3.2. FishBase references numbers for the functional traits and categories used to identify functional entities and assess the functional vulnerability of 121 each reef fish species sampled in the Galápagos Archipelago in 2015. Corresponding references are below in Table S3.3.

genus_species	gen_sp	Body size references	Trophic ecology references						Ecological niche and within-reef mobility references							Social behaviour references		
<i>Abudefduf troschelii</i>	Abud_tro	55763	69278		5592	57615			5592	28023	9334	57615					28023	57615
<i>Acanthocybium solandri</i>	Acan_sol	30573	69278	168	6769				51243	168	53568						168	6769
<i>Acanthurus nigricans</i>	Acan_nig	2334	69278	57615	57615				1602	275	57615	58302	58652	58534			275	90102
<i>Acanthurus xanopterus</i>	Acan_xan	4795	69278	3921	1602	48637	5543		9267	1920	48637	57615	1602	48673	58302		1920	1602
<i>Aetobatus narinari</i>	Aeto_nari	58048	33	33	9862				51243	33	58534	58302	6871	9862			33	7251
<i>Alectis ciliaris</i>	Alec_ciliar	30573	69278	9137	9283				37816	5217	58302	58534					5217	
<i>Aluterus monoceros</i>	Alut_monoc	26340	46593	30573	30573				90102	3592	53568	58534	58302	9318	48637		3592	9318
<i>Aluterus scriptus</i>	Alut_scrip	9710	33	33	26165				36484	33	53568	58534	57616				33	
<i>Anisotremus interruptus</i>	Anis_in	55763	69278	57615	9114				5227	9114	57615	A1					9114	205
<i>Anisotremus scapularis</i>	Anis_sc	11482	53696		28023				5227	28023							28023	5227
<i>Apogon spp</i>	Apog_spp	11482	69278	57615					5227	28023	57615						28023	
<i>Archosargus pourtalesii</i>	Arch_po	5590	69278		28023				5227	28023	A2						28023	
<i>Arothron hispidus</i>	Arot_hispi	30874	55797	1602	11889				90102	1602	57615	11889					1602	11889
<i>Arothron meleagris</i>	Arot_melea	9710	3921	3921	57615				89467	3921	53568	57615	58302	A1			3921	90102

Supplementary information

genus_species	gen_sp	Body size references	Trophic ecology references						Ecological niche and within-reef mobility references								Social behaviour references	
<i>Aulostomus chinensis</i>	Aulo_chi	2334	69278	3921	9275				1602	3921	53568	57615	58472	58302			3921	48635
<i>Balistes polylepis</i>	Bali_polyl	2850	69278		5227				91172	28023	2850	57615	28023			28023		
<i>Bodianus diplotaenia</i>	Bodi_diplo	5592	69278	57615	57615				9311	9823	57615					9823	9311	
<i>Bodianus eclancheri</i>	Bodi_eclan	5592	69278		28023				5227	28023	A2					28023	205	
<i>Bothus leopardinus</i>	Both_leopard	911972	69278		28023				9281	28023	5227					28023		
<i>Calamus taurinus</i>	Cala_taurin	11482	69278		28023				5227	28023	11482					28023		
<i>Canthidermis maculata</i>	Cant_mac	9276	69278		88972				9710	13385	43538	37816	1602	7251	44187	13385	205	
<i>Caranx caballus</i>	Cara_caballu	estimate*	69278	9283	9283	57615			9283	57615						9283		
<i>Caranx caninus</i>	Cara_caninus	estimate*	69278		28023	9283			51243	28023	9283					28023	9283	
<i>Caranx lugubris</i>	Cara_lugubri	7251	33	4887	4887	5213	57615		51243	7300	57615	9283	26938			7300	9283	
<i>Caranx melampygus</i>	Cara_melampy	estimate*	6057	6057	6057	9283	9710		9710	6057	53568	57615	58302	7300	9283	6057	90102	
<i>Caranx sexfasciatus</i>	Cara_sexfasc	9987	6932	6932	6932	90102			57178	4887	57615	44894	9283	58534		4887	90102	
<i>Carcharhinus falciformis</i>	Carc_fal	9997	37512	244	37816	37816			51243	244	58302					244	26340	
<i>Carcharhinus galapagensis</i>	Carc_gal	1602	33559	26464	26464	244	28023		58302	26464	12400	244				26464	244	
<i>Carcharhinus limbatus</i>	Carc_lim	27169	33559		11889	5578	37816	5485	51243	11889	26970	244	58302			11889		
<i>Caulolatilus princeps</i>	Caul_prin	2850	69278		5227				5227	9119	9952					9119	5227	
<i>Cephalopholis panamensis</i>	Ceph_pan	89707	69278	57615	57615	89707			55763	5222	57615	A1				5222		
<i>Chaetodon humeralis</i>	Chae_hume	5592	69278		28023	57615			37955	28023	4858	57615	A1			28023	9286	
<i>Chanos chanos</i>	Chan_chan	estimate*	12509	49	49	11889			51243	49	119549					49	12868	
<i>Chilomycterus reticulatus</i>	Chil_ret	estimate*	69278	9680	9680				9680	53568	30573	9680	A1			9680	30573	
<i>Chromis alta</i>	Chro_alta	estimate*	69278		9334				9334				A1			9334		
<i>Chromis atrilobata</i>	Chro_atrilo	59088	69278	57615	57615				9334	28023	57615	28023	A1			28023	205	
<i>Cirrhichthys oxycephalus</i>	Cirr_oxyce	9289	69278	57615		37955			9710	58534	37955					58534		
<i>Cratinus agassizii</i>	Crat_agass	55763	69278			28023			55763	28023	5227					28023		
<i>Dasyatis brevis</i>	Dasy_brevi	40637	69278	7445		37955			37955	7445	12591	5227				7445		
<i>Dasyatis longus</i>	Dasy_longu	9254	69278	12951	57615	114953			117334	57615	12951					117334		
<i>Dermatolepis dermatolepis</i>	Derm_derm	5222	69278	57615		28023			5222	28023	57615	A1				28023		
<i>Elagatis bipinnulata</i>	Elag_bipin	26340	69278	275	57615	9283	26145		9710	275	53568	57615	58534	9283	48635	90102	275	48635
<i>Enchelycore lichenosa</i>	Ench_li	11114	69278	9137	9137				5227	9137	28023					9137		

Supplementary information

genus_species	gen_sp	Body size references	Trophic ecology references						Ecological niche and within-reef mobility references								Social behaviour references	
<i>Epinephelus labriformis</i>	Epin_la	11035	69278	5222	5592	57615			89707	5222	57615	11035					5222	5592
<i>Euthynnus lineatus</i>	Euth_line	estimate*	69278	168	168				51243	168	11035						168	168
<i>Fistularia commersonii</i>	Fist_com	9301	26908	26908	36710	36327	37816	57615	58302	26908	53568	57615	58472	36710	41878	A1	26908	9710
<i>Galeocerdo cuvier</i>	Gale_cuv	58784	37512	33	33	9997	37816		51243	4805	2683	9137					4805	
<i>Girella freminvillei</i>	Gire_fremin	11482	69278		28023				11482	28023	A1						28023	5227
<i>Gobioclinus dendriticus</i>	Gobio_den	11482	69278	28023					5227	28023	A1						9313	
<i>Gymnothorax dovii</i>	Gymn_do	5227	69278			A1			5227									
<i>Gymnothorax flavimarginatus</i>	Gymn_fl	48635	69278	3921	3921	30573	89972		1602	57615	58302	48635					1602	90102
<i>Haemulon scudderii</i>	Haem_scudd	9114	69278	57615	57615				5227								5227	205
<i>Halichoeres dispilus</i>	Hali_disp	9311	69278		28023	9311			9311	28023	57615	A1					28023	5227
<i>Halichoeres nicholsi</i>	Hali_nich	9311	69278	57615	57615	28023			9311	28023	57615	A1					9311	205
<i>Halichoeres notospilus</i>	Hali_noto	5592	69278	57615	57615				9311	57615	A1						28023	205
<i>Hemilutjanus macrophthalmos</i>	Hemi_mac	28023	53696		53696	28023			104864	28023							28023	
<i>Heteroconger klausewitzii</i>	Hete_klau	11482	69278		28023				11482	28023							247	28023
<i>Heterodontus quoyi</i>	Hete_quoy	5227	69278	28023	28023				5227	247	A1						28023	5227
<i>Holacanthus passer</i>	Hola_pass	5592	69278		28023	57615	38503		5227	28023	57615	A1	A2				28023	9333
<i>Hoplopagrus guentherii</i>	Hopl_guen	9313	46593	46593	46593	9313			55763	28023	57615	9313	A1				9286	
<i>Johnrandallia nigrirostris</i>	John_nig	9286	69278	57615	57615	9286			9286	57615	5227	205	A1				28015	205
<i>Kyphosus analogus</i>	Kyph_analo	559	28015	559					51243	28015	53568	58652	559				28023	28023
<i>Kyphosus elegans</i>	Kyph_elag	55763	69278		28023				55763	28023	57615	A1					5227	95491
<i>Kyphosus ocyurus</i>	Kyph_ocyur	38398	69278	57615	57615	95491			89972	5227	57615	58302	95491				28023	559
<i>Lutjanus aratus</i>	Lutj_aratu	55763	69278	9313	9313				55763	9313	A1						55	9313
<i>Lutjanus argentiventris</i>	Lutj_argen	40637	69278	55	9313				9313	55	57615						55	9313
<i>Lutjanus guttatus</i>	Lutj_gutta	9313	37029	9313	9313	57615			91172	55	57615	9313					28023	9313
<i>Lutjanus novemfasciatus</i>	Lutj_novem	9313	69278	57615	57615	9313			9313	28023	57615	A1					28023	
<i>Lutjanus viridis</i>	Lutj_virid	55	69278	57615	57615				5227	28023	57615	A1					33	9313
<i>Melichthys niger</i>	Meli_nig	5217	33	33	1602	48637	33499	5213	9710	33	41878	9276	48637				275	33
<i>Mobula birostris</i>	Mobu_biros	58048	69278	9137	9137	9911			51243	275	9137	9911	58302	12951			117334	12951
<i>Mobula spp</i>	Mobu_spp	4442	69278		6679				51243	4442								

Supplementary information

genus_species	gen_sp	Body size references	Trophic ecology references						Ecological niche and within-reef mobility references								Social behaviour references	
<i>Mola ramsayi</i>	Mola_ram	4424	69278		4925	48637			86942	117334							28023	
<i>Mugil galapagensis</i>	Mugi_galapa	11482	69278		28023	11482			11482	28023	A1						205	
<i>Mulloidichthys dentatus</i>	Mull_dent	2850	69278	57615	57615				5227	4930	9322	57615	A1				2850	5227
<i>Muraena argus</i>	Mura_arg	57763	69278		57615	6852	A1		5227								28023	
<i>Muraena clepsydra</i>	Mura_clepsy	57763	69278		57615	6852	A1		57763								6930	
<i>Muraena lentiginosa</i>	Mura_lentig	5590	69278	57615	57615	6852			9324	28023	57615						9257	
<i>Mycteroperca olfax</i>	Myct_olf	5222	69278	6930	6930	11295			11295	6930	5222						3921	
<i>Myliobatis spp</i>	Mylio_spp	2850	69278	6253		9257			96339	9257	2850						28023	2334
<i>Ogcocephalus darwini</i>	Ogco_darw	estimate*	69278		28023				5227	28023	40824						28023	205
<i>Ophioblennius steindachneri</i>	Ophi_stein	28023	69278	57615	57615	28023			5227	28023	57615						5227	5590
<i>Oplegnathus insignis</i>	Ople_insig	55763	53696			28023			55763	28023	5227	A1					3921	205
<i>Orthopristis forbesi</i>	Orth_forb	estimate*	69278		25	9626	A1		5227	A1							33482	52884
<i>Paralabrax albonotatus</i>	Para_albo	estimate*	69278		33482				33482	11295	A2	A1					28023	57615
<i>Paranthias colonus</i>	Para_col	5592	69278	57615	57615				5222	28023	57615	A2					78172	205
<i>Plagiotremus azaleus</i>	Plag_aza	11482	69278	57615	57615	5227	28023		5227	28023	57615						27115	
<i>Prionurus laticlavus</i>	Prio_lati	55763	69278	57615					5227	27115	55763	57615	28023	9267	A1		4858	
<i>Prognathodes carlhubbsi</i>	Prog_carl	9286	69278	4930					4858	5227							9263	
<i>Remora remora</i>	Remo_remo	26340	33	33	33	35388			86942	33	41878	58302	33				12951	
<i>Rhinoptera steindachneri</i>	Rhin_stein	28023	69278	9263					51243	9263	12951						168	12951
<i>Rypticus bicolor</i>	Rypt_bicol	5227	69278		57615	5227			5227	57615	11482						5227	
<i>Sarda orientalis</i>	Sard_orient	estimate*	69278	168	168				51243	168	A2						6110	9340
<i>Scarus compressus</i>	Scar_comp	55763	69278	57615	57615				5227	57615	A1						28023	205
<i>Scarus ghobban</i>	Scar_ghob	90102	69278	6110	6110	5227	43650	57615	89642	6110	58652	58534	5490	1602	4821	48636	26993	48636
<i>Scarus perrico</i>	Scar_perr	5592	69278	57615	57615				5227	28023	57615	A1					168	205
<i>Scarus rubroviolaceus</i>	Scar_rubro	2334	69278	26993	26993	30573	57615		5227	26993	43539	58534	26993	48636			33	48636
<i>Scomberomorus sierra</i>	Scom_sier	estimate*	46593	168	168				51243	168	11035						42311	11035
<i>Scorpaena plumieri</i>	Scor_plum	5288	33	33	33				5228	33	42268	9710					9654	
<i>Semicossyphus darwini</i>	Semi_darw	11295	53696		42311	11295			11295	42311	A1						205	
<i>Seriola lalandi</i>	Seri_lalan	27865	69278	9654	9654	27121			4517	9654	53568	2850	9563	6390			4887	27865

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genus_species	gen_sp	Body size references	Trophic ecology references						Ecological niche and within-reef mobility references							Social behaviour references		
<i>Seriola rivoliana</i>	Seri_rivo	estimate*	50226	4887	4887	57615			90102	4887	9283	57615	58534	26235			58302	4887
<i>Serranus psittacinus</i>	Serr_psit	9342	69278		57615				5227	57615	9342						28023	9342
<i>Sphoeroides angusticeps</i>	Spho_angu	9349	69278			A1			5227	9349								
<i>Sphoeroides annulatus</i>	Spho_anna	9349	69278	75737	75737				91172	28023	9349						28023	
<i>Sphyraena idiaestes</i>	Sphy_idia	5590	69278		28023				5227	28023	A1						13562	58784
<i>Sphyrna lewini</i>	Sphy_lewi	26938	33559	568	568	6871	37816	30573	51243	568	58302	11230	244				12400	205
<i>Stegastes leucurus</i>	Steg_leuc	estimate*	69278	28023	9334				9334	7247							9311	
<i>Sufflamen verres</i>	Suff_verr	9276	69278	28023	28023	5227	57615		5227	28023	57615	9276					28023	
<i>Taeniurops meyeri</i>	Taen_mey	30573	69278	9137	9137	5578			37816	12400	75154	9137	1602					
<i>Thalassoma grammaticum</i>	Thal_gra	9311	69278	9311	9311	57615			9311	57615							9311	5227
<i>Thalassoma lucasanum</i>	Thal_luc	9311	69278	57615	57615	9311			9311	28023	A1						9311	
<i>Thunnus albacares</i>	Thun_alba	estimate*	27003	168	168				51243	168	6390	48637					568	9283
<i>Trachinotus stilbe</i>	Trac_stil	estimate*	69278		A1				5227								244	2850
<i>Trachurus murphyi</i>	Trac_symm	2850	40330	6262	6262	9283			51243	6262							2850	
<i>Triaenodon obesus</i>	Tria_obe	244	33559	568	568	244			244	568	9137	6871	37816	58302				
<i>Triakidae</i> spp	Tria_spp	244	69278	28023					244	6252								
<i>Umbrina galapagorum</i>	Umbr_gala	9118	120179	A1					9118									
<i>Uraspis helvola</i>	Uras_helv	7251	69278		4887				51243	2850	A2						30573	
<i>Xanthichthys mento</i>	Xant_ment	estimate*	69278		1602	89972			89972	1602	A2						2850	9710
<i>Zanclus cornutus</i>	Zanc_cornut	6113	6110	6110	6110	6113	59308	57615	9710	53568	58534	6110	1602	48637			9267	48637
		*total length estimated from models by Fishbase																

Table S3.3. FishBase references for the reference numbers in Table S3.2.

FishBase reference number	Author	Year	Title	Source
25	Darcy, G.H.	1983	Synopsis of biological data on the pigfish, <i>Orthopristis chrysoptera</i> (Pisces: Haemulidae).	FAO Fish. Synop. (134); NOAA Tech. Rep. NMFS Circ. (449).
33	Randall, J.E.	1967	Food habits of reef fishes of the West Indies.	Stud. Trop. Oceanogr. Miami 5:665-847.
55	Allen, G.R.	1985	FAO Species Catalogue. Vol. 6. Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date.	FAO Fish. Synop. 125(6):208 p. Rome: FAO.
168	Collette, B.B. and C.E. Nauen	1983	FAO Species Catalogue. Vol. 2. Scombrids of the world. An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date.	Rome: FAO. FAO Fish. Synop. 125(2):137 p.
205	Breder, C.M. and D.E. Rosen	1966	Modes of reproduction in fishes.	T.F.H. Publications, Neptune City, New Jersey. 941 p.

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FishBase reference number	Author	Year	Title	Source
244	Compagno, L.J.V.	1984	FAO Species Catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2 - Carcharhiniformes.	FAO Fish. Synop. 125(4 2):251-655. Rome: FAO.
275	Hiatt, R.W. and D.W. Strasburg	1960	Ecological relationships of the fish fauna on coral reefs of the Marshall Islands.	Ecol. Monogr. 30(1):65-127.
559	Masuda, H., K. Amaoka, C. Araga, T. Uyeno and T. Yoshino	1984	The fishes of the Japanese Archipelago. Vol. 1.	Tokai University Press, Tokyo, Japan. 437 p. (text).
568	Wetherbee, B.M., S.H. Gruber and E. Cortes	1990	Diet, feeding habits, digestion, and consumption in sharks, with special reference to the lemon shark, <i>Negaprion brevirostris</i> .	p. 29-47. In H.L. Pratt, Jr., S.H. Gruber and T. Taniuchi (eds.) Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Tech. Rep. NMFS 90. 517 p.
1602	Myers, R.F.	1991	Micronesian reef fishes.	Second Ed. Coral Graphics, Barrigada, Guam. 298 p.
1920	Randall, J.E.	1956	A revision of the surgeonfish genus, <i>Acanthurus</i> .	Pac. Sci. 10(2):159-235.
2334	Randall, J.E., G.R. Allen and R.C. Steene	1990	Fishes of the Great Barrier Reef and Coral Sea.	University of Hawaii Press, Honolulu, Hawaii. 506 p.
2683	Schneider, W.	1990	FAO species identification sheets for fishery purposes. Field guide to the commercial marine resources of the Gulf of Guinea. Prepared and published with the support of the FAO Regional Office for Africa.	Rome: FAO. 268 p.
2850	Eschmeyer, W.N., E.S. Herald and H. Hammann	1983	A field guide to Pacific coast fishes of North America.	Boston (MA, USA): Houghton Mifflin Company. xii+336 p.
3592	Harmelin-Vivien, M.L. and J.C. Quero	1990	Monacanthidae.	p. 1061-1066. In J.C. Quero, J.C. Hureau, C. Karrer, A. Post and L. Saldanha (eds.) Check-list of the fishes of the eastern tropical Atlantic (CLOFETA). JNICT, Lisbon; SEI, Paris; and UNESCO, Paris. Vol. 2.
3798	Courtenay, W.R. and H.F. Sahlman	1978	Pomadasyidae.	In W. Fischer (ed.) FAO species identification sheets for fishery purposes. Western Central Atlantic (Fishing Area 31), Volume 4. FAO, Rome.
3921	Randall, J.E.	1985	Guide to Hawaiian reef fishes.	Harrowood Books, Newtown Square, PA 19073, USA. 74 p.
3978	Cohen, D.M.	1986	Argentinidae.	p. 215-216. In M.M. Smith and P.C. Heemstra (eds.) Smiths' sea fishes. Springer-Verlag, Berlin.
4424	Heemstra, P.C.	1986	Molidae.	p. 907-908. In M.M. Smith and P.C. Heemstra (eds.) Smiths' sea fishes. Springer-Verlag, Berlin.
4442	McEachran, J.D. and B. Seibert	1990	Mobulidae.	p. 73-76. In J.C. Quero, J.C. Hureau, C. Karrer, A. Post and L. Saldanha (eds.) Check-list of the fishes of the eastern tropical Atlantic (CLOFETA). JNICT, Lisbon; SEI, Paris; and UNESCO, Paris. Vol. 1.
4517	Hureau, J.C.	1991	La base de données GICIM : Gestion informatisée des collections ichthyologiques du Muséum.	p. 225-227. In Atlas Préliminaire des Poissons d'Eau Douce de France. Conseil Supérieur de la Pêche, Ministère de l'Environnement, CEMAGREF et Muséum national d'Histoire naturelle, Paris.
4805	Randall, J.E.	1992	Review of the biology of the tiger shark (<i>Galeocerdo cuvier</i>).	Aust. J. Mar. Freshwat. Res. 43(1):21-31.
4821	Bagnis, R., P. Mazellier, J. Bennett and E. Christian	1972	Fishes of Polynesia.	Les Editions du Pacifique, Tahiti. 368 p.
4858	Allen, G.R.	1985	Butterfly and angelfishes of the world. Vol. 2.	3rd edit. in English. Mergus Publishers, Melle, Germany.
4887	Honebrink, R.	1990	Fishing in Hawaii: a student manual.	Education Program, Division of Aquatic Resources, Honolulu, Hawaii. 79 p.
4925	Clemens, W.A. and G.V. Wilby	1961	Fishes of the Pacific coast of Canada.	2nd ed. Fish. Res. Bd. Canada Bull. (68):443 p.
5213	Fischer, W., I. Sousa, C. Silva, A. de Freitas, J.M. Poutiers, W. Schneider, T.C. Borges, J.P. Feral and A. Massinga	1990	Fichas FAO de identificação de espécies para actividades de pesca. Guia de campo das espécies comerciais marinhas e de águas salobras de Moçambique.	Publicação preparada em colaboração com o Instituto de Investigação Pesqueira de Moçambique, com financiamento do Projecto PNUD/FAO MOZ/86/030 e de NORAD. Roma, FAO. 1990. 424 p.
5217	Cervigon, F., R. Cipriani, W. Fischer, L. Garibaldi, M. Hendrickx, A.J. Lemus, R. Merquez, J.M. Poutiers, G. Robaina and B. Rodriguez	1992	FAO species identification sheets for the purposes of fishing. Field guide to commercial marine and brackish aquatic species on the northern coast of South America.	FAO, Rome. 513 p. Prepared with financing from the Commission of the European Communities and NORAD.

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FishBase reference number	Author	Year	Title	Source
5222	Heemstra, P.C. and J.E. Randall	1993	FAO Species Catalogue. Vol. 16. Groupers of the world (family Serranidae, subfamily Epinephelinae). An annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper and lyretail species known to date.	Rome: FAO. FAO Fish. Synop. 125(16):382 p.
5227	Humann, P. and N. Deloach	1993	Reef fish identification. Galápagos.	New World Publications, Inc., Florida. 267 p.
5228	Smith, D.G.	1990	Derichthyidae.	p. 193-194. In J.C. Quero, J.C. Hureau, C. Karrer, A. Post and L. Saldanha (eds.) Check-list of the fishes of the eastern tropical Atlantic (CLOFETA). JNICT, Lisbon; SEI, Paris; and UNESCO, Paris. Vol. 1.
5288	Edwards, A.	1990	Fish and fisheries of Saint Helena Island.	Centre for Tropical Coastal Management Studies, University of Newcastle upon Tyne, England.
5485	Bass, A.J., P.C. Heemstra and L.J.V. Compagno	1986	Carcharhinidae.	p. 67-87. In M.M. Smith and P.C. Heemstra (eds.) Smiths' sea fishes. Springer-Verlag, Berlin.
5490	Randall, J.E.	1986	Scaridae.	p. 706-714. In M.M. Smith and P.C. Heemstra (eds.) Smiths' sea fishes. Springer-Verlag, Berlin.
5543	Dalzell, P.	1989	The biology of surgeon fishes with particular emphasis on <i>Acanthurus nigricauda</i> and <i>A. xanthopterus</i> from northern Papua New Guinea.	University of Newcastle Upon Tyne, England. 285 p. M.S. thesis.
5578	Compagno, L.J.V., D.A. Ebert and M.J. Smale	1989	Guide to the sharks and rays of southern Africa.	New Holland (Publ.) Ltd., London. 158 p.
5590	Merlen, G.	1988	A field guide to the fishes of Galápagos.	Wilmot Books, London, England 60 p.
6057	Sudekum, A.E., J.D. Parrish, R.L. Radtke and S. Ralston	1991	Life history and ecology of large jacks in undisturbed, shallow, oceanic communities.	Fish. Bull. 89:493-513.
6110	Sano, M., M. Shimizu and Y. Nose	1984	Food habits of teleostean reef fishes in Okinawa Island, southern Japan.	University of Tokyo Bulletin, no. 25. v,128p. University of Tokyo Press, Tokyo, Japan. 128 p.
6113	Anderson, C. and A. Hafiz	1987	Common reef fishes of the Maldives. Part 1.	Novelty Press, Republic of Maldives. 83 p.
6252	Talent, L.G.	1976	Food habits of the leopard shark, <i>Triakis semifasciata</i> , in Elkhorn Slough, Monterey Bay, California.	Calif. Fish Game 62(4):286-298.
6253	Talent, L.G.	1982	Food habits of the gray smoothhound, <i>Mustelus californicus</i> , the brown smoothhound, <i>Mustelus henlei</i> , the shovelnose guitarfish, <i>Rhinobatos productus</i> , and the bat ray, <i>Myliobatis californica</i> , in Elkhorn Slough, California.	Calif. Fish Game 68(4):224-234.
6262	Konchina, Y.V.	1983	The feeding niche of the hake, <i>Merluccius gayi</i> (Merlucciidae), and the jack mackerel, <i>Trachurus symmetricus</i> (Carangidae), in the trophic system of the Peruvian coastal upwelling.	J. Ichthyol. 23(2):87-98.
6390	Kailola, P.J., M.J. Williams, P.C. Stewart, R.E. Reichelt, A. McNee and C. Grieve	1993	Australian fisheries resources.	Bureau of Resource Sciences, Canberra, Australia. 422 p.
6679	McEachran, J.D. and C. Capape	1984	Mobulidae.	p. 210-211. In P.J.P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (eds.) Fishes of the north-eastern Atlantic and the Mediterranean. UNESCO, Paris. Vol. 1.
6769	Collette, B.B.	1986	Scombridae (including Thunnidae, Scomberomoridae, Gasterochismatidae and Sardidae).	p. 981-997. In P.J.P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (eds.) Fishes of the north-eastern Atlantic and the Mediterranean, Volume 2. Unesco, Paris.
6852	Thomson, D.A., L.T. Findley and A.N. Kerstitch	1979	Reef fishes of the Sea of Cortez. The rocky-shore fishes of the Gulf of California.	John Wiley and Sons, New York. 302 p.
6871	Last, P.R. and J.D. Stevens	1994	Sharks and rays of Australia.	CSIRO, Australia. 513 p.
6932	Salini, J.P., S.J.M. Blaber and D.T. Brewer	1994	Diets of trawled predatory fish of the Gulf of Carpentaria, Australia, with particular reference to predation on prawns.	Aust. J. Mar. Freshwat. Res. 45(3):397-411.
7247	Allen, G.R.	1991	Damselfishes of the world.	Mergus Publishers, Melle, Germany. 271 p.
7251	Robins, C.R. and G.C. Ray	1986	A field guide to Atlantic coast fishes of North America.	Houghton Mifflin Company, Boston, U.S.A. 354 p.
7300	Paxton, J.R., D.F. Hoese, G.R. Allen and J.E. Hanley	1989	Pisces. Petromyzontidae to Carangidae.	Zoological Catalogue of Australia, Vol. 7. Australian Government Publishing Service, Canberra, 665 p.
9114	McKay, R.J. and M. Schneider	1995	Haemulidae. Burros, corocoros, chulas, gallinazos, roncos.	p. 1136-1173. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para Identificación de Especies para lo Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.

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FishBase reference number	Author	Year	Title	Source
9118	Chao, L.N.	1995	Sciaenidae. Corvinas, barbiches, bombaches, corvinatas, corvinetas, corvinillas, lambes, pescadillas, roncachos, verrugatos.	p. 1427-1518. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de especies para los fines de la pesca. Pacífico Centro-oriental., 3 volúmenes. 1813 p.
9119	Schneider, W. and F. Krupp	1995	Malacanthidae. Blanquillos, matajuelos.	p. 1266-1271. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de Especies para lo Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
9137	Masuda, H. and G.R. Allen	1993	Meeresfische der Welt - Gro ÷df -Indopazifische Region.	Tetra Verlag, Herrenteich, Melle. 528 p.
9254	McEachran, J.D.	1995	Dasyatidae. Rayas-latigo.	p. 752-755. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de Especies para los Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
9257	McEachran, J.D. and G. Notarbartolo di Sciara	1995	Myliobatidae. Aguilas marinas.	p. 765-768. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de Especies para los Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
9263	McEachran, J.D. and G. Notarbartolo di Sciara	1995	Rhinopteridae. Gavilanes.	p. 782-783. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de Especies para los Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
9267	Krupp, F.	1995	Acanthuridae. Sangradores, cirujanos, navaones.	p. 839-844. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de Especies para lo Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
9275	Fritzsche, R.A.	1995	Aulostomidae. Trompetas.	p. 904. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de Especies para lo Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
9276	Bussing, W.A.	1995	Balistidae. Pejepuercos, calafates, gatillos.	p. 905-909. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de Especies para lo Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
9281	Hensley, D.A.	1995	Bothidae. Lenguados.	p. 931-936. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de Especies para lo Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
9283	Smith-Vaniz, W.F.	1995	Carangidae. Jureles, pámpanos, cojinúas, zapateros, cocineros, casabes, macarelas, chicharros, jorobados, medregales, pez pilota.	p. 940-986. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de Especies para lo Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
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9289	Bussing, W.A. and R.J. Lavenberg	1995	Cirrhitidae. Chinos, halcones.	p. 1007-1010. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de Especies para lo Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
9301	Fritzsche, R.A. and M. Schneider	1995	Fistulariidae. Cornetas.	p. 1104-1105. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de Especies para lo Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
9311	Gomon, M.F.	1995	Labridae. Viejas, doncellasas, señoritas.	p. 1201-1225. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de Especies para lo Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
9313	Allen, G.R.	1995	Lutjanidae. Pargos.	p. 1231-1244. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guía FAO para identificación de

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9318	Bussing, W.A. and R.J. Lavenberg	1995	Monacanthidae. Cachuas, lijas.	p. 1278-1280. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guia FAO para Identificación de Especies para lo Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
9322	Schneider, M.	1995	Mullidae. Salmonetes.	p. 1299-1300. In W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter and V. Niem (eds.) Guia FAO para Identificación de Especies para lo Fines de la Pesca. Pacífico Centro-Oriental., 3 Vols. FAO, Rome.
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120179	Froese, R., N. Demirel, G. Coro, K.M. Kleisner and H. Winker	2017	Estimating fisheries reference points from catch and resilience	Fish and Fisheries 18(3):506-526
AlternativeRefs				
A1	Robertson, D. R. and G. R. Allen	2015	Shorefishes of the Tropical Eastern Pacific: online information system	https://biogeodb.stri.si.edu/sfstep/en/findafish
A2	Humann, P. and N. Deloach	2003	Reef Fish Identification: Galápagos	New World Publications, Inc., Florida. 240p.

Supplementary information

Table S3.4. Working definitions and ecosystem effects of the five functional traits used to identify functional entities and assess the functional vulnerability of 121 reef fish species sampled in the Galápagos Archipelago in 2015.

Functional trait category	Functional trait	Trait levels	Source	Working definitions	Ecosystem effects
Body size	Maximum total length (cm) (ML)	very-small (vs, 0-20cm) small (sm, 20.01-50cm) medium (me, 50.01-100cm) large (la, 100.01-200cm) very-large (vl, 200.01cm+)	Estimated using maximum total length measurements from FishBase.	Total length: The greatest length of the whole body between the most anterior point of the body and the most posterior point, in a straight line, not over the curve of the body.	Body size is a primary indicator of reef fish ecological niche (Fisher, Frank, & Leggett, 2010; Lokrantz, Nyström, Thyresson, & Johansson, 2008; Wilson, 1975). Body size indicates resource depletion through energy requirements with relation to body mass (Munday & Jones, 1998), growth rates (Brown, Gillooly, Allen, Savage, & West, 2004) and mortality rates (Munday & Jones, 1998). Body size also indicates resource contributions through secondary production (Woodward et al., 2005).
Trophic ecology	Diet (DI)	Herbivorous (he) Invertivorous (in) Planktivorous (pl) Piscivorous (pi) Omnivorous (om) Filter-feeding (fi)	Estimated using trophic level, trophic level standard error and feeding habit (that integrates main food type and feeding method) from FishBase.	Trophic level: Position in the food chain, determined by the number of energy-transfer steps to that level. Feeding habit: Integrates main food type with feeding method. Herbivorous: primarily consumes detritus and algae Invertivorous: primarily consumes invertebrates Planktivorous: primarily consumes individually picked planktonic organisms Piscivorous: primarily consumes fish Omnivorous: consumes a variety of food types Filter feeder: filters plankton from the water column using cephalic fins and specialised gill plates	Diet is the other primary indicator of reef fish ecological niche (Bellwood, Wainwright, Fulton, & Hoey, 2006; Burkepile & Hay, 2008). Diet indicates resource depletion and subsequently, addition, through trophic interactions, specifically, predator-prey relationships, and nutrient recycling (Burkepile et al., 2013; Vanni, 2002). Diet also indicates resource availability, specifically, habitat requirements, because some resources are only available at particular habitats (Brandl & Bellwood, 2013).

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Functional trait category	Functional trait	Trait levels	Source	Working definitions	Ecosystem effects
Ecological niche	Water column position	Demersal (de) Benthic (be) Benthopelagic (bp) Pelagic (pe)	Estimated using distribution information and biological descriptions relating to feeding and mobility in FishBase.	Preferred vertical position in the water column for living and feeding. Pelagic: Living and free swimming within the middle depths or near the surface not in association with the bottom. Feeding in the open sea; associated with the surface or middle depths of a body of water. Benthopelagic: Living near the bottom as well as in midwaters or near the surface and feeding on benthic as well as free swimming organisms. Benthic: Living near and relating to, the bottom of a body of water feeding on benthic organisms Demersal: Living on or in the bottom substrate and feeding on benthic organisms	Water column position in reef fish indicates ecological connectivity and nutrient cycling both within-reefs through benthic-pelagic coupling (Schaus & Vanni, 2000) and between-reefs through home-ranges (Rijnsdorp, Peck, Engelhard, Möllmann, & Pinnegar, 2009) and prey availability (Bellwood et al., 2006). Water column position also indicates resource depletion because pelagic species are likely to be more mobile than demersal species, thereby having more significant energy needs (Norman & Jones, 1984).
Within-reef mobility	Substrate preference	Soft (so) Hard (ha) Hard and soft (hs) Open-water (px)	Estimated using substrate and habitat associations and biological descriptions relating to feeding and mobility in FishBase.	Preferred substrate for living and feeding. Soft: living and feeding on or in soft sediment habitats such as sand and mud. Hard: living and feeding on or in hard substrate habitats such as rocky and coral reefs. Both: moving between soft sediment and hard substrates for living and feeding. Open-water: Pelagic lifestyle, mostly found in the water-column.	Within-reef mobility and substrate preference in reef fishes indicate resource depletion and subsequently, addition through smaller scale nutrient transfer and recycling (Meyer & Schultz, 1985; Nagelkerken, Dorenbosch, de la Moriniere, & Van der Velde, 2000). Within-reef mobility also indicates resource and prey availability.
Social behaviour	Largest common group size	Solitary or pairing (so) Small group (sg) Large group (lg)	Estimated using social behaviour information and biological descriptions in FishBase.	Predominant social behaviour with regards to other fish and fish species. Solitary to pairing: Mostly occur alone or in pairs for living and feeding. Small group: Can live or	Social behaviour in reef fishes indicates resource depletion because larger groups instigate rapid nutrient cycling and also, resource addition because larger groups indicate an abundance of prey (Foster, 1985; Meyer & Schultz, 1985). Social behaviour can also indicate prey vulnerability and avoidance (Hoare,

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Functional trait category	Functional trait	Trait levels	Source	Working definitions	Ecosystem effects
				<p>aggregate into small groups of up to 20 individuals, not in schools or shoals.</p> <p>Large group: Behaviourally group together with other individuals and species, living and moving together as a group and acting as a school.</p>	<p>Krause, Peuhkuri, & Godin, 2000; Stier, Geange, & Bolker, 2013).</p>

Supplementary information

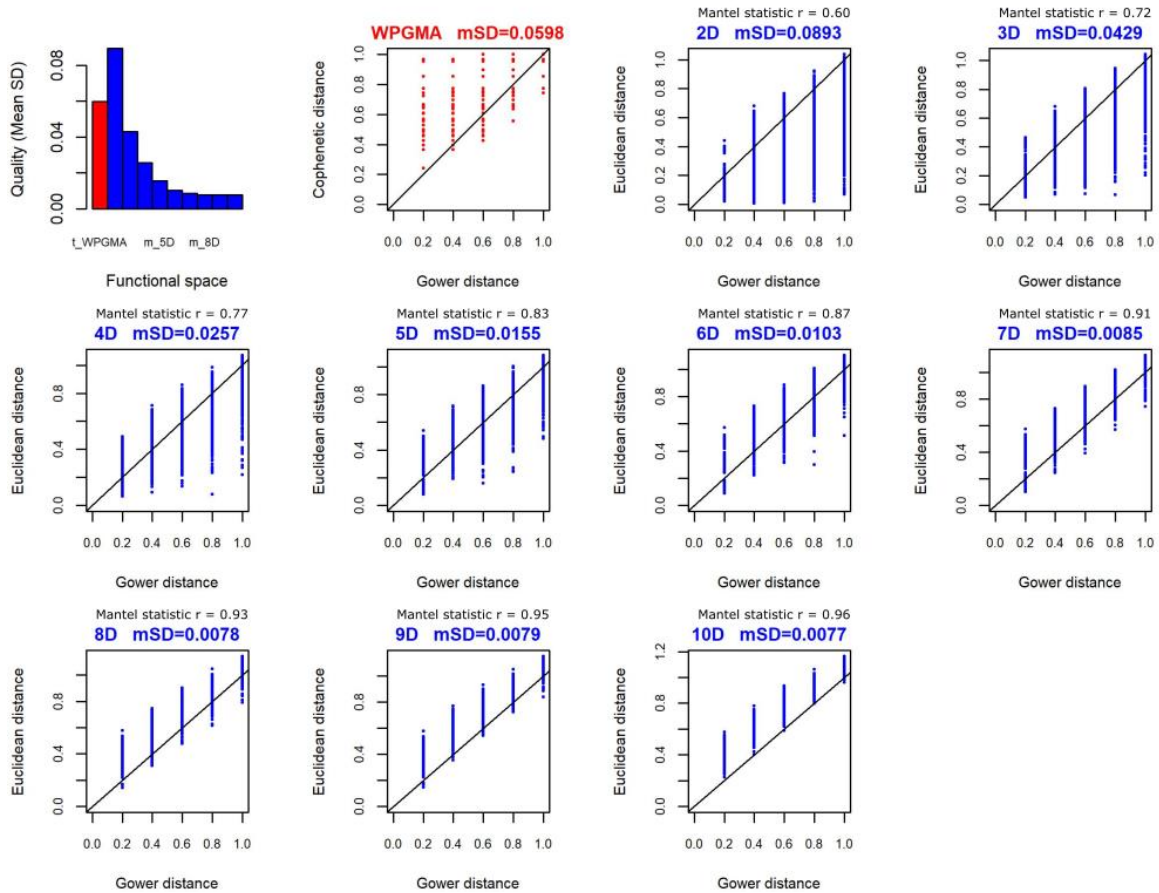


Figure S3.1. The quality of functional spaces used to compute the functional originality index for Galápagos reef fish assemblages sampled in 2015. The top-left panel shows the mean squared deviation for the ten functional spaces. The remaining ten panels show the correlation between the initial Gower's distances and the standardised distances in each of the ten functional spaces including a functional dendrogram built from the unweighted pair group method with arithmetic mean (UPGMA) clustering algorithm and the 2D-10D multidimensional spaces built using principal coordinates analysis (PCoA) for two to 10 axes. Mantel tests between the original Gowers matrix and resulting species positions are also included. Each point represents a species.

Table S3.5. Summary of the five alternative distance-based linear models (DistLMs) within two AIC units of the best models used to model the abundance of FEs using environmental variables, the best selection procedure and AICc selection criteria. The Pseudo-F statistic, P-value and Proportion of variance explained by each explanatory variable in each mode are also presented.

Model number, number of variables	R ²	RSS	AICc	Variables	Pseudo-F	P-value	Proportion explained
1, 3	0.303	41155	304.2	Latitude SST Bottom Incline	3.462 8.326 4.655	0.001 <0.001 <0.001	7.78 16.88 10.12
2, 4	0.351	38321	303.7	Latitude Longitude SST Bottom Incline	3.462 4.658 8.326 4.655	0.001 <0.001 <0.001 <0.001	7.78 1.02 16.88 10.12
3, 5	0.391	35971	303.69	Latitude Mean fetch Macroalgae cover Bottom Incline Distance to ports	3.462 2.513 6.785 4.655 3.838	0.001 0.010 <0.001 <0.001 <0.001	7.78 5.77 14.20 10.20 8.56
4, 6	0.426	33921	304.04	Latitude Mean fetch	3.462 2.513	0.001 0.010	7.78 5.77

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Model number, number of variables	R ²	RSS	AICc	Variables	Pseudo- F	P- value	Proportion explained
				Hard coral cover Macroalgae cover Bottom incline Distance to ports	2.345 6.785 4.655 3.838	0.010 <0.001 <0.001 <0.001	1.04 14.20 10.20 8.56
5, 7	0.458	32037	304.61	Latitude Mean fetch Cholorophyll a Hard coral cover Macroalgae cover Bottom incline Distance to ports	3.462 2.513 2.422 2.345 6.785 4.655 3.838	0.001 0.010 0.014 0.010 <0.001 <0.001 <0.001	7.78 5.77 5.57 1.04 0.14.20 10.20 8.56

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