

Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

# Spatial patterns in the taxonomic and dietary diversity of New Zealand rocky reef fishes

A thesis presented in partial fulfilment of the requirements for the degree of Master of Science in Biological Sciences at Massey University, Albany, New Zealand.

Odette Ruth Howarth

2018

## Abstract

Latitudinal gradients of high species richness from the tropics declining towards the poles are well documented for many terrestrial and marine species. However, these broad scale patterns of numbers of species observed don't inform as to how related these species are, or how they use food resources. By understanding taxonomic relationships between observed species I can predict how resilient these assemblages are and how environmental processes impact their distribution. Dietary diversity between species describes patterns related to mechanisms of food availability and preference of habitats or environmental niches.

Marine fishes are speciose and well known taxonomically, and so comprise a useful system for studying broad-scale patterns in biodiversity. Here I examined five indices of diversity—species richness, average taxonomic distinctness, variation in taxonomic distinctness, average diet diversity and variation in diet diversity—using a historical dataset on the presence/absence of rocky reef fishes spanning most of New Zealand. I modelled these indices using boosted regression trees and mapped their distributions to the coastline at a 1km scale resolution. Additionally, I developed a new quantitative methodology to classify coastal, rocky reef fishes into homogenous diet guilds using hierarchical clustering of nine broad food items and SIMPROF multivariate analysis and modelled species richness of three of the diet guilds (herbivore, invertivore and piscivore/benthic invertivores) using boosted regression trees.

This research has broadened our understanding of patterns of fish diversity, spatial patterns in diversity of diets in coastal rocky reef fishes in New Zealand. I found the indices of overall species richness, species richness of herbivores and invertivores, and average taxonomic distinctness to be highly correlated with increased wintertime sea-surface temperature indicating a latitudinal gradient to their distributions. Decreased turbidity increased average dietary diversity and species richness of the piscivore/benthic invertivore guild. Average fetch or exposure had a positive relationship with variation in diet diversity and a negative relationship with variation in taxonomic distinctness. Of secondary importance I found the indices of overall species richness, species richness of invertivores, average taxonomic distinctness and variation in diet diversity to be adversely affected by increased turbidity. Variation in taxonomic distinctness and species richness of the

herbivore diet guild increased with variable and increasing salinity (respectively) while average diet diversity increased with exposure.

Lastly the piscivore/benthic invertivore guild had a positive relationship with increased wintertime sea-surface temperature. Overall I found broad and fine scale environmental processes affected the species richness and taxonomic diversity of NZ reef fishes as did food availability, resource use and habitat preferences.

## Acknowledgements

First and foremost, I would like to thank Adam Smith and Libby Liggins. Adam, for taking a chance on one of his worst statistics students who wanted to embrace the dark-side (statistics) of science and for (usually) believing both of us would actually get through this. Libby, for constantly expanding my understanding of how the world works, what can be achieved and to constantly form questions (all of which may not be immediately apparent). You have both been unwavering, solid columns of support, always with the mantra of 'keep going' (definitely Libby). I have been unbelievably lucky to have both Adam and Libby supporting me through this experience and I would not have made it here without them. I would also like to thank Clinton Duffy. Without his data (meticulously) collected over many years, as a testament of his passion for NZ flora and fauna conservation, this project would never have existed.

I would also like to thank my family, Lorraine and Paul Howarth for putting up with me throughout this experience and always being on the end of the phone when it all got a bit much. I love you very dearly. To my siblings Brett, Shannon and Chris Howarth for the late night phone calls, you got me through and I thank you.

In addition to my amazing supervisors, I have been lucky enough to be a student of and advised by some amazing people. Dave Aguirre who is always willing (maybe not always) to help with code and usually a well-needed dose of reality. You have supported and taught me how to science and I will am more thankful than you know. Karen Stockin for her unwavering support of me, always, all the time. I can only hope I deserve your faith in me. Emma Betty for listening to me moan and always a sympathetic ear. Mat Pawley, because deep down he still wants to be a biologist, as well as Daniel Thomas and Anne Wignall, whose knowledge and passion always motivated me to want to know more.

Lastly, I'd like to thank my long suffering friends. Kate for being a master formatter and partner in study and Cass for the constant check-ups on my mental health. Also Mel and Mikey, Dan and Sam, Bek and Chris, Christine, Fletcher, Bran and Emily, Amber and Pete, Jan, Freeman and Mark for being my support crew for the last 5 years. I would not have made it without you and I am forever grateful. Lastly to my new work crew, Margaret, Jarod, Natasha, Kathi and Rachel you have been amazingly tolerant and I thank you!

## TABLE OF CONTENTS

Chapter 1 General Introduction .....	10
1.1 Biodiversity gradients.....	10
1.2 Predictors of biodiversity .....	11
1.3 Indices of diversity.....	11
1.4 Glossary of Indices.....	12
Thesis overview .....	13
1.6 Spatial patterns of species and taxonomic diversity of New Zealand rocky reef fishes.....	13
1.7 Quantitative classification of New Zealand rocky reef fishes into diet guilds.....	14
1.8 Regional and local processes as drivers of diet diversity in New Zealand rocky reef fish species .....	15
General Discussion .....	16
Chapter 2 Spatial patterns of species and taxonomic diversity of New Zealand rocky reef fishes .....	17
2.1 Introduction .....	17
2.2 Materials and Methods .....	19
Collection of data and predictor variables.....	19
Species richness .....	20
Average Taxonomic Distinctness .....	20
Variation in Taxonomic Distinctness.....	20
Boosted regression Tree models .....	21
2.3 Results .....	23
2.4 Discussion.....	35
Chapter 3 Quantitative classification of New Zealand rocky reef fishes into diet guilds .....	39
3.1 Introduction .....	39
3.2 Methods and theory.....	41
Data on species diets .....	41
Classifying species based on diets .....	42
3.3 Results .....	43
3.4 Discussion.....	47
Chapter 4 Regional and local processes as drivers of diet diversity in New Zealand rocky reef fish species.....	49
4.1 Introduction .....	49
4.2 Materials and Methods .....	52
Collection of data and predictor variables (see previous chapters) .....	52
Species richness of Diet Guilds .....	52
Average and Variation in Diet Diversity .....	53
Boosted regression tree models .....	53
4.3 Results .....	54

Species Richness of Diet Guilds.....	59
4.4 Discussion.....	71
Chapter 5 General Discussion and overall chapter synthesis .....	76
5.1 Chapter 2 conclusions .....	76
5.2 Chapter 3 conclusions .....	76
5.3 Chapter 4 conclusions .....	77
5.4 General Discussion .....	78
5.5 Future directions .....	80
References .....	81
Appendix.....	87

## TABLE OF FIGURES

FIGURE 2.1 LOCATIONS OF 467 DIVE SURVEY SITES. THERE WERE NO SAMPLING SITES AT ANY OF THE OTHER ISLAND GROUPS THAT ARE NOT SHOWN HERE, INCLUDING THE CHATHAM ISLANDS. ....	22
FIGURE 2.2: INFLUENCE OF INDIVIDUAL PREDICTOR VARIABLES ON RESPONSE VARIABLE OF SPECIES RICHNESS, INCLUDING THE COMBINED VARIABLE OF 'TURB1 AND TURB2' AND THE VISIBILITY ANOMALY 'VISANOM'. THE Y-AXIS OF "FITTED FUNCTION" HOLDS ALL OTHER VARIABLES CONSTANT AND PREDICTS FOR A RANGE OF VALUES OF THE ONE VARIABLE AGAINST THE RESPONSE VARIABLE 'SPECIES RICHNESS'. SPECIES RICHNESS WAS SQUARE-ROOTED. ....	24
FIGURE 2.3: BAR PLOT SHOWING RELATIVE INFERENCE OF ENVIRONMENTAL, GEOGRAPHICAL AND DIVE RELATED VARIABLES FOR PREDICTED SPECIES RICHNESS USING BOOSTED REGRESSION TREES. ....	25
FIGURE 2.4: INFLUENCE OF INDIVIDUAL PREDICTOR VARIABLES ON RESPONSE VARIABLE OF AVERAGE TAXONOMIC DISTINCTNESS (DELTA) INCLUDING THE COMBINED VARIABLE OF 'TURB1 AND TURB2' AND THE VISIBILITY ANOMALY 'VISANOM'. THE Y-AXIS OF "FITTED FUNCTION" HOLDS ALL OTHER VARIABLES CONSTANT AND PREDICTS FOR A RANGE OF VALUES OF THE ONE VARIABLE AGAINST THE RESPONSE VARIABLE 'TAXONOMIC DISTINCTNESS'. ....	26
FIGURE 2.5: BAR PLOT SHOWING RELATIVE INFERENCE OF ENVIRONMENTAL, GEOGRAPHICAL AND DIVE RELATED VARIABLES FOR PREDICTED AVERAGE TAXONOMIC DISTINCTNESS USING BOOSTED REGRESSION TREES. ....	27
FIGURE 2.6: INFLUENCE OF INDIVIDUAL PREDICTOR VARIABLES ON RESPONSE VARIABLE OF 'VARIATION OF TAXONOMIC DISTINCTNESS' (SQUARE-ROOTED) INCLUDING THE COMBINED VARIABLE OF 'TURB1 AND TURB2' AND THE VISIBILITY ANOMALY 'VISANOM'. THE Y-AXIS OF 'FITTED FUNCTION' HOLDS ALL OTHER VARIABLES CONSTANT AND PREDICTS FOR A RANGE OF VALUES OF THE ONE VARIABLE AGAINST THE RESPONSE VARIABLE 'VARIATION IN TAXONOMIC DISTINCTNESS'. ....	28
FIGURE 2.7: BAR PLOT SHOWING RELATIVE INFERENCE OF ENVIRONMENTAL, GEOGRAPHICAL AND DIVE RELATED VARIABLES FOR PREDICTED VARIABLE TAXONOMIC DISTINCTNESS USING BOOSTED REGRESSION TREES. ....	29
FIGURE 2.8: GEOGRAPHIC MAP OF PREDICTED SPECIES RICHNESS OF NEW ZEALAND ROCKY REEF FISH. KEY INDICATES NUMBER OF SPECIES EXPECTED TO BE SEEN IN EACH REGION/AREA. INSETS SHOW THE KERMADec ISLANDS (TOP LEFT) AND CHATHAM ISLANDS (BOTTOM LEFT). ....	30
FIGURE 2.9: GEOGRAPHIC MAP OF PREDICTED AVERAGE TAXONOMIC DISTINCTNESS OF NEW ZEALAND ROCKY REEF FISH. KEY INDICATES HOW TAXONOMICALLY DIFFERENT THE SPECIES IN EACH REGION/AREA ARE BY AVERAGING THE PATH LENGTHS THROUGH A TAXONOMIC TREE. INSETS SHOW THE KERMADec ISLANDS (TOP LEFT) AND CHATHAM ISLANDS (BOTTOM LEFT). .	31
FIGURE 2.10: GEOGRAPHIC MAP OF PREDICTED VARIATION IN TAXONOMIC DISTINCTNESS OF NEW ZEALAND ROCKY REEF FISH. KEY INDICATES HOW VARIABLE THE TAXA IN EACH REGION/AREA ARE. INSETS SHOW THE KERMADec ISLANDS (TOP LEFT) AND CHATHAM ISLANDS (BOTTOM LEFT). ....	32
FIGURE 2.11: FUNNEL PLOT OF 'AVERAGE TAXONOMIC DISTINCTNESS' OF EACH SAMPLE SITE'S FISH SPECIES IN RELATION TO NUMBER OF FISH SPECIES FOUND AT EACH SITE INCLUDING A 95% CONTOUR.....	33
FIGURE 2.12: FUNNEL PLOT OF 'VARIATION IN TAXONOMIC DISTINCTNESS' OF EACH SAMPLE SITE'S FISH SPECIES IN RELATION TO NUMBER OF FISH SPECIES FOUND AT EACH SITE INCLUDING A 95% CONTOUR. ....	34
FIGURE 3.1: SHADE-PLOT OF RAW DATA SHOWING SCORES OF 9 FOOD ITEMS ACROSS ALL 158 SPECIES. BLACK SHADING INDICATES THAT THE FOOD SOURCE IS PRESENT IN SPECIES DIET. ....	44
FIGURE 3.2: NON-METRIC MULTIDIMENSIONAL SCALING OF SPECIES GAMMA+ DISSIMILARITIES BASED ON WHETHER OR NOT THEY CONSUME EACH OF NINE FOOD ITEMS. EACH POINT IS A SPECIES, EACH CLASSIFIED INTO ONE OF EIGHT DIET GUILDS. THE BLUE VECTORS REPRESENT CORRELATIONS (TO 1 AT CIRCLE) BETWEEN THE MDS AXES AND THE FOOD ITEMS. ....	45
FIGURE 3.3: BOXPLOTS OF THE EIGHT DIET GUILDS ILLUSTRATING THE VARIANCE OF EACH MEMBER SPECIES TROPHIC LEVELS. ....	46

FIGURE 4.1: INFLUENCE OF INDIVIDUAL PREDICTOR VARIABLES ON RESPONSE VARIABLE OF AVERAGE DIET DIVERSITY INCLUDING THE COMBINED VARIABLE OF 'TURB1 AND TURB2' AND THE VISIBILITY ANOMALY 'VISANOM". THE Y-AXIS OF "FITTED FUNCTION' HOLDS ALL OTHER VARIABLES CONSTANT AND PREDICTS FOR A RANGE OF VALUES OF THE ONE VARIABLE AGAINST THE RESPONSE VARIABLE 'SPECIES RICHNESS'. SPECIES RICHNESS WAS SQUARE-ROOTED. ....	55
FIGURE 4.2: GEOGRAPHIC MAP OF PREDICTED AVERAGE DIET DIVERSITY OF NEW ZEALAND ROCKY REEF FISH. KEY INDICATES PREDICTED DIVERSITY OF DIETS FOUND IN EACH REGION/AREA. INSETS SHOW THE KERMADEC ISLANDS (TOP LEFT) AND CHATHAM ISLANDS (BOTTOM LEFT). THE Y-AXIS OF "FITTED FUNCTION' HOLDS ALL OTHER VARIABLES CONSTANT AND PREDICTS FOR A RANGE OF VALUES OF THE ONE VARIABLE AGAINST THE RESPONSE VARIABLE 'AVERAGE OF DIET DIVERSITY'. ....	56
FIGURE 4.3: INFLUENCE OF INDIVIDUAL PREDICTOR VARIABLES ON RESPONSE VARIABLE OF VARIATION IN DIET DIVERSITY INCLUDING THE COMBINED VARIABLE OF 'TURB1 AND TURB2' AND THE VISIBILITY ANOMALY 'VISANOM". THE Y-AXIS OF "FITTED FUNCTION' HOLDS ALL OTHER VARIABLES CONSTANT AND PREDICTS FOR A RANGE OF VALUES OF THE ONE VARIABLE AGAINST THE RESPONSE VARIABLE 'TAXONOMIC DISTINCTNESS'. ....	58
FIGURE 4.4: GEOGRAPHIC MAP OF PREDICTED VARIATION IN DIET DIVERSITY OF NEW ZEALAND ROCKY REEF FISH SPECIES. KEY INDICATES PREDICTED VARIATION IN FOOD ITEMS CONSUMED FOUND IN EACH REGION/AREA. INSETS SHOW THE KERMADEC ISLANDS (TOP LEFT) AND CHATHAM ISLANDS (BOTTOM LEFT). THE Y-AXIS OF "FITTED FUNCTION' HOLDS ALL OTHER VARIABLES CONSTANT AND PREDICTS FOR A RANGE OF VALUES OF THE ONE VARIABLE AGAINST THE RESPONSE VARIABLE 'VARIATION IN DIET DIVERSITY'. ....	59
FIGURE 4.5: INFLUENCE OF INDIVIDUAL PREDICTOR VARIABLES ON RESPONSE VARIABLE OF SPECIES RICHNESS OF HERBIVORES, INCLUDING THE COMBINED VARIABLE OF 'TURB1 AND TURB2' AND THE VISIBILITY ANOMALY 'VISANOM". THE Y-AXIS OF "FITTED FUNCTION' HOLDS ALL OTHER VARIABLES CONSTANT AND PREDICTS FOR A RANGE OF VALUES OF THE ONE VARIABLE AGAINST THE RESPONSE VARIABLE 'SPECIES RICHNESS OF HERBIVORES' ....	60
FIGURE 4.6: GEOGRAPHIC MAP OF PREDICTED DISTRIBUTION OF HERBIVOROUS NEW ZEALAND ROCKY REEF FISH. KEY INDICATES PREDICTED ABUNDANCE OF HERBIVOROUS SPECIES FOUND IN EACH REGION/AREA. INSETS SHOW THE KERMADEC ISLANDS (TOP LEFT) AND CHATHAM ISLANDS (BOTTOM LEFT).....	62
FIGURE 4.7: INFLUENCE OF INDIVIDUAL PREDICTOR VARIABLES ON RESPONSE VARIABLE OF SPECIES RICHNESS OF INVERTEBRATE CONSUMERS, INCLUDING THE COMBINED VARIABLE OF 'TURB1 AND TURB2' AND THE VISIBILITY ANOMALY 'VISANOM". THE Y-AXIS OF "FITTED FUNCTION' HOLDS ALL OTHER VARIABLES CONSTANT AND PREDICTS FOR A RANGE OF VALUES OF THE ONE VARIABLE AGAINST THE RESPONSE VARIABLE 'SPECIES RICHNESS OF INVERTIVORES'. ....	63
FIGURE 4.8: GEOGRAPHIC MAP OF PREDICTED DISTRIBUTION OF NEW ZEALAND ROCKY REEF FISH INVERTIVORE SPECIES. KEY INDICATES HOW MANY INVERTIVORE SPECIES PREDICTED TO BE FOUND IN EACH REGION/AREA. INSETS SHOW THE KERMADEC ISLANDS (TOP LEFT) AND CHATHAM ISLANDS (BOTTOM LEFT).....	65
FIGURE 4.9: INFLUENCE OF INDIVIDUAL PREDICTOR VARIABLES ON RESPONSE VARIABLE OF SPECIES RICHNESS OF PISCIVORE/BENTHIC INVERTIVORES, INCLUDING THE COMBINED VARIABLE OF 'TURB 1 AND TURB 2' AND THE VISIBILITY ANOMALY 'VISANOM". THE Y-AXIS OF "FITTED FUNCTION' HOLDS ALL OTHER VARIABLES CONSTANT AND PREDICTS FOR A RANGE OF VALUES OF THE ONE VARIABLE AGAINST THE RESPONSE VARIABLE 'SPECIES RICHNESS OF PISCIVORE/BENTHIC INVERTIVORES'. ....	67
FIGURE 4.10: GEOGRAPHIC MAP OF PREDICTED DISTRIBUTION OF NEW ZEALAND ROCKY REEF FISH SPECIES THAT CONSUME FISH AND BENTHIC INVERTEBRATES. KEY INDICATES HOW MANY PISCIVORE/BENTHIC INVERTIVORE SPECIES ARE PREDICTED TO BE FOUND IN EACH REGION/AREA. INSETS SHOW THE KERMADEC ISLANDS (TOP LEFT) AND CHATHAM ISLANDS (BOTTOM LEFT). ....	68
FIGURE 4.11: FUNNEL PLOTS OF AVERAGE DIET DIVERSITY OF THE FOOD-ITEMS CONSUMED BY FISH SPECIES FOUND AT EACH SITE IN RELATION TO THE NUMBER OF FISH SPECIES FOUND AT EACH SITE INCLUDING A 95% CONTOUR. ....	69
FIGURE 4.12: FUNNEL PLOTS OF VARIATION IN DIET DIVERSITY (SQUARE-ROOTED) OF THE FOOD-ITEMS CONSUMED BY FISH SPECIES FOUND AT EACH SITE IN RELATION TO THE NUMBER OF FISH SPECIES FOUND AT EACH SITE INCLUDING A 95% CONTOUR. ....	70
FIGURE 5.1: PAIRS PLOTS OF THE CORRELATIONS BETWEEN AVERAGE TAXONOMIC DISTINCTNESS, VARIATION IN TAXONOMIC	

DISTINCTNESS, SPECIES RICHNESS, AVERAGE DIET DIVERSITY AND VARIATION IN DIET DIVERSITY ACROSS 467 SITES IN NEW ZEALAND. .... 79

LIST OF TABLES

TABLE 2.1 LIST OF THE ORIGINAL 15 VARIABLES AND THEIR UNITS IN THREE CATEGORIES OFFERED TO THE MODEL. ‘TURB1’ AND ‘TURB2’ WERE OBTAINED BY COMBINING ‘CHLA2’, ‘LOGSUSPARTMAT’ & ‘LOGDISORGM’ TO CREATE A PRINCIPAL COMPONENT ANALYSIS OF TURBIDITY, WHICH WAS LINEARLY RELATED TO ‘VIS’. A LINEAR MODEL PREDICTING VISIBILITY USING TURBIDITY WAS THEN BUILT. ‘VISANOM’ WAS TAKEN AS THE RESIDUALS FROM THIS MODEL, AND REPRESENTS THE DIFFERENCE IN VISIBILITY ON EACH DIVE RELATIVE TO WHAT WAS EXPECTED FOR THAT GEOGRAPHICAL LOCATION. .... 22

# Chapter 1

## General Introduction

### *1.1 Biodiversity gradients*

Patterns and gradients in biodiversity have interested ecologists for centuries. As early as the 1840's renowned explorer Alfred Wallace (1853) noted greater abundances and diversities of many taxa (especially Lepidoptera) in tropical, equatorial regions compared to temperate England. A few pervasive gradients have been identified (such as latitude, altitude, depth) which are also influenced by contributing processes such as energy/resources, temperature and isolation (Hildebrand, 2004a; Gaston, 1996). The drivers of biodiversity gradients are the product of a wide range of mechanisms at both broad and fine spatial scales.

Understanding species distributions in relation to environmental processes (in addition to inter- and intra-species interactions) enables researchers to identify crucial species specific drivers that proportionally influence large and fine scale biodiversity gradients and therefore, overall species richness. Underlying causative mechanisms of broad, global patterns of species richness may not always be the contributing processes that drive finer scale regional or local patterns of species richness. For example, farmland bird assemblages across Europe differ geographically more so than as a result of local agricultural intensification, however, farm size and yield also influence habitat availability and quality, and as a result, taxonomic diversity of farmland bird assemblages (Guerrero et al, 2011). Studies at local spatial scales reveal patterns of biodiversity that are not always immediately apparent. At higher resolutions, biodiversity patterns become more complex with geographic, a/biotic and local environmental variables seemingly more influential compared to broader global scales. At finer spatial scales, the need for comprehensive data-rich resources to facilitate quantitative analysis of multiple variables becomes apparent.

## *1.2 Predictors of biodiversity*

Early ecologists realised morphology and traits influenced species interactions with the environment and other species in expected and measurable ways. In the 'Origin of species' (1869), Darwin notes a dichotomy inherent in ecology. Species that are closely related and have a shared ancestry should be ecologically similar, requiring similar habitats thus driving co-occurrence. However, closely related species that are ecologically similar should also be strongly competitive for habitat and resources (limiting co-occurrence). Therefore, phenotypical similarities and differences among species that share environmental requirements will determine species interactions driving environmental niches and resource partitioning (Chase & Leibold, 2003; Cavender-Bares et al, 2009).

The most speciose vertebrate group on the planet are fishes and fish populations have been used to model, analyse and understand broad-scale patterns in diversity (Oberdorff et al, 1995). Geographically, New Zealand (NZ) is an isolated, temperate region made up of multiple island formations covering an extensive latitudinal gradient. MacArthur and Wilsons, (1967) seminal 'Theory of Island Biogeography' discusses the fundamental processes (dispersal, invasion, competition, adaptation and extinction) behind why regions such as NZ produce unique flora and fauna. These ecological processes operate across geological and global scales down to regional and local scales. In NZ, fish assemblages have been well studied at national and regional scales (Francis, 1996; Anderson and Millar, 2004; Russell, 1983) and reef fish species richness (in both hemispheres) has been shown to follow a latitudinal gradient from high in the tropics, declining towards the poles (Rohde, 1992; Floeter et al, 2004) although, other ecological processes can influence species distribution or deviations from this overall pattern. By employing alternative indices of diversity, I can understand other mechanisms that can affect species richness, particularly at smaller spatial scales, especially in isolated regions or areas that are particularly environmentally heterogenic (Thiollay, 1990; Ricklefs, 1987).

## *1.3 Indices of diversity*

Commonly, I measured diversity using the index of species richness (see Glossary), however, other indices of diversity can incorporate additional information to give a more detailed picture of diversity. These indices can better describe inter- and intra-species

relationships and ecological function with regards to taxonomic (phylogenetic) diversity (Vane-Wright et al, 1991) and functional traits (Diaz and Cabido, 2001) as well as quantifying disparities between indices of diversity or analysing combinations of indices (Webb et al, 2002). Quantifying diversity only in terms of species richness leads to complications when research has not been standardised by sampling effort or number of individuals collected (Gotelli and Colwell, 2001). By considering multiple indices of diversity, I can reveal underlying relationships that provide a more nuanced understanding into the many contributing mechanisms of species diversity.

#### *1.4 Glossary of Indices*

Throughout this thesis I analysed the data using five different diversity indices. Species richness, average taxonomic distinctness, and variation in taxonomic distinctness are all well-known and commonly utilised measurements of species diversity. I devised the indices of 'average diet diversity' and 'variation in diet diversity' by using the consumed food items hierarchy in place of the fish species phylogeny for the TAXDTEST in PRIMER v7. This food-item hierarchy clusters scavengers closer to piscivores, piscivores close to invertebrates and algae consumers on its own branch. These diet indices describe the relatedness of a pair of species found at a site in terms of the food items they consume.

Species richness - the number of species recorded in a sampling unit) (Spellerberg, 1991; Spellerberg and Fedor, 2003; Shannon, 1949).

Average taxonomic distinctness - measures how taxonomically diverse an assemblage is, by taking the average of the distances through the taxonomic tree across each pair of species found in a sampling unit. Because it is an average, it is generally unrelated to species richness. Markedly less sample-size dependent than other common diversity measures such as species richness and evenness. The 'distinctness weight' given to taxa across the full range, the path length linking pairs of species in the hierarchy, then taxonomic diversity of taxa is defined as all species in different phyla simply as the average (weighted) path length between a pair of individuals (Warwick & Clarke, 1995), or the average path-length between two species.

Variation in taxonomic distinctness - measure purely of taxonomic distinctness, without the contribution from species diversity, which is the mean path length through the taxonomic tree connecting every pair of species in the list, variance of these pairwise path lengths and reflects the unevenness of the taxonomic tree (Clarke & Warwick, 2001)

Average diet diversity – A new index of diversity in diet based on weighted hierarchy of food items between pairs of species calculated with the analysis of ‘average taxonomic distinctness’.

Variation in diet diversity – A new index of variation or unevenness/evenness of species based on the hierarchy of diet items consumed by individual species calculated with the analysis of ‘average taxonomic distinctness’ and ‘variation in’ taxonomic distinctness.

## **Thesis overview**

In this thesis, I address the following ideas using the coastal rocky reef fishes of New Zealand, using data on observed fish species over an 18-year period (Nov 1986-Dec 2004) during 467 SCUBA dives (Smith et al, 2013). Although 212 species were observed, only 158 species were retained in the final data set; species that were pelagic, cryptic or soft-sediment dwellers were excluded because they were not consistently recorded (Smith et al., 2013).

Three categories of predictor variables were available for the model: environmental, geographic, and dive-specific (13 were retained). The environmental and geographic variables were developed as part of the New Zealand Marine Environment Classification (NZMEC). The NZMEC provides environmental and geographical frameworks using several spatial data layers that describe the physical environment (Snelder et al., 2005).

### ***1.6 Spatial patterns of species and taxonomic diversity of New Zealand rocky reef fishes***

Chapter 2 models diversity of rocky reef fish using the indices of species richness, average taxonomic distinctness, and variation in taxonomic distinctness. I hypothesised that the latitudinal gradient of decreasing reef fish species-richness from north to south will

be reflected in relationships with environmental variables associated with this gradient. Additionally, I tested whether the latitudinal gradient is also reflected in the indices of taxonomic diversity, with high taxonomic distinctness of phyla in low latitudes decreasing with higher latitudes. I aimed to quantify whether species-rich regions contain many taxonomically distinct species or many species that are closely related. I also examined whether distinct taxa followed a latitudinal gradient (with decreasing diversity from the tropics to the poles), or are lost resulting in only closely related species in species-poor regions. Much research has been collated on species distributions of NZ rocky reef fish utilising various methodologies, including trawling and underwater visual census (Francis, 1996; Russell, 1983). Francis, (1996) looked at regional species lists on a nationwide scale while Anderson and Millar, (2004) provided quantitative research of species richness and taxonomic diversity of NZ reef fish to the nor-eastern climes. I wanted to provide a fine resolution, nation-wide quantitative analysis of diversity that included not only a traditional species richness index of diversity but also implemented phylogenetic analysis to employ multiple indices of diversity. By including a multi-index approach to biodiversity, I hoped to garner a broader understanding of species richness at both a national and local spatial scale that would explain gradients of diversity in terms of not only traditional latitudinal environmental gradients, but also by reference to environmental variables that drive diversity at finer spatial scales. To enable this, I modelled multiple indices of diversity which explained deviance within these multiple diversity indices. Areas such as the outer Marlborough Sound and Fiordland have predicted greater than expected taxonomic diversity based on environmental variables. The models predicted that water temperature, turbidity, exposure and salinity to be the most influential variables, suggesting local and regional processes, habitat heterogeneity and potentially food resources as important in driving patterns in species diversity.

### *1.7 Quantitative classification of New Zealand rocky reef fishes into diet guilds*

Chapter 3 examines the variation in the food items consumed by the study species. I aimed to provide a new objective method for categorising groups of reef fishes based on similarities in their diet. Data on the presence and absence of a nine broad food item

categories in the diets of NZ rocky reef fish species were sourced from the literature and clustered hierarchically based on their similarities. Our SIMPROF analysis yielded eight homogenous diet guilds across multiple species based on the similarity of food items consumed. Research of diet in NZ rocky reef fish has previously focused on expert opinion (Francis, 1996; Anderson and Millar, 2004; Russell, 1983; Thompson; 1981) with diet data collected by either under-water visual census or biological sampling of stomach contents. These methodologies are time consuming, costly and taxonomically based. By using a purely quantitative, *posteriori* analysis of diet to understand resource partitioning of NZ temperate reef systems based on diet similarities that could then be used to further understand the food resources requirements of New Zealand's rocky reef fishes.

#### *1.8 Regional and local processes as drivers of diet diversity in New Zealand rocky reef fish species*

Chapter 4 uses the data frame of food items utilised by fish species to further understand the distribution of fish assemblages on New Zealand's rocky reefs and the role that local food resources may have in shaping patterns of species richness. I expected some guilds (e.g. piscivores), to be more strongly associated with environmental variables than others. In these cases, I expected that spatial patterns of species richness for these guilds would be reflected by spatial patterns in food item diversity. In contrast, I expected that some guilds, such as the herbivores, to be limited directly by environmental factors, such as a minimum critical temperature they require for metabolism as well as the defined environmental limitations of a kelp habitat and primary food resources (kelp intolerance to low salinity and low temperature). Overall, I found that the two of the three diet guilds (herbivores, invertivores) studied here reflected a strong latitudinal gradient in species richness with the piscivore/benthic invertivores to a far lesser degree. I employed a new analysis of diet diversity based on taxonomic distinctness, variation in taxonomic distinctness (Clarke and Warwick, 2008). By modelling overall diet diversity and variation of diet diversity of assemblages found at each site, I predicted fish assemblages with higher than expected diversity of diets in the regions of the Kermadec Islands and Poor Knights Islands. I also found substantial unevenness of diet diversity in the Hauraki Gulf with much

lower than expected diet diversity by species habituating the area. Turbidity, salinity and temperature were environmental variables that were most strongly correlated to diet diversity.

### *1.8 General Discussion*

In Chapter 5, I review the major findings of each chapter and synthesise the results. I discuss the emergent findings of my research in the context of the broader literature and offer some future direction for studies on rocky reef fishes in New Zealand and species richness patterns more generally.

## Chapter 2

# Spatial patterns of species and taxonomic diversity of New Zealand rocky reef fishes

Odette Howarth  
Massey University, Auckland

---

### 2.1 Introduction

Understanding the patterns and drivers of biodiversity is fundamental to ecology. Several environmental and geographic gradients exist in species diversity. Latitudinally, from the equator to the poles, a decrease in the number of species has been found in a range of taxa (e.g., Willig et al, 2003; Hillebrand, 2004a). This latitudinal gradient is hypothesised to be driven by a number of different factors, such as isolation, island geography, temperature and resources (MacArthur & Wilson, 1967; Hillebrand, 2004a&b; Ricklefs, 2004). These patterns are well documented on a broad global, spatial scale (tropical vs temperate regions); however, on a finer regional or local resolution these patterns or gradients of diversity may not be so well recorded or understood (Hillebrand, 2004a&b). By focusing on regional scales and processes (environmental niches, habitat heterogeneity and anthropogenic impacts) I can assess the proximate environmental causes of species richness which may inform the ultimate drivers and conditions (such as evolutionary duration and diversification) contributing to diverse species assemblages (Dobzhansky, 1950; Willig et al, 2003; Mittelbach et al, 2007).

Species diversity is commonly measured by species richness—the number of species observed in a sample. Richness is an important and intuitive index of diversity; however, there are many other aspects of diversity that are not captured by this index (Warwick and Clarke 1995, 2001). For example, species richness ignores the phylogenetic relationships among species; yet, a set of closely-related species can be considered less diverse than the same number of distantly-related species (Clarke and Warwick, 2001). Several measures have been developed to quantify phylogenetic diversity. The average taxonomic distinctness (AveTD) of a list of species observed in a sample may be calculated as the average phylogenetic or taxonomic relatedness of every pair of species present within a

sample (Warwick and Clarke, 1995, 2001; Clarke and Warwick, 1998; Tolimeri and Anderson, 2010). AveTD is useful over large spatial scales as heterogeneity of habitat can influence patterns of biodiversity (Thiollay, 1990). Another index of diversity is 'variation in taxonomic distinctness' (VarTD). This measure is complementary to AveTD, it reflects the taxonomically 'unevenness' of an assemblage (Clarke and Warwick, 2001) in terms of the distribution of species, whether there is a large variation in the number of species within higher taxonomic units, or whether species are similarly dispersed across multiple taxa. Both these indices are robust to having different numbers of species or varying effort across the sampling units, so they can be considered as complementary to species richness (Clarke and Warwick, 2001). Relatively few studies have examined spatial patterns in taxonomic indices of diversity, and how they relate to the environmental gradients that have been observed for species richness (Gray, 2002). Warwick and Clarke, (2001) found significant negative relationships with turbidity/anthropogenic disturbance with the taxonomic indices of AveTD and VarTD while salinity and depth showed positive correlations particularly with AveTD (Zintzen et al, 2011; Mouillot et al, 2005).

Fishes are ideal taxa for research on diversity as they are conspicuous, exploited and well known taxonomically (Stuart-Smith et al., 2013). Previous studies of fish biogeography across NZ have been completed at only very broad, regional scales (Francis, 1996; Russell, 1998; Leathwick et al, 2006). The rocky reef fauna includes tropical, subtropical and temperate species, reflecting NZ's broad latitudinal range, with diversity generally declining with increasing latitude (Stuart-Smith et al., 2013; Floeter et al., 2005).

Here, I developed predictive models of the diversity of fishes in shallow, subtidal, rocky reef habitats around coastal NZ using a range of environmental and geographic variables at a fine, 1km scale. In addition to 'species richness', I have modelled 'average taxonomic distinctness' and 'variation in taxonomic distinctness' to predict geographic distributions and patterns of phylogenetic diversity.

Specifically, I aim to:

- Build predictive models of reef fish diversity using environmental and geographic variables, and examine which variables are most correlated with reef fish diversity;
- Compare the relationships between environmental/geographic variables and diversity among the three indices.

## 2.2 Materials and Methods

### *Collection of data and predictor variables*

Presence/absence data on observed fish species were collected over an 18-year period (Nov 1986-Dec 2004) during 467 SCUBA dives (Figure 1) around the coast of New Zealand (median maximum depth of 17m and median length of dive 46 minutes) (Smith et al., 2013). Although 212 species were observed, only 158 species were retained in the final data set; species that were pelagic, cryptic or soft-sediment dwellers were excluded because they were not consistently recorded (Smith et al., 2013).

Three categories of predictor variables were available for the model: environmental, geographic, and dive-specific (15 predictor variables in total; see Table 1). The environmental and geographic variables were developed as part of the New Zealand Marine Environment Classification (NZMEC) and obtained as GIS raster layers. The NZMEC is a hierarchical spatial classification of NZ's Estuary Environment Classification (EEC). During the project, several spatial environmental variables were developed, which I used here as predictor variables to model a range of diversity measures for rocky reef fishes.

The dive specific variables were included to control for differences in the scope and duration of the surveys, but were assigned standardised values for prediction. Three environmental variables relating to turbidity—namely, 'chl<sub>a</sub>2', 'suspended particulate matter' and 'dissolved organic matter'—were found to be highly correlated. This was addressed by doing a Principal Component Analysis (PCA) of these variables. The first and second axes from this PCA (named 'turb1' and 'turb2', respectively) were used as predictors instead of the original variables. The dive-specific variable 'visibility' was also related to

turbidity. I fitted a linear regression of visibility on turb1; the residuals of this regression were taken as a new variable 'visanom' (visibility anomaly), representing the difference in visibility on each dive relative to what was expected given the turbidity at that geographical location. Average fetch was calculated as the average distance to land in all directions and was used here as a proxy for wave exposure (Smith et al., 2013). As Smith et al., (2013) describes, average fetch was "calculated using the method developed by E. Villouta and R. Pickard (described by Fletcher et al. 2005), where the distance to land was measured along 36 radial lines radiating from a point at 10 degrees intervals. Where land was not encountered the lines were cropped at 10 km. Where Fletcher et al., (2005) used the sum of the distances in each direction, we instead used the average distance".

### *Species richness*

Species richness was estimated by counting the number of species observed per site.

### *Average Taxonomic Distinctness*

Average Taxonomic Distinctness (AveTD) is a measure of the average taxonomic paths or distances through a Linnean classification tree between all pairs of species in an assemblage (Warwick and Clarke, 1995). In our analysis, this included all levels from species to class. The maximum path length of 100 was between classes (the highest classification), and the lengths of the steps between each level of the tree (class to order to family to genus to species) were set to be equal (20) (Warwick and Clarke, 1995). Using PRIMER v7, I calculated AveTD (delta) for all sites dived. I used the TAXDTEST procedure in PRIMER v7 (Clarke and Gorley, 2006) to produce plots of average and variation in taxonomic distinctness of each site sampled compared to the number of species found per site, with 95% bounds made from calculating AveTD and VarTD under the null model of taking random samples of species. I then used these values to make predictions using boosted regression trees and mapped these predictions onto the New Zealand coastline.

### *Variation in Taxonomic Distinctness*

Variation in Taxonomic Distinctness (VarTD), calculated using PRIMER v7, is a diversity index based on the variability of the taxonomic relatedness across the species recorded in a sampling unit. Although complementary to AveTD, it differs in that VarTD

reflects the variance of the pairwise path lengths throughout the Linnean taxonomic tree (Clarke and Warwick, 2001). Therefore, it reflects the degree to which species are unevenly distributed through the taxonomic tree.

### *Boosted regression Tree models*

Boosted regression trees (BRTs; using the *dismo* package for R 3.4.9) were used to model the species richness (SPR), average taxonomic distinctness (AveTD) and variation in taxonomic distinctness (VarTD) of rocky reef fish assemblages. BRTs combine two algorithms to produce a large number of simple tree models fitted sequentially; or an 'ensemble' of trees (Elith, et al., 2006). At each iteration, the boosting algorithm re-weights the data set giving larger weight to poorly fitted observations yielding greater predictive power. The BRT models were fitted using a Gaussian error distribution with both species richness and variation in taxonomic distinctness square-root transformed.

To control over-fitting of the model, the number of trees was determined based on a ten-fold cross-validation (CV) procedure. The data were randomly assigned to one of ten folds. For each five new trees added to the ensemble, the CV procedure removed each fold in turn and trained a model using the remaining 90% of data. The predictive accuracy of the model was then evaluated with the withheld fold. Sites that were clustered geographically (within c. 1km) were always assigned to the same fold to ensure that models were not tested using data from the same location. Individual trees were constrained to complexity of 5 (i.e., the depth of the trees), and by a learning rate (shrinkage) of 0.002 (Elith et al., 2008).

Predictions of species richness, AveTD and VarTD of reef fishes were made using boosted regression trees. Predictions were mapped on the New Zealand coastline using the *sp* and *raster* packages in R at the 1 km scale of the original predictor variables of the New Zealand Marine Environment Classification (NZMEC). Predictions are shown only for grid cells that are known to contain rocky reef (see Smith et al. 2013 for further details). PRIMER v7 produced funnel plots of the AveTD and VarTD of each site sampled compared to the number of species found per site sorted by geographic regions.

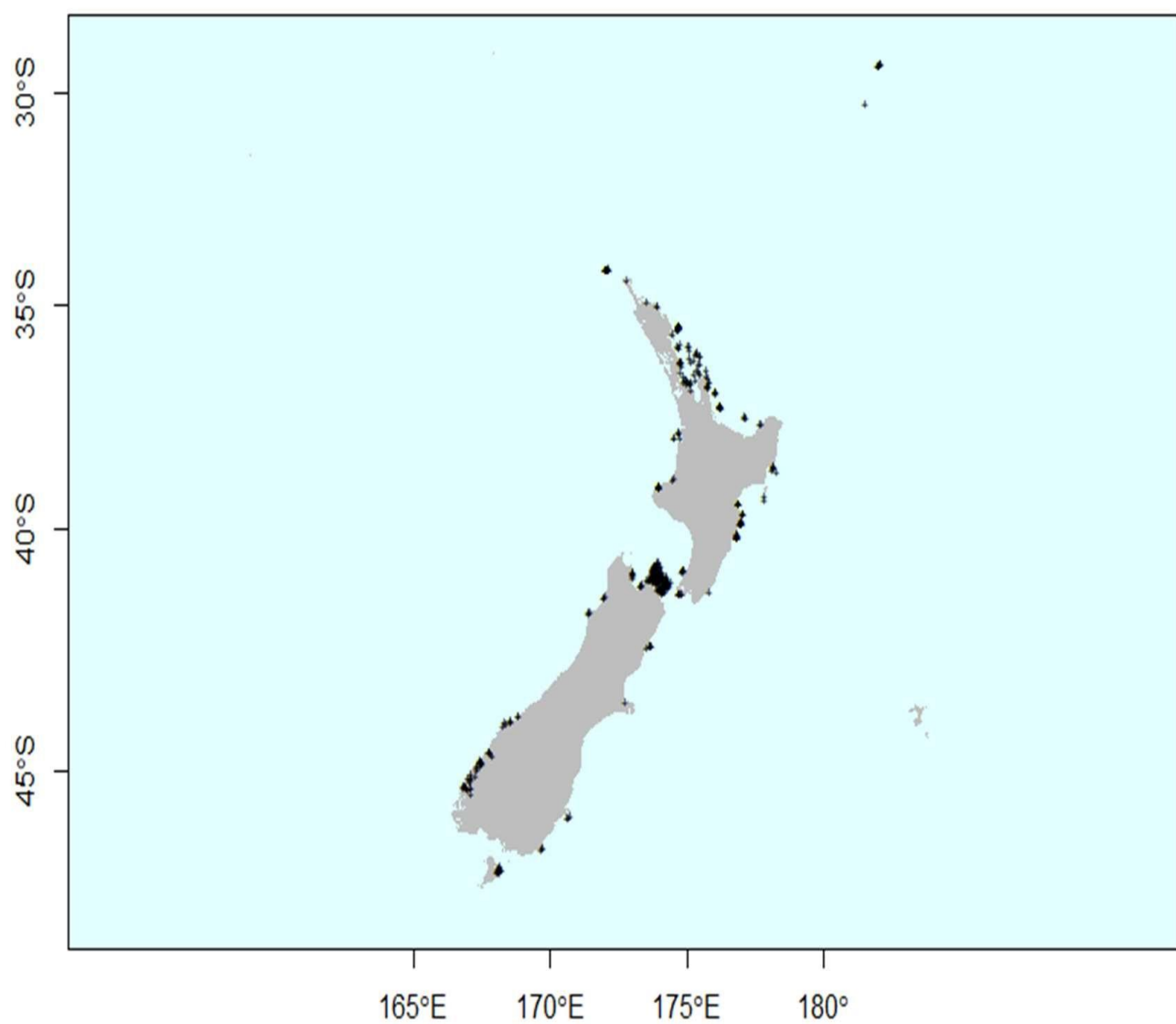


Figure 2.1 Locations of 467 dive survey sites. There were no sampling sites at any of the other island groups that are not shown here, including the Chatham Islands.

Table 2.1 List of the original 15 variables and their units in three categories offered to the model. ‘Turb1’ and ‘Turb2’ was obtained by combining ‘chla2’, ‘logsuspartmat’ & ‘logdisorgm’ to create a principal component analysis of turbidity, which was linearly related to ‘vis’. A linear model predicting visibility using turbidity was then built. ‘Visanom’ was taken as the residuals from this model, and represents the difference in visibility on each dive relative to what was expected for that geographical location.

TYPE	ABBREVIATION	EXPLANATION	UNITS
Environmental	sstwint	Wintertime sea surface temperature	°C
	seabedsal	Salinity at the sea bed	psu
	sstanamp	Annual amplitude of sea surface temperature	°C
	logdisorgm	Log of dissolved organic matter	Dimensionless
	logtidalspeed	Log of tidal speed	
	logsuspartmat	Log of suspended particulate matter	Approx. g/m3
	sstanom	Sea surface temperature anomaly	°C
	logsstgrad	Log of sea surface temperature gradient	°C/km
	chla2	Concentration of chlorophyll a	ppm
Geographic	avefetch	Average fetch	m
	dcoast	Shortest distance to land	m
Dive-specific	dmax	Maximum depth of dive	m
	dur	Duration of dive	min
	dmin	Minimum depth of dive	m
	visanom	Visibility of dive	m

## 2.3 Results

The BRT model of species richness used 1890 trees and explained 90% of the deviance for withheld data. The environmental and geographical variables collectively accounted for 84% of the explanatory power for species richness in this model (Figure 2.2 and 2.3). The most important of these variables was SSTwint (55.3%) which showed a positive relationship with SPR, with a particularly steep increase in predicted SPR between the values of 14-16°C. The second most important variable was turbidity (turb 1-PCA axis 1) (10.6%) which saw a significantly higher species richness with decreased turbidity in the water (lower levels of dissolved particulate, organic matter and chlorophyll). Average fetch or distance to land (5.4%) had a slight positive effect on SPR. With increasing salinity, a slight increase in species richness (3.5%) is observed. As ‘log tidal speed’ decreases, a small positive effect on species richness (3.1%) with a decreasing sea-surface temperature gradient slightly decreasing

species richness (2.9%). The rest of the environmental and geographic variables make up less than 4% of the deviance in the model.

The dive-specific variables accounted for 16% of the explanatory power (Figure 2.2 and 2.3). More species were found in deeper dives (6.1%), although this relationship between species richness and maximum dive depth plateaued at 40-45m. This positive relationship is also observed in the ‘duration of dive’ variable (5.2%), the longer the dive the more species I predicted I would see. If visibility on the dive was higher than expected in a geographic area I also found more species (3.6%).

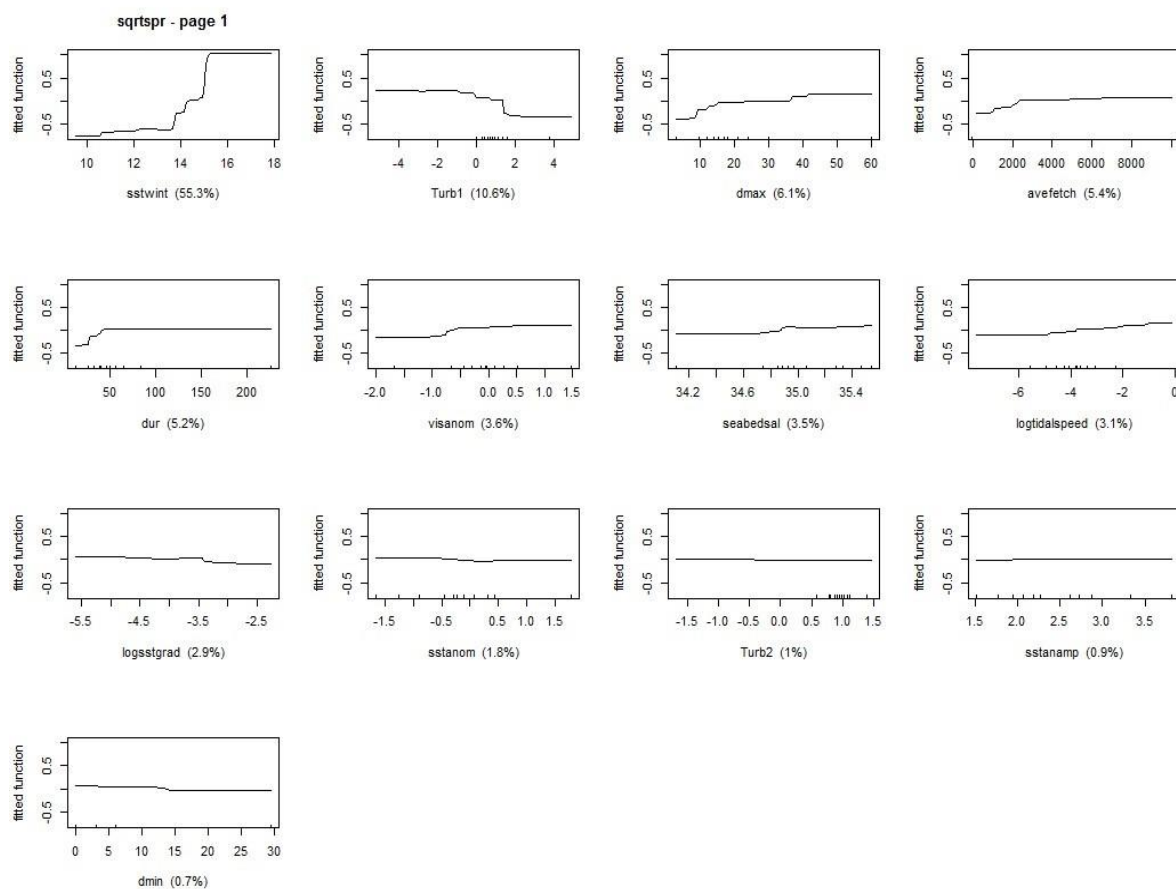


Figure 2.2: Influence of individual predictor variables on response variable of species richness, including the combined variable of ‘turb1 and turb2’ and the visibility anomaly ‘visanom’. The y axis for each plot represents the marginal effects of a particular predictor variable on the response variable. It is calculated by comparing predictions across the range of the predictor variable in question, while holding all other predictor variables constant at their median values.

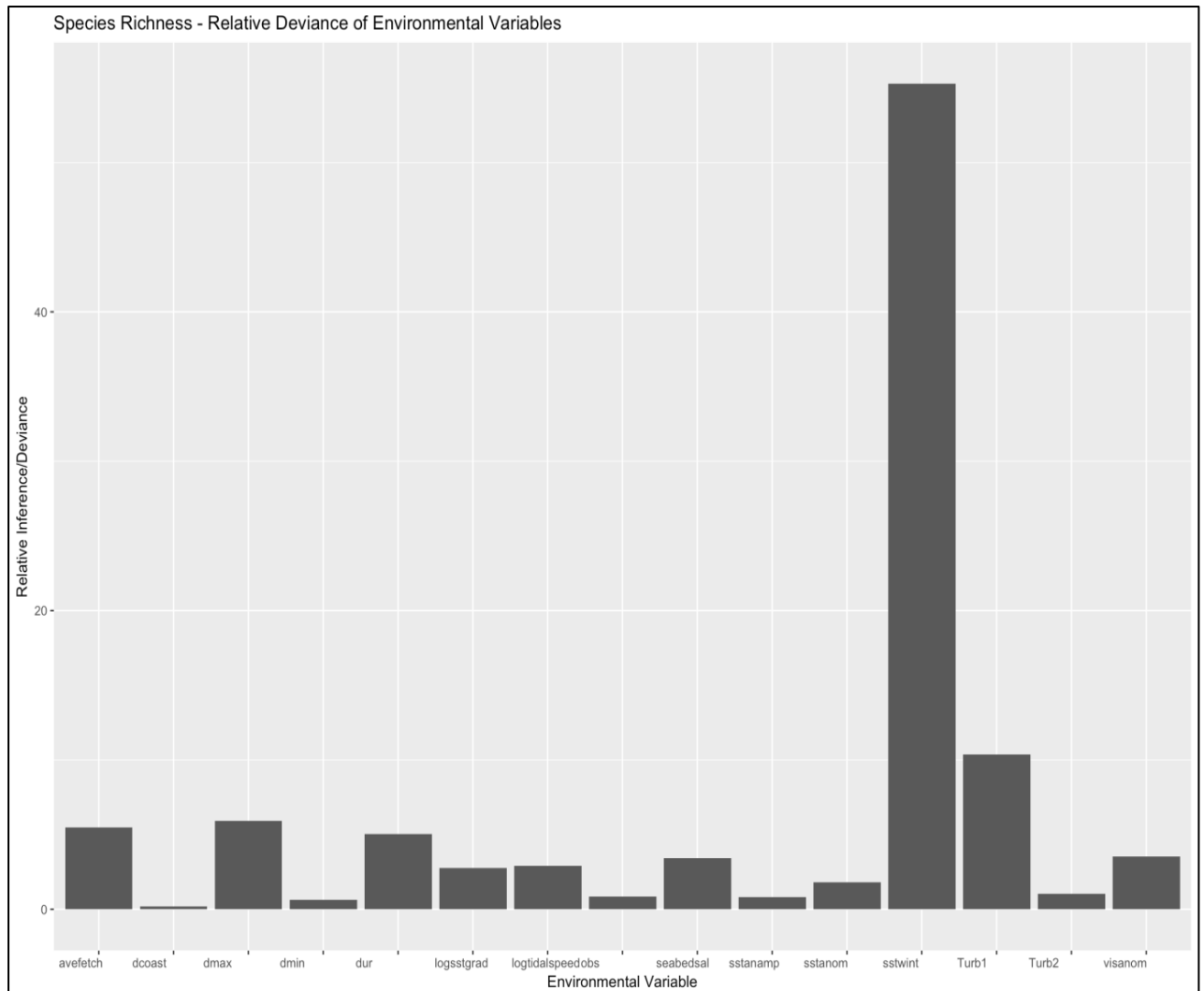


Figure 2.3: Bar plot showing relative inference of environmental, geographical and dive related variables for predicted species richness using boosted regression trees.

The model AveTD explained 70% of the deviance for withheld data were obtained by fitting 860 trees. The environmental and geographical variables collectively accounted for 81% of the explanatory power for species AveTD in this model (Figure 2.4 and 2.5). The most important of these variables was winter sea-surface temperature (34.5%) which showed a positive relationship with AveTD with a significant increase between 12-15°C (see Figure 4). The second most important variable was turbidity (turb 1 - PCA axis 1) (12.3%) with increasing turbidity decreasing the number of distinct taxa observed. Increasing salinity (10%) and exposure (7.9%) both have a noticeable positive effect on how many distinct taxa are found (exposure plateaus after 6kms from shore). Decreasing tidal speeds (7.7%) as well as decreasing water temperature gradients or variability (3.1%) saw an increase in

number of taxa predicted. The rest of the environmental and geographic variables make up less than 6% of the deviance in the model.

The dive-specific variables accounted for 19% of the explanatory power (Figure 2.4 and 2.5). Greater than expected visibility on a dive saw a higher number of distinct taxa observed. Both duration of dive and maximum depth of dive increased the predicted number of distinct taxa found, although this plateaued after 50 minutes and approximately 18-20 metres.

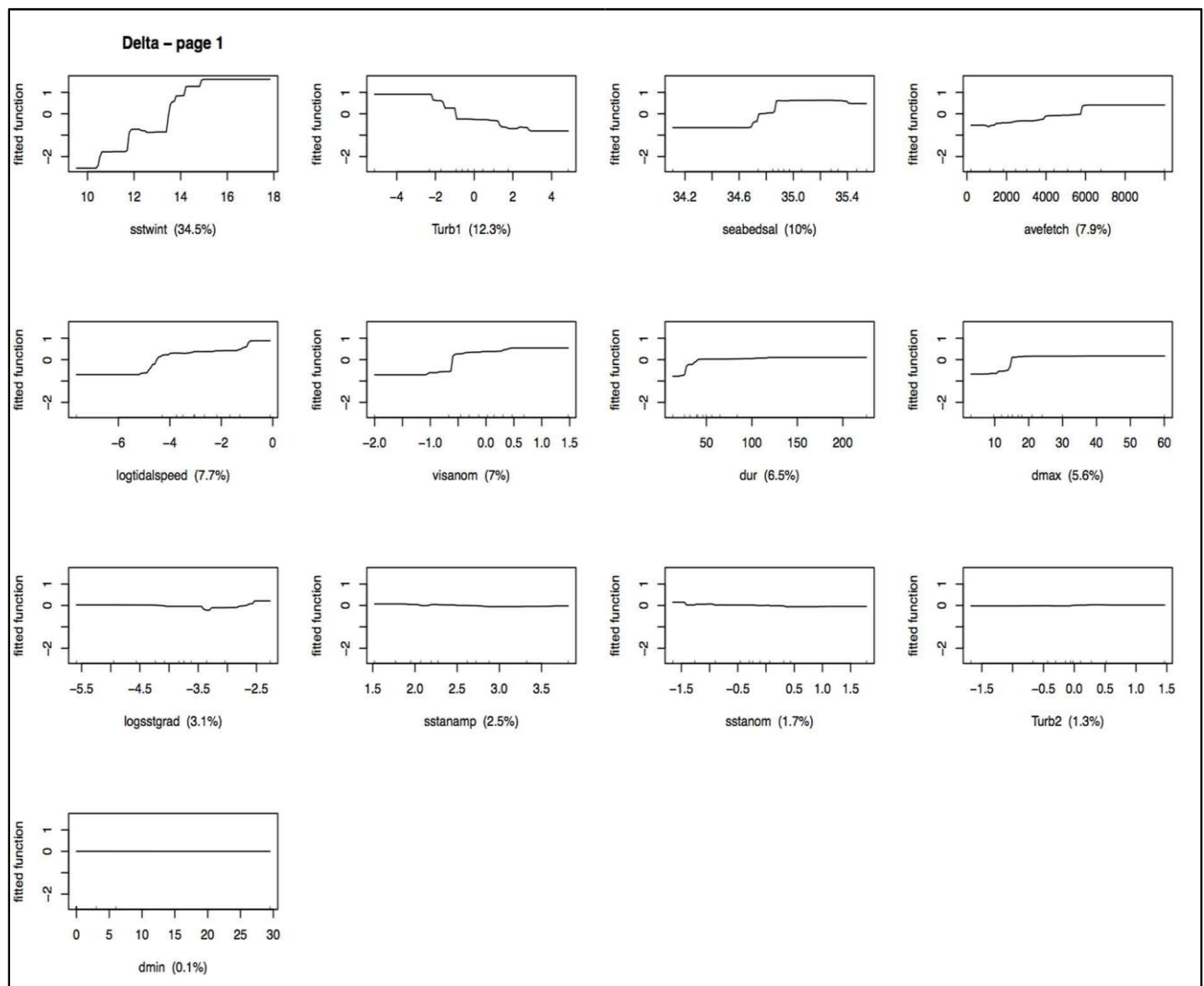


Figure 2.4: Influence of individual predictor variables on response variable of average taxonomic distinctness (Delta) including the combined variable of 'turb1 and turb2' and the visibility anomaly 'visanom'. The y axis for each plot represents the marginal effects of a particular predictor variable on the response variable. It is calculated by comparing predictions across the range of the predictor variable in question, while holding all other predictor variables constant at their median values.

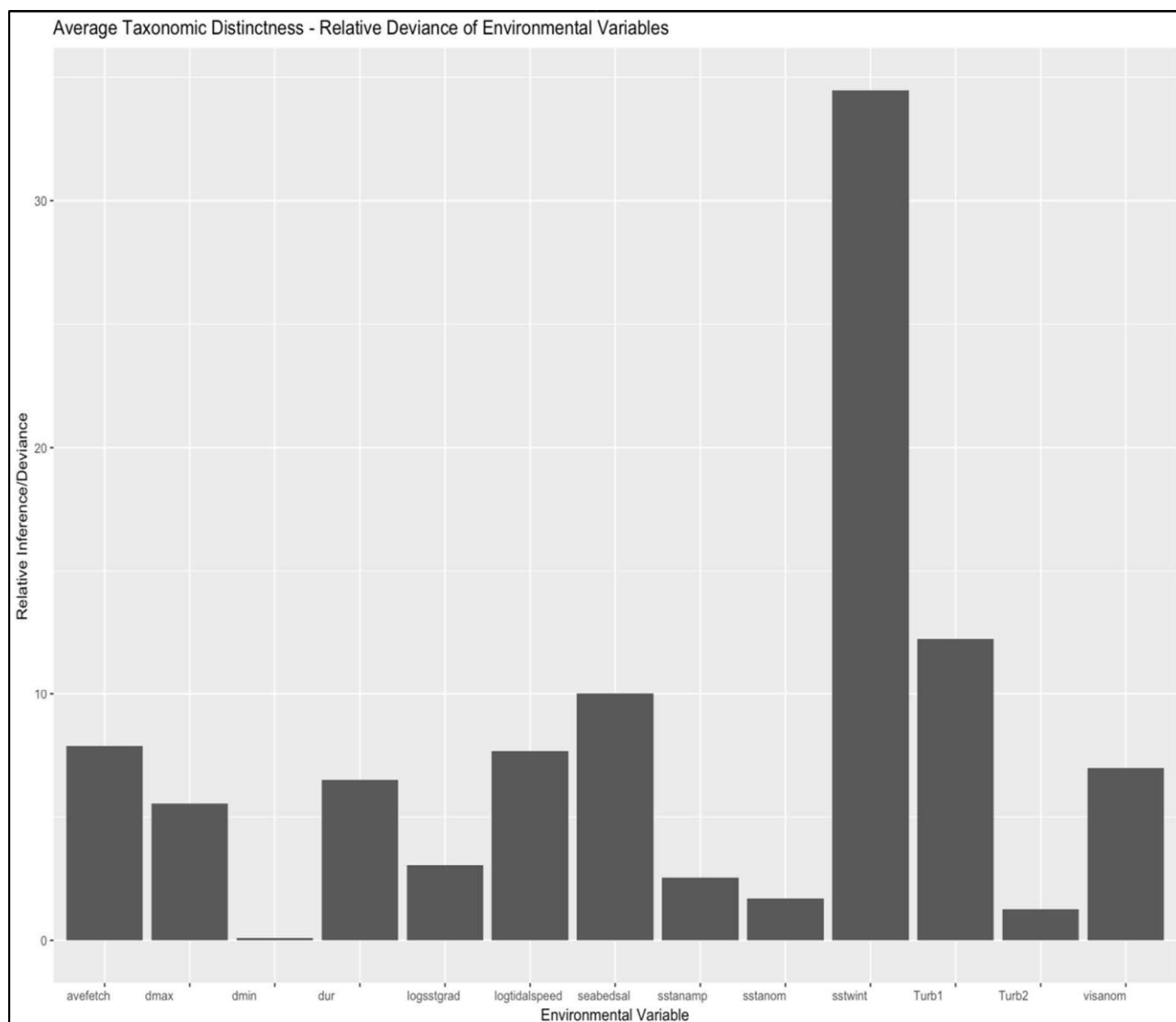


Figure 2.5: Bar plot showing relative inference of environmental, geographical and dive related variables for predicted average taxonomic distinctness using boosted regression trees.

For VarTD, the model explained 66% of the deviance for withheld data obtained by fitting 765 trees. The environmental and geographical variables collectively accounted for 90% of the explanatory power for VarTD in this model (Figure 2.6 and 2.7). The most important of these variables was reduced exposure (34.9%). I found more closely related, clustered taxa compiled the species assemblage in sheltered areas. Salinity (19.3%) was the second most important variable but the shape of the function was not linear, with an increase and then decrease in variation between 34.6 - 35.4psu. Increasing turbidity (6.7%) predicted that more closely related species would be found as well as increasing water temperature (6.6%). The shape of the function for water temperature stepped with a slight

increase of VarTD at between 10-14°C but then dropped back to previous levels. Increasing turbidity (PCA axis 1) slightly increased the clustering of the taxa found (6.7%). Areas with a high gradient in water temperature (6.4%) had relatively high VarTD. Increasing annual amplitude of water temperature (5.5%) and tidal speed (5.3%) were associated with decreases in VarTD. Increasing turbidity on PCA axis 2 (3.5%) seems to correlate positively with VarTD.

The dive-specific variables accounted for 10% of the explanatory power (Figure 2.6 and 2.7). Deeper dives increased the chance of encountering more closely related species (6.9%) although this levelled out at 15-20 metres. The other dive-specific variables combined accounted for less than 3.5% of the overall deviance within the model.

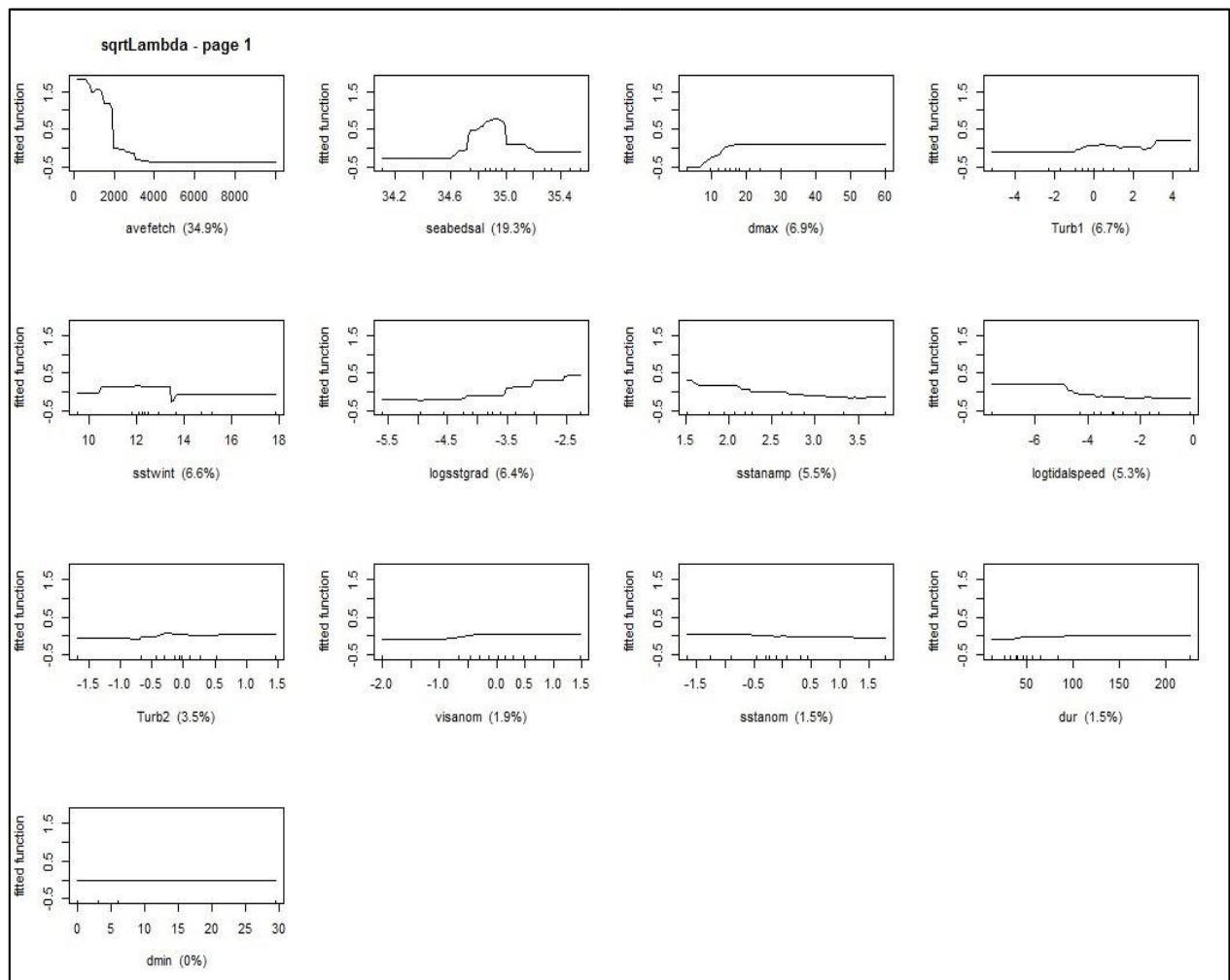


Figure 2.6: Influence of individual predictor variables on response variable of 'variation of taxonomic distinctness' (square rooted) including the combined variable of 'turb1 and turb2' and the visibility anomaly 'visanom'. The y axis for each plot represents the marginal effects of a particular predictor variable on the response variable. It is calculated by comparing predictions across the range of the predictor variable in question, while holding all other predictor variables constant at their median values.

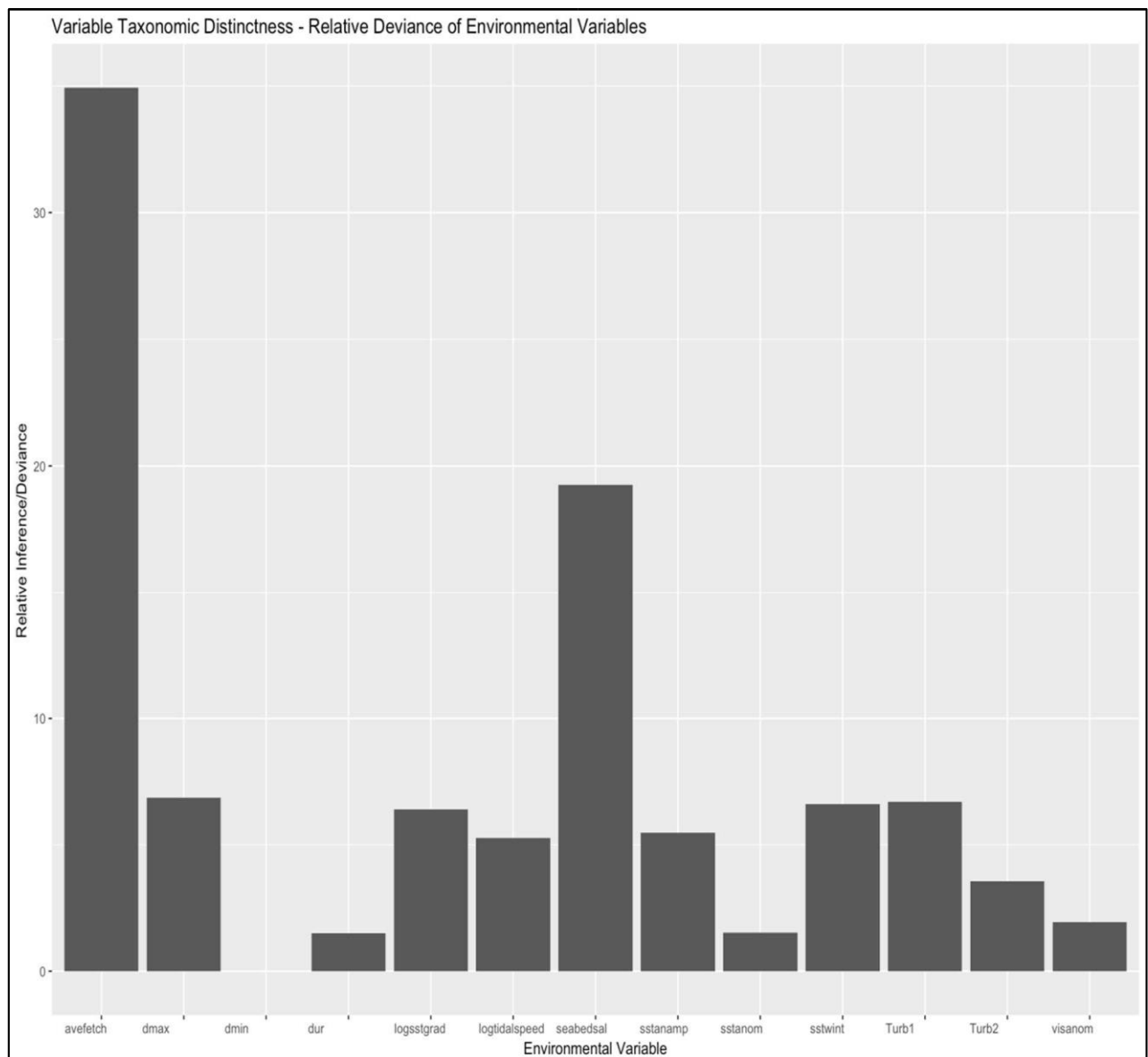


Figure 2.7: Bar plot showing relative inference of environmental, geographical and dive related variables for predicted variable taxonomic distinctness using boosted regression trees.

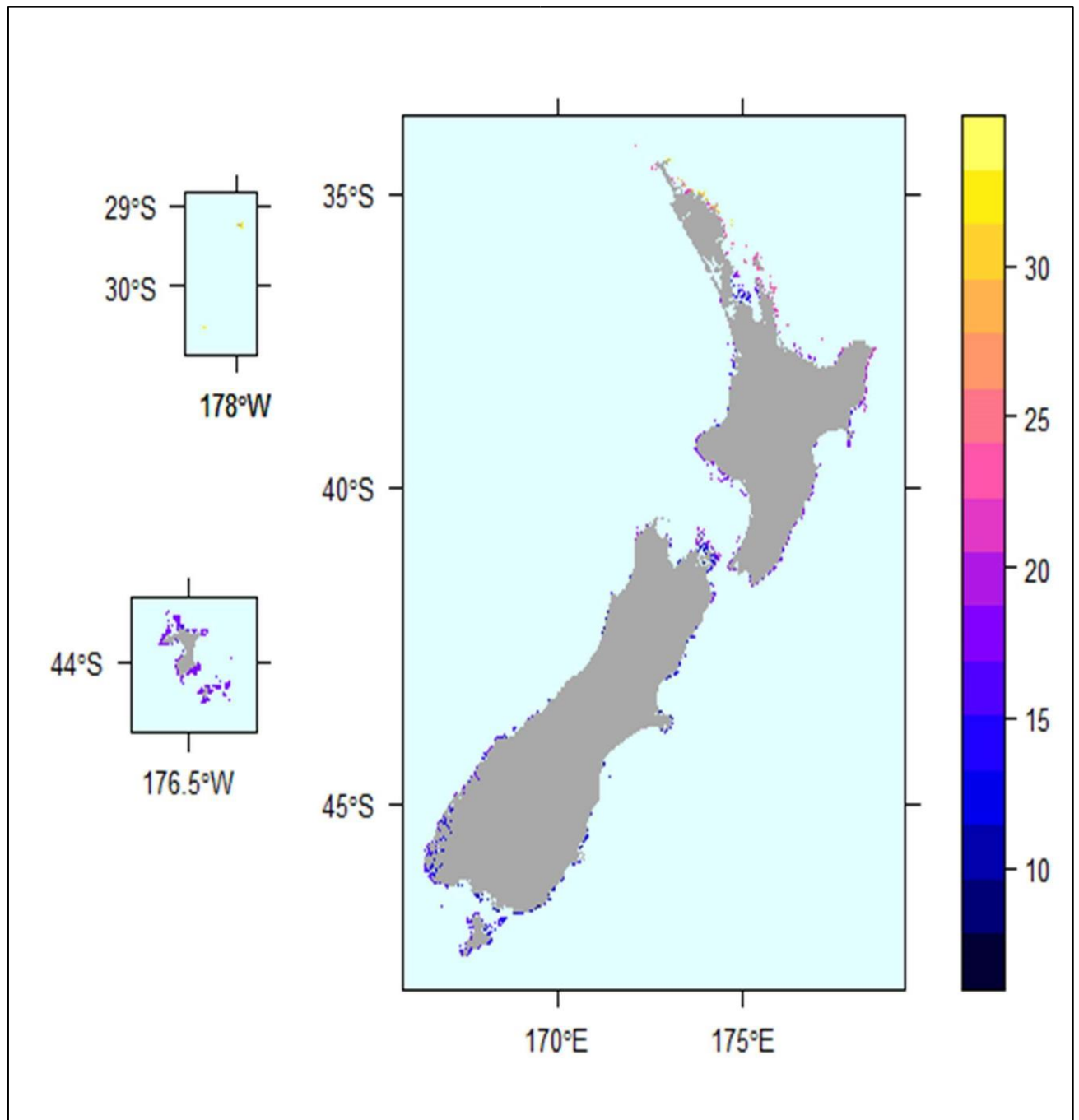


Figure 2.8: Geographic map of predicted species richness of New Zealand rocky reef fish. Key indicates number of species expected to be seen in each region/area. Insets show the Kermadec Islands (top left) and Chatham Islands (bottom left).

Figure 2.8 shows species richness predictions mapped to the NZ coastline. High species richness (30+ species) is seen in the Kermadec Islands and the north east of the North Island with decreasing species richness with increasing latitude. The Chatham Islands are predicted values from the model as no actual data was obtained from the area. The model predicted 15-20 species would be expected at the Chatham Islands.

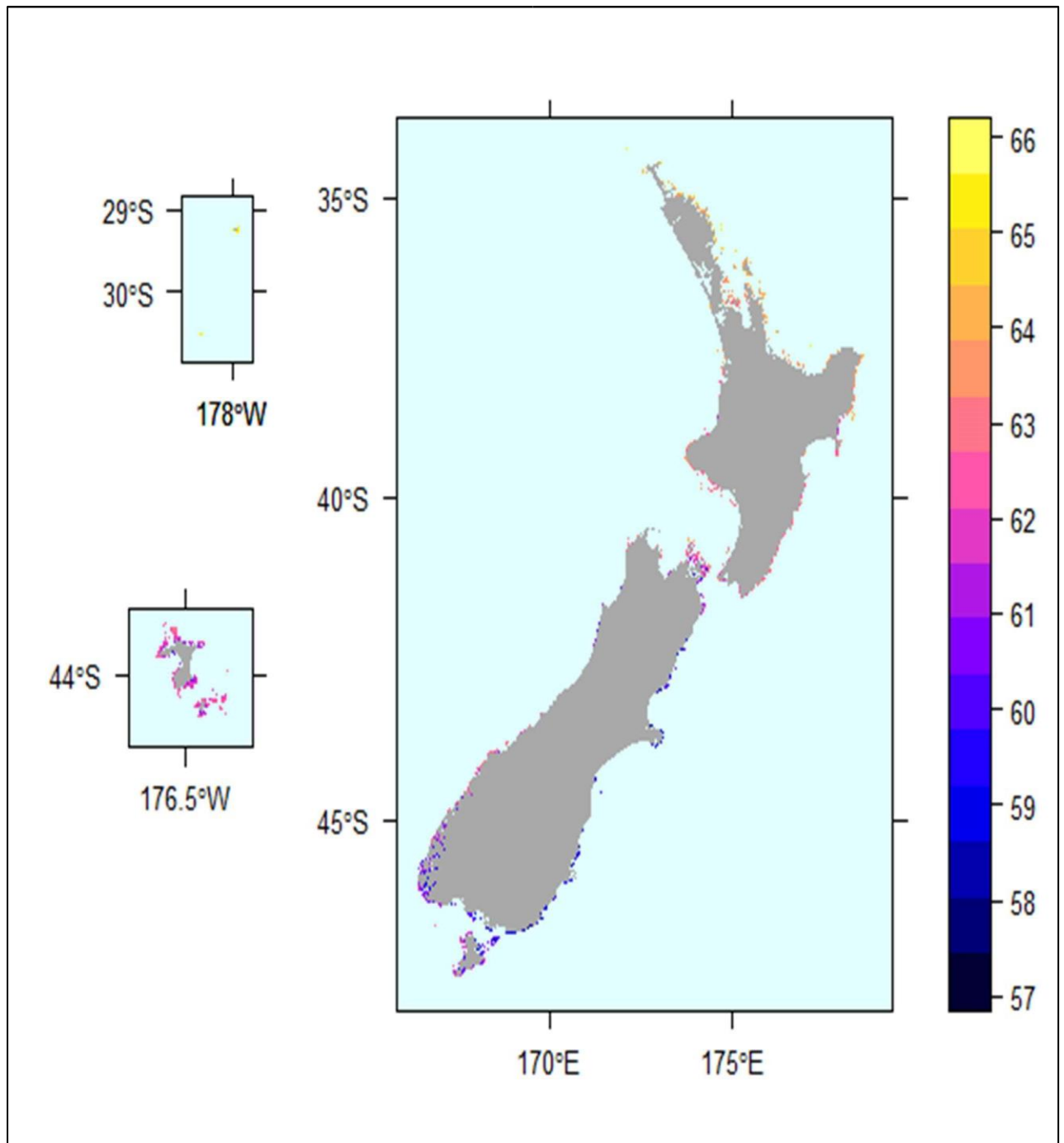


Figure 2.9: Geographic map of predicted average taxonomic distinctness of New Zealand rocky reef fish. Key indicates how taxonomically different the species in each region/area are by averaging the path lengths through a taxonomic tree. Insets show the Kermadec Islands (top left) and Chatham Islands (bottom left).

Figure 2.9 shows average taxonomic distinctness predictions mapped to the NZ coastline. High average taxonomic distinctness (mean path length longer than 65) is seen in the Kermadec Islands and the north east of the North Island. A decreasing AveTD with an

increasing latitudinal gradient is not particularly delineated. The Chatham Islands are again predicted values from the model with AveTD path lengths around 62-63.

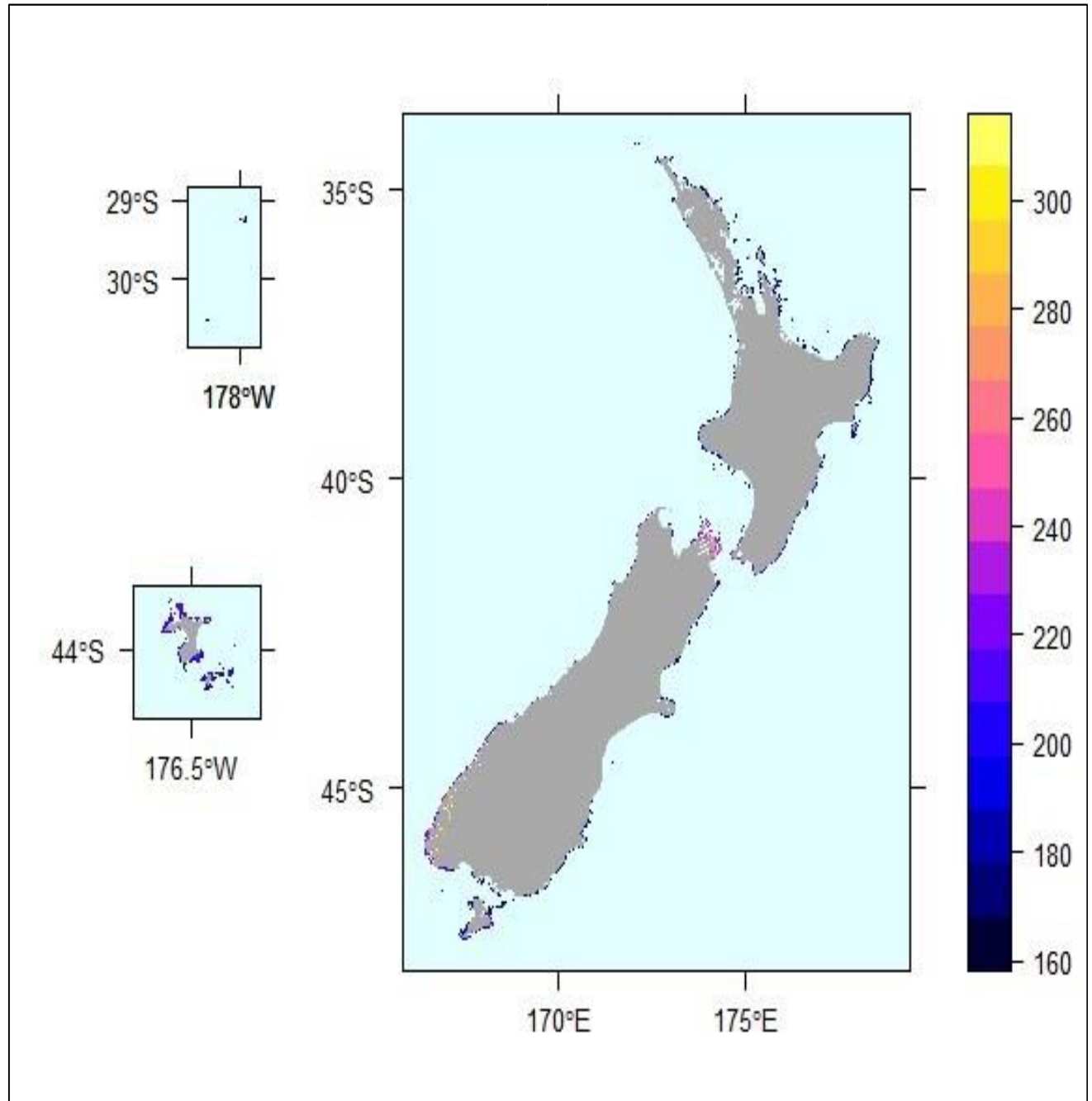


Figure 2.10: Geographic map of predicted variation in taxonomic distinctness of New Zealand rocky reef fish. Key indicates how variable the taxa in each region/area are. Insets show the Kermadec Islands (top left) and Chatham Islands (bottom left).

Figure 2.10 shows variable taxonomic distinctness predictions mapped to the NZ coastline. High variation in taxonomic distinctness (yellow) is seen in Fiordland and Outer

Marlborough Sounds. The Chatham Islands are again predicted values with rather low VarTD.

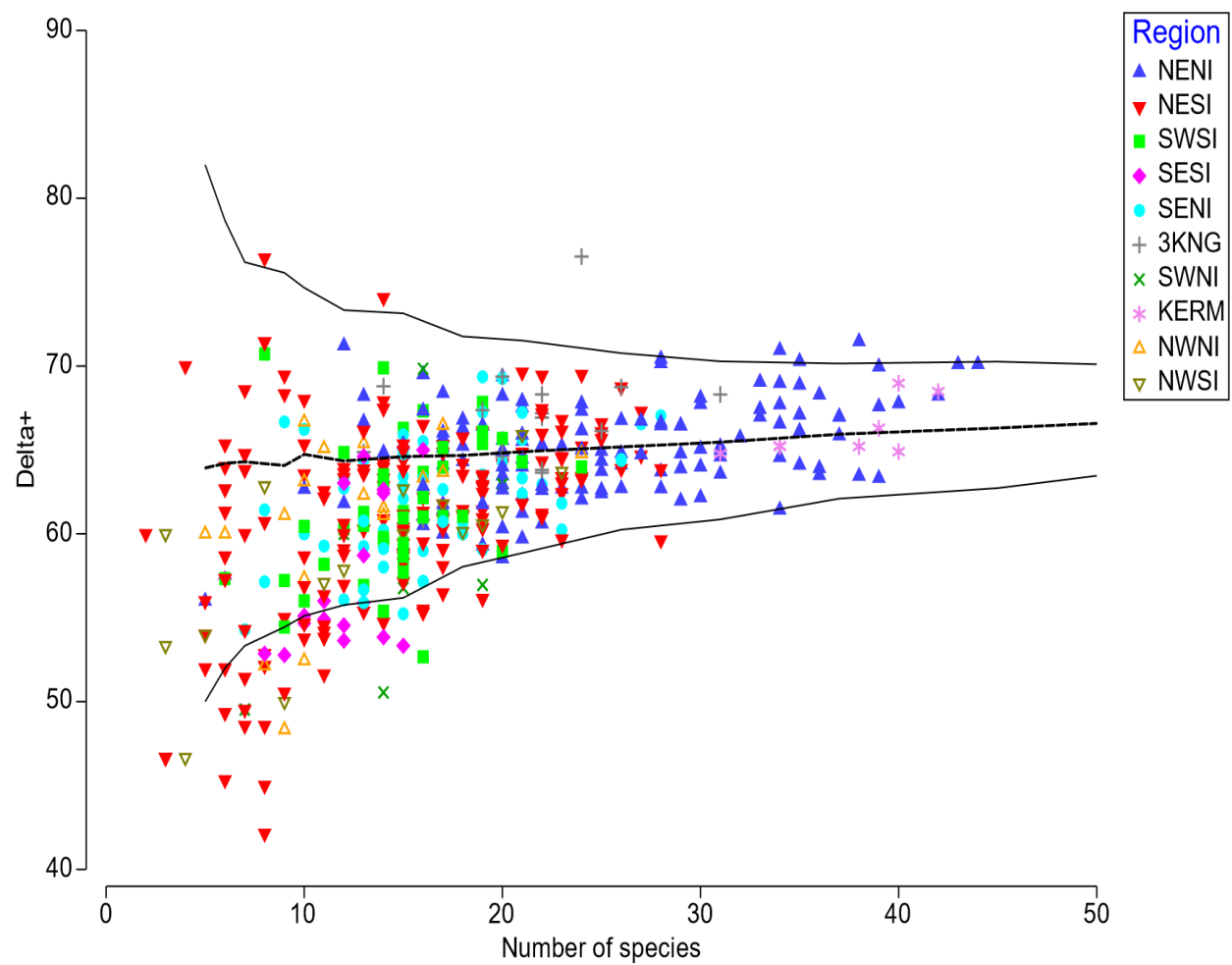


Figure 2.11: Funnel plot of 'average taxonomic distinctness' of each sample site's fish species in relation to number of fish species found at each site including a 95% contour.

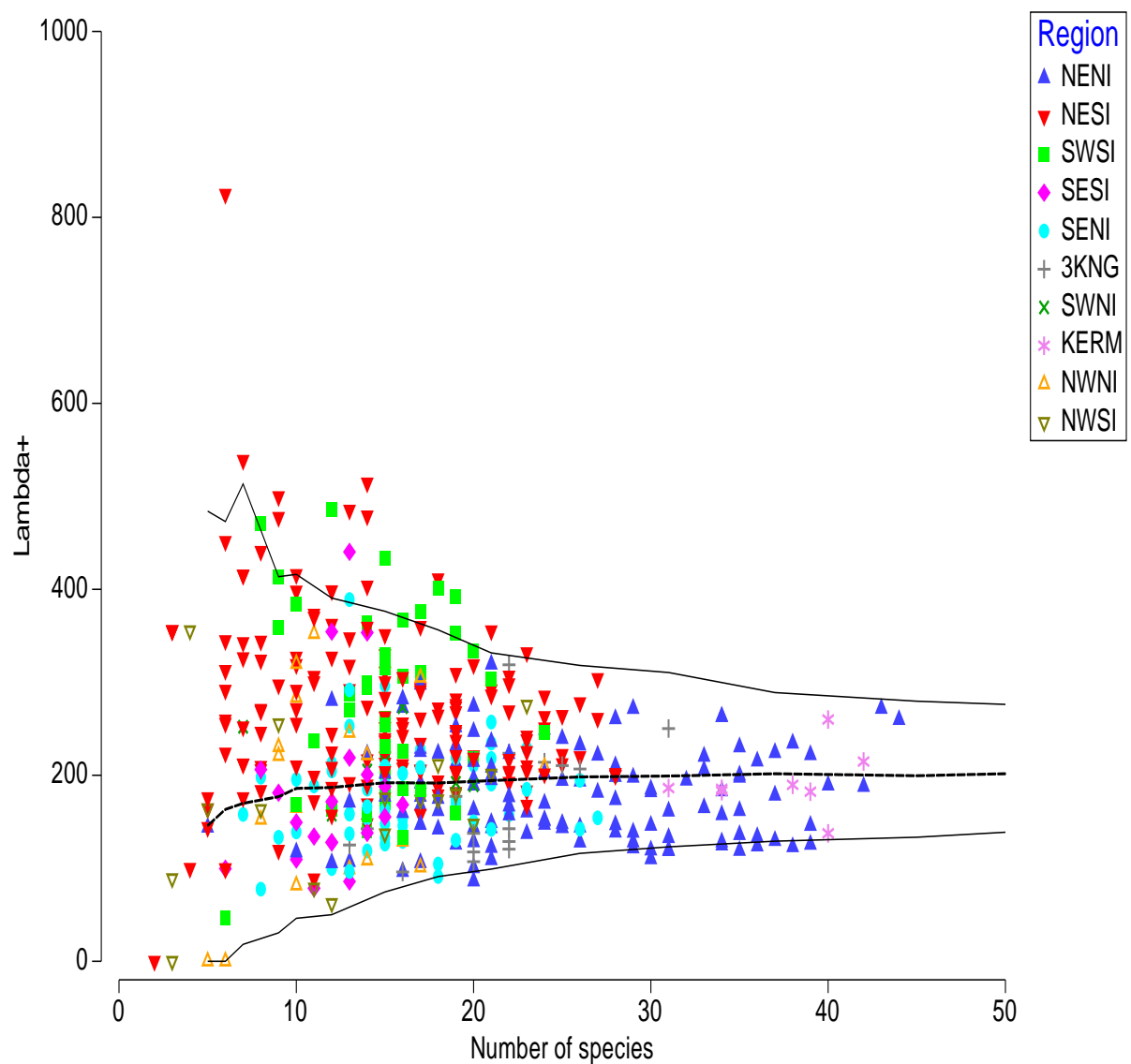


Figure 2.12: Funnel plot of 'variation in taxonomic distinctness' of each sample site's fish species in relation to number of fish species found at each site including a 95% contour.

The funnel plot of AveTD (Figure 2.11) illustrates that the spread of AveTD is relatively consistent with north east North Island, north east South Island and the Three Kings regions over the 95% contour of expected AveTD. This indicates these regions have higher than expected number of species from distinct taxa. For VarTD funnel plot (Figure 2.12), greater than expected unevenness of species found in the north east of the South Island and the south west of the South Island (surpassing the 95% contour).

## 2.4 Discussion

Using assemblages of NZ fishes, I modelled three indices of diversity ‘species richness’, ‘average taxonomic distinctness’ and ‘variation in taxonomic distinctness’ to compare similarities across the broad range of latitudes and environmental conditions of NZ’s rocky reefs. The index of species richness ‘SPR’ (numbers of species observed) and average taxonomic distinctness (AveTD) showed similar spatial patterns at the national scale (Figures 2.8 & 2.9), with comparable relationships with environmental predictor variables (Figures 2.2 & 2.4). In contrast, variance of taxonomic distinctness (i.e., the evenness of the taxonomic relatedness of individuals in a sample, or VarTD) showed different spatial patterns and relationships with predictor variables to that of SPR and AveTD (Figures 2.6 & 2.10).

Wintertime sea-surface temperature (SSTwint) was the most important predictor variable for both SPR and AveTD. A positive association was exhibited for both indices, however, they differed in the shape of the function (see Figures 2.2 & 2.4). This relationship of SSTwint with SPR and AveTD reflects a dominant latitudinal species diversity gradient (Hillebrand, 2004a&b, Gaston, 1996) with lower latitudes supporting more tropical and sub-tropical species compared to higher latitudes. SPR and AveTD were highest in north east North Island and Kermadec Islands where tropical and subtropical species are present (Stuart-Smith et al, 2013). This latitudinal gradient of diversity shows not only an overall decrease in species numbers but also a reduction in the numbers of higher taxonomic groups (e.g., genera, families, orders) that are represented. The decreasing latitudinal gradient was more gradual for AveTD than for SPR, with areas in the lower North Island still retaining moderate to high numbers of taxonomically distinct species (Figure 2.9). Behrens and Lafferty, (2007), Floeter et al. (2005) and Trip et al, (2014) all described a latitudinal gradient of decreasing species richness with increasing latitude, with particular reference to the scarcity of herbivorous species in more temperate waters. Physiological, metabolic constraints in herbivorous fishes may restrict some species to warmer latitudes. With increased energy expenditure in temperate or polar waters, omnivorous or predatory life history traits can be more successful for meeting their energetic demands (Floeter et al., 2005). With a reduction in herbivorous species present comes a correlated reduction in

predators of herbivorous species. As predatory and omnivorous fish are usually quite specialised, (Sale, 2006) a decrease in the distribution of these predator species would also contribute to declining species richness in increasing latitudes.

In contrast, SSTwint was not an important predictor variable for VarTD and therefore, did not reflect the strong latitudinal gradient observed in the other two indices. VarTD proved to be fairly stable across latitudes, and thus appeared to be driven by more localised environmental factors. Increasing turbidity significantly decreased SPR and AveTD, a negative association for both indices. Predictions of low SPR in the Hauraki Gulf may be indicative of an effect of increased turbidity. I expect SPR around Auckland to be significantly higher especially when compared to areas of the same latitude that are not as densely populated, such as the Coromandel Peninsula (Figure 2.8). Clarke and Warwick, (1998) found anthropogenic disturbance (sewage, heavy metal contamination) to be a significant contributing factor to decreased AveTD and increased nutrients in aquatic environments have been well documented for their adverse effects on species diversity (Terlizzi et al, 2005).

Average fetch (a proxy for exposure) was the most important variable for predicting VarTD and fourth for predicting SPR and AveTD. Exposure showed a negative association with VarTD while SPR and AveTD displayed a positive correlation with exposure (although the shape of the function differed). High VarTD is evident in significantly sheltered waters such as Fiordland and the Marlborough Sounds while increased 'maximum dive depth' also exhibited high VarTD, as shelves are commonly dominated by a single species rather than assemblages (Zintzen et al, 2011). This increase in variation could be indicative of early evolutionary divergence (Andriashev, 1953) and specialisation within specific taxa over depth (Tolimeri & Anderson, 2010). Fetch was positively correlated with the indices of SPR and AveTD, increasing both. The Kermadec Islands displayed high SPR and AveTD, while the Chatham Islands showed high AveTD, however, these highly exposed areas could also be a proxy for isolation (MacArthur and Wilson, 1967) which would encourage both high SPR and high AveTD although to confirm this would require further research.

VarTD showed a positive association with turbidity. Areas with higher values of VarTD (such as Fiordland and the Marlborough Sounds) may be characteristic of an island fauna or a reduction in habitat diversity (Clarke and Warwick, 2001). While Fiordland is isolated, the Marlborough Sound is relatively impacted anthropogenically, which supports the suggestion made by Clark and Warwick, (2001) that these conditions would support assemblages with higher VarTD. Disturbance and pollution are seen to be main drivers of a decrease in both AveTD and VarTD (from a loss of the normal spread of higher taxa) but also highly divergent unusual taxa tend to have fewer subordinate branches, therefore, restricting the range of higher taxa with relatively speciose lower branches in comparison (Clarke and Warwick, 2001). Compromised marine environments have also shown to become abundant in indicator species (certain benthic invertebrates) when enrichment levels are particularly high (Pearson & Rosenberg, 1978) contributing to a substantial increase in tolerant species (with a corresponding decrease in intolerant species) which may contribute to high VarTD.

The relationships between seabed salinity and the indices of diversity were more variable. Increased salinity revealed a positive correlation with high AveTD, while VarTD saw a significant relationship with salinity levels that were variable, in that the function was stepped, with a sharp increase then decline in taxonomic variation. These results are consistent with that of Moulliot et al (2005), who found salinity to be the key predictor of variation in taxonomic distinctness in macrophyte communities in coastal lagoon environments, the driver seems to be the variation of salinity in estuarine environments however and difficult to accurately assess in the marine environment.

Competition is thought to be more severe between more closely related species (Darwin, 1859). Clarke and Warwick, (2001) surmised that elevated VarTD with clusters of closely related species across multiple taxa, is representative of habitat homogeneity and characteristic of island biogeography. Areas of high VarTD, Fiordland and the Outer Marlborough Sounds (Figure 2.10), are representative of isolated, specialised coastal environments. Spatial scales are important in understanding assemblage phylogenetic structure, as biogeographic rather than ecological processes may be at play (Webb et al,

2002; Soininen et al, 2007). The fourth chapter will further expand these ideas of average and variable taxonomic distinctness of species in a context of diet to better understand which ecological drivers may be present in these environments

This work has provided new knowledge of the complex relationships between biodiversity and broad-scale environmental conditions and produced predictions of species richness and the average and variance of taxonomic distinctness for shallow coastal rocky reefs in New Zealand at a fine spatial resolution. Studies of diversity at fine resolution and broad spatial extent, and identify the variables that correlate with such patterns, are still relatively rare, yet they can be an important platform for the development of theory on the biological processes that generate and maintain diversity.

# Chapter 3

## Quantitative classification of New Zealand rocky reef fishes into diet guilds

Odette Howarth  
Massey University

---

### 3.1 Introduction

The structure and diversity of functional traits of communities of species are seen as key drivers of the function of ecosystems (Villegger et al., 2008). Loss of diversity has increasingly been discussed more meaningfully in terms of functional traits rather than just the taxonomic identities of species (Bellwood et al., 2002; Wright et al., 2006). Thus, analysing species in terms of their functional traits can help us to understand the structure and function of ecosystems, such as resource partitioning and functional redundancy.

Functional traits comprise a range of ecological attributes from morphology to resource use (Bellwood et al, 2002; Wright et al, 2006). Recently, Zurell et al. (2016) highlighted the importance of considering functional traits when trying to understand patterns in species richness in relation to biogeography and environmental conditions. In particular, classifying species into diet guilds can provide a framework for understanding the breadth and redundancy of ecological functions within an ecosystem (Root, 1967; Simberloff, 1991).

Using diet guilds to classify species within an assemblage allows us to describe the species' functions and use of resources in an ecosystem without regard to their taxonomy (Root, 1967; Simberloff, 1991). Diet guilds have long been used to categorise broad groups of species; from gut microbiota of insects (Colman et al, 2012), polychaetes (Fauchauld & Jumars, 1979) and anurans (Toft, 1981) to bats (Bernard and Fenton, 2002) and birds (Greenberg et al, 1997). Globally, diet guilds have also been used to describe both marine and freshwater fish assemblages (Bonato et al 2012; Novakowski et al, 2008; Platell and Potter, 2001). Traditionally, studies that have focused on diet classifications in NZ have relied on biological sampling of fish stomach contents (by various methods) or diver underwater visual census (Francis, 1996; Russell, 1982; Thompson, 1997). These classifications (Francis, 1996; Russell, 1982; Thompson, 1997) have been compiled by

qualitative, expert opinion rather than quantitative analysis. Biological sampling of stomach contents is precise but restricted by the number of individuals and species sampled and the sampling methods undertaken (content weight, percentage or proportion of total biomass). Additionally, there are limitations with analyses using these sampling methods in both their capacity to compare diet categories across studies as well as between multiple fish species.

Diet guilds in rocky reef fishes have previously been observed in New Zealand (NZ), although not specifically researched (Sale, 1996). NZ is geographically isolated with a broad latitudinal gradient. Previous studies of the diets of rocky reef fishes in NZ have been limited to small scale studies of particular species or regions, not on a national scale (Anderson and Millar, Russell, 1983). Furthermore, like for many systems, previous analyses of diets across broad numbers of NZ fishes have been based on expert opinion or broad qualitative *a priori* groups (Francis, 1996; Russell, 1982). These classifications tend to be subjective rather than objective, with little assurance of consistency across studies. Without robust quantitative methods to objectively categorise diet and species function within an assemblage, reliable comparisons of diet between multiple species is difficult.

Here, I introduce here a new approach to diet classification based on quantitative analysis of broadly available data. I demonstrate this methodology for NZ fishes based on quantitative analysis of broad food-item categories taken from a range of published sources. Use of broad food-item categories allowed us to include a large number of species in the analysis whilst still retaining accurate comparisons between species. More specifically, I defined diet guilds using hierarchical clustering and similarity profile analysis (SIMPROF) (Clarke and Somerfield, 2008) to construct homogenous categories or guilds based on the similarity of these food items within each species' diet, regardless of *a priori* groupings. This clustering allows us to look across family or order and build a comprehensive diet guild to quite a fine classification, in contrast to traditional groupings such as 'omnivore', 'generalist' or 'opportunistic'. This chapter aims to classify species of fish that inhabit shallow, coastal rocky reefs of New Zealand into relatively homogeneous diet guilds.

This research aims to:

- Develop a quantitative multivariate approach to classify 158 New Zealand rocky reef fish species into diet guilds broadly based on food items each species is known to consume.
- This quantitative approach will be based on a hierarchical cluster analysis of pairwise between species-dissimilarities in diet with the final classification chosen using Similarity Profiles (SIMPROF) to test for homogenous multivariate structure within diet guilds.

### 3.2 Methods and theory

#### *Data on species diets*

The list of New Zealand rocky reef fishes used in this study was taken from a national survey of rocky reef fishes at 467 locations (Smith et al., 2013). The original dataset contained 212 species; 158 species were retained after pelagic, cryptic, or soft-sediment species were excluded (Smith et al., 2013).

The diet data comprised for each species was the presence (0) or absence (1) of each of nine broad food-item categories; namely, algae, plankton, parasites, micro-benthic invertebrates (body size < 1 mm), meso-benthic invertebrates (1-20 mm), macro-benthic invertebrates (> 20 mm), small fish (as quantified by Malcolm Francis in Coastal Fishes of NZ, 1996), medium/large fish, and scavengers (dead animal material). Diet information was sourced from published books (Francis, 1996; Roberts et al. 2015) and primary literature (Russell, 1996; Thompson, 1981). Species without specific diet information, I sought expert opinion (Clinton Duffy, pers. comm.). For the species *Gobiopsis atrata*, *Gilloblennius abditus* and *Thalasseleotris iota*, I used diet information from the 'closest' species based on genus, environment and behaviour, as diet data on these species is depauperate. I also compiled the trophic index for each species from fishbase.org, as a supplementary, univariate measure that could be compared with our analyses based on diets.

### *Classifying species based on diets*

A matrix of the dissimilarities of the diets between each pair of species was produced using the Gamma+ dissimilarity measure (Clarke and Somerfield, 2008). Gamma+ is normally used as a measure of dissimilarity between pairs of samples, based on the nearest taxonomic relatives from each assemblage to the next. Here, Gamma+ was used to compare diets between species while incorporating the 'similarity' of the nine food items. The food items were assigned to a hierarchy based on similarity and the location of the food items in the water column. This allowed more distinct pairs of food items (e.g., fish vs algae) to contribute more to the dissimilarity than more similar pairs of food items (e.g., benthic micro- vs benthic meso-invertebrates) when comparing species diets.

Hierarchical clustering was applied to the Gamma+ diet-dissimilarity matrix to produce a classification. I then used similarity profile analysis (SIMPROF; Clarke et al. 2008) to test for multivariate structure in the diets within groups of fish species delineated by the hierarchical cluster analysis. Beginning at the top of the dendrogram, with all species in one group, the profile of the observed ranked between-species similarities in the group were compared with those generated under permutation of the data within food items across the species (i.e., to simulate the null hypothesis of homogeneity of diets in a group of species). If the observed dissimilarities in the group failed to differ significantly ( $p < 0.05$ ) from those obtained under permutation, the group was deemed a coherent diet guild. If the null hypothesis was rejected, it meant that the group contained multivariate structure (heterogeneity) and SIMPROF was applied to the two groups following the subsequent split in the dendrogram. Thus, separate SIMPROF tests were applied at each hierarchical node, beginning at the top where all species belonged to a single group, and finishing when all groups failed to show significant multivariate heterogeneity in their diets. The groups returned by SIMPROF were deemed 'diet guilds', which were then examined and given names according to the types of food items consumed by their member species.

The diet guilds were shown on a non-metric multi-dimensional scaling (nMDS) ordination of the Gamma+ dissimilarity matrix in order to visualise associations among species and diet guilds in relation to the original food items. The range of trophic scores of species within guilds were also plotted.

### 3.3 Results

The 158 NZ rocky reef fish species we classified into eight diet guilds. These were labelled as Generalist carnivores (8 species), Omnivore/Scavengers (3 species); Invertivores (80 species); Piscivore/Scavengers (6 species); Herbivore/Benthic Invertivore/Piscivores (2 species); Herbivores (9 species); Piscivore/Benthic Invertivores (40 species) Herbivore/Invertivore/Scavengers (10 species).

The nMDS (Figure 2) shows the eight diet guilds and the strength of the correlation of each of the nine food items across these guilds. Axes one of the nMDS illustrates the distance between the food item algae and benthic macro-invertebrates with axes two separating fish and benthic meso-invertebrates. Herbivores and piscivore scavengers display the strongest correlations. The nMDS provides an overview of the guilds and their associations with the food items (Figure 3.2). Axis 1 separates herbivores from carnivores, while Axis 2 separates the animal food items between higher (fishes) and lower (invertebrates) trophic levels and the size of the prey consumed, the guilds with the strongest correlations being within the herbivore guild, and the piscivore/benthic invertivore species.

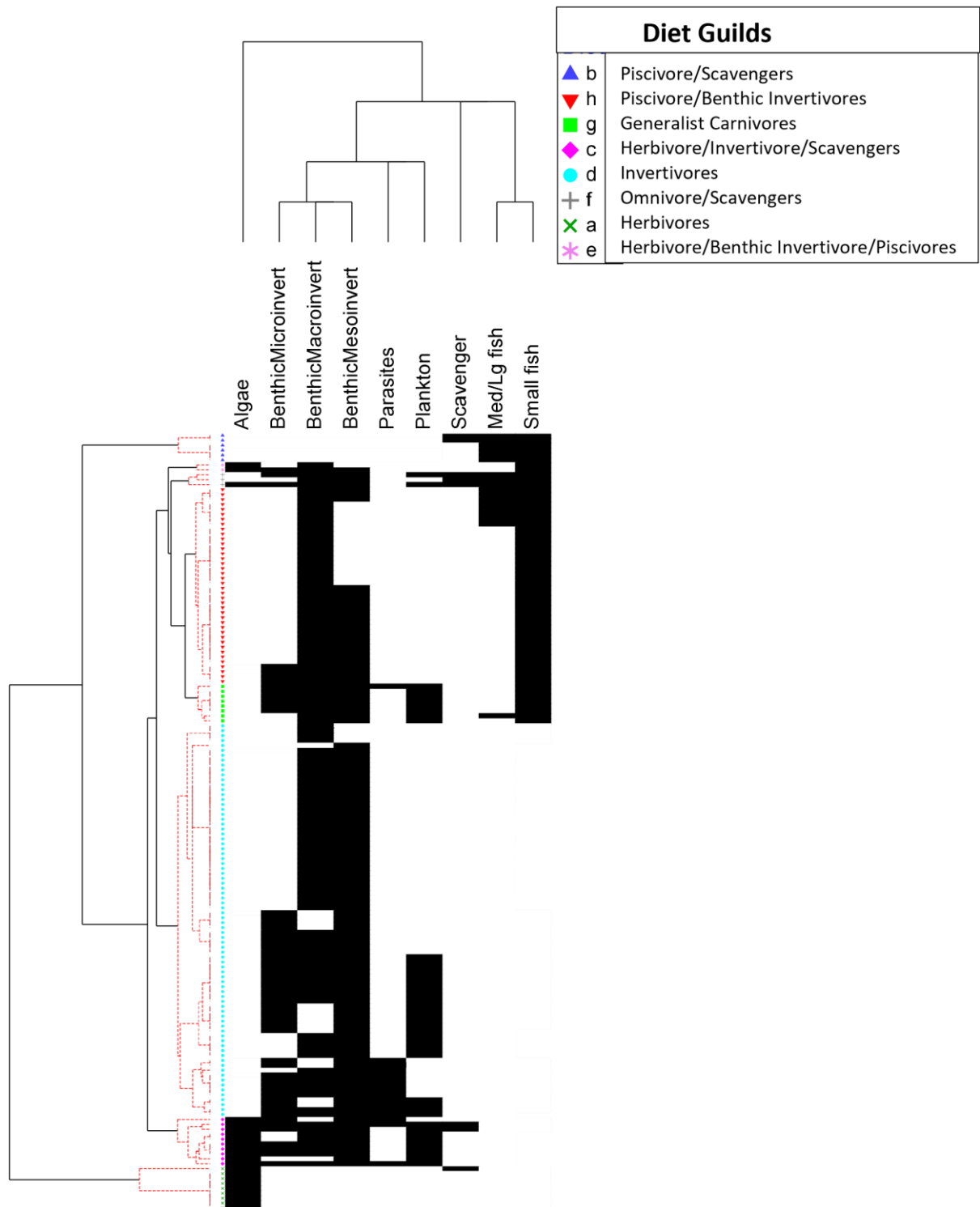


Figure 3.1: Shade-plot of raw data showing scores of 9 food items across all 158 species. Black shading indicates that the food source is present in species diet. The red-dotted lines group the fish species resulting in the dendrogram of the cluster analysis of the 8 diet guilds

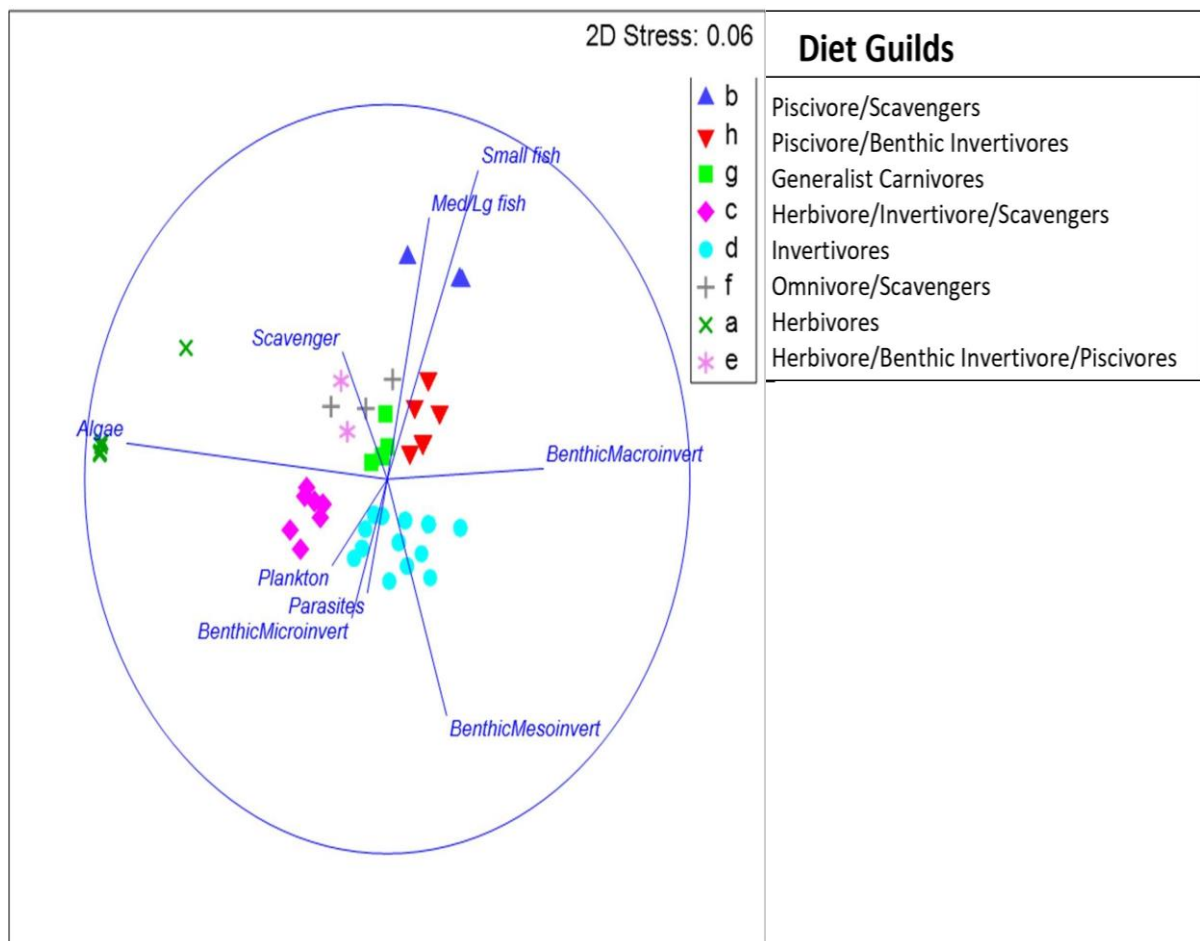


Figure 3.2: Non-metric multidimensional scaling of species Gamma+ dissimilarities based on whether or not they consume each of nine food items. Each point is a species, each classified into one of eight diet guilds. The blue vectors represent correlations (to 1 at circle) between the MDS axes and the food items.

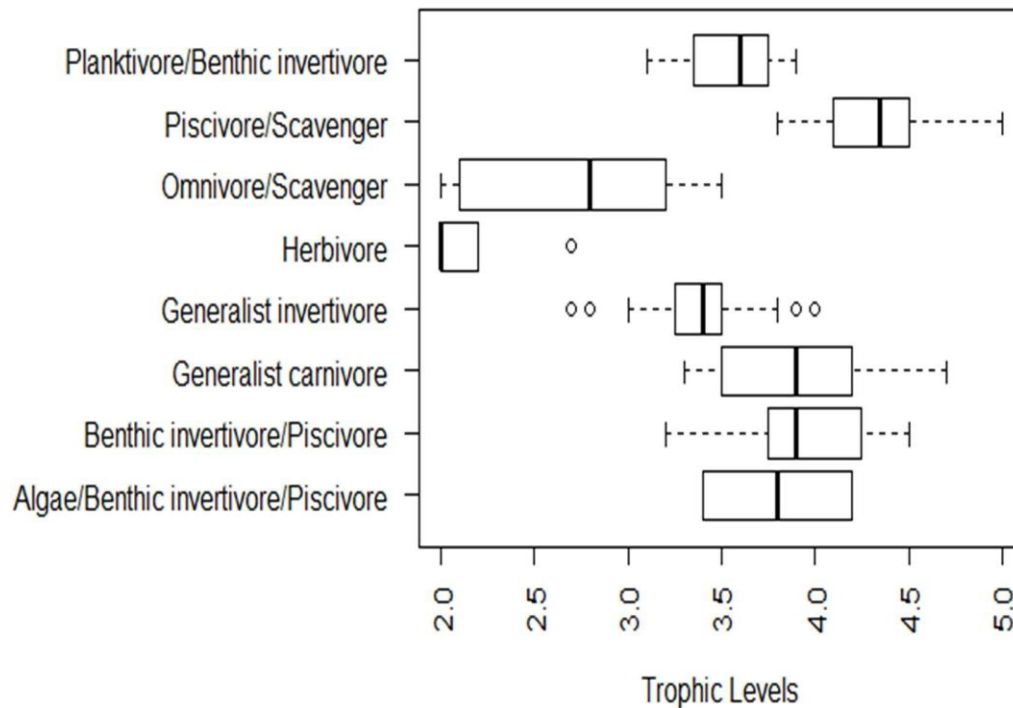


Figure 3.3: Boxplots of the eight diet guilds illustrating the variance of each member species trophic levels.

The Omnivore/Scavenger (Figure 3.3) guild has a large spread of trophic levels, from maximum 3.5 to minimum with Herbivores' trophic levels constrained to between 2 and 2.6 (although this maximum can be considered an outlier). Piscivore/Scavengers have the highest average trophic level but with a large spread of between 3.5 and 5. The five other guilds average around trophic values of 3 and 4, with Generalist carnivores (between 3.3 and 4.7) and Benthic invertivore/Piscivore consumers (3.25 – 4.5) having the largest spread of trophic levels. Generalist invertivores have a relatively small spread of trophic levels although they are consuming a wide range of prey from many niches (albeit all invertebrates) with minimum and maximum outliers.

### 3.4 Discussion

I present a quantitative multivariate classification of 158 New Zealand rocky reef fish species into eight diet guilds based on a simple dataset of the presence or absence of nine broad food-item categories. The approach was based on hierarchical cluster analysis of pair-wise between species-dissimilarities in food items with the final classification chosen using SIMPROF.

The most speciose diet guild found by our method were invertivores, which comprise 80 out of 158 species. The abundance of invertivores may reflect the diversity of habitats and invertebrate prey offered by NZ's temperate rocky reefs (see Russell 1983 for more details), and the ability of fishes to adapt to and exploit the multitude of niches. The presence of so many species in this single diet guild does not necessarily indicate functional redundancy within that group (Petchey and Gaston, 2002; Micheli and Halpern, 2005), especially given the broad spatial scale and breadth of this study. Indeed, the dendrogram (Figure 3.1) shows some potential further structure within the invertivore guild, though it was not deemed significant by the SIMPROF test; more detailed diet data may reveal finer delineation among invertivore diets

A distinct guild of only eight herbivorous species was identified. There is a well described expectation that the geographic distribution of herbivorous species will be more prevalent in tropical or sub-tropical waters than in temperate waters, with urchin species more often filling this ecological niche at higher latitudes (Jones and Andrew 1990; Floeter et al, 2005). Several mechanisms are thought to be responsible for this reduction of herbivorous species at higher latitudes, such as colder waters imposing physiological constraints on digestion and increased metabolic requirements, as well as decreasing nutritional value of algae with increasing latitudes (Floeter et al., 2005). The isolation and island geography of New Zealand and its outlying islands may be responsible for the large number of herbivorous species (MacArthur & Wilson, 1967) possibly due to the variability of environmental niches (Thiollay, 1990). Russell, (1977) found herbivorous species to comprise a substantial percentage of (51%) of the biomass or total weight of fishes in the Cape Rodney-Okakari Point Marine Reserve, albeit in dense kelp areas. Three of these eight species are relatively

rare and two are only found at the Kermadec Islands (*Parma kermadecensis* and *Girella fimbriata*), with the other (*Odax cyanoallix*) found only at the Three Kings Islands.

The smallest guild contained only two members *Notothenia angustata* and *Ostracion cubicus*, labelled algae/piscivore/benthic invertivores. These species consume both fish and algae, making them distinct enough to warrant their own diet guild. They are similar both morphologically and behaviourally, and have a similar size range (maximum length 470 and 450 mm respectively) with similar feeding strategies and behaviour (slow-moving, ambush predation, solitary, and cave-dwelling). These two species fill similar ecological niches but differ in spatial distributions

Quantitative, objective classifications of species into diet guilds are possible when only coarse information on diet is available, and without any need for *a priori* groupings of the species of interest. Data-driven classifications are preferable to expert opinion, which can be predetermined and subjective. Quantitative analysis provides objective descriptors of diet guilds based on data. Previous diet studies of rocky reef fish in NZ have relied on biological sampling, visual census and expert opinion which have resulted in classifications such as 'carnivore' and 'omnivore' or 'generalist' and 'specialist'. With our approach, the classification into diet guilds were based solely on diet data, without any preconceived notion of what the guilds should be. A qualitative classification can struggle to provide any further information on resource partitioning or community assemblage of a given population and any comparisons between species or classifications can be misleading. Further analysis using this methodology could incorporate variables such as size, morphology and depth to advance understanding of these guild relationships. In the next chapter I will build on this research and look at spatial distributions of these guilds and the underlying local and regional processes that drive diversity gradients in relation to food resources.

In conclusion, I have demonstrated a useful method, based on applying cluster analysis and SIMPROF to broad data on diets, for classifying rocky reef fishes into diet guilds. I consider that this robust quantitative methodology could be used more broadly to compare functional similarities of fauna in other systems and geographic locations across multiple species.

# Chapter 4

## Regional and local processes as drivers of diet diversity in New Zealand rocky reef fish species

Odette Howarth

Massey University, Auckland

---

### 4.1 Introduction

Gradients in diversity are shaped by a variety of biotic and abiotic factors. These factors affect the ranges and distribution of species over space and time (Cavender-Barnes et al, 2009). For example, studies of mangroves in Africa show that species distributed throughout the region form distinct zones depending on tide levels (Davis, 1940). In this case, species may exist in different tidal zones according to the amount of air exposure they can physiologically handle. In contrast, distributions of humpback whales in the Southern Hemisphere are seasonal, with annual winter migration to Antarctic feeding grounds and winter migrations back to breeding grounds (Dawbin, 1956; 1966) driven by access to resources. Understanding the complex processes that both directly and indirectly determine diversity gradients is key to recognising how species adapt to environmental change and the opportunities and pressures species face. Comprehending diversity gradients beyond species distribution ranges must also consider the physiology, ecology and resource partitioning of the individual species.

On a global scale, reef fishes show a latitudinal gradient in species richness, with tropical, low latitude regions displaying high diversity which decreases towards higher latitudes of temperate and polar-regions (Hillebrand, 2004a&b; Macarthur & Wilson, 1967; Gaston, 1996). Globally, it is likely this latitudinal gradient is driven by the culmination of a number of factors and mechanisms; such as species environment and habitat use, availability and partitioning of resources and energy as well as larval dispersal and connectivity/migration. New Zealand (NZ) has a latitudinal gradient that encompasses a total of approximately 13° of latitude. My research has revealed that the global latitudinal gradient evident in fish species richness and diversity persists to some degree at a national scale in NZ (Chapter 2). The models for New Zealand revealed that environmental variables that were inversely associated with latitude, such as wintertime sea surface temperature

(SSTwint), were positively correlated with species richness, while environmental variables of turbidity and salinity seem to operate as mechanisms at smaller scales (Chapter 2). Akin et al, (2005) found that turbidity and salinity affected the composition of fish assemblages, mediated by the tolerance or specialisation of species to low salinity and high turbidity environments. Additionally, on an individual species level, my models indicate both positive and negative relationships with environmental variables such as SSTwint, turbidity, salinity and fetch. However, when an individual species displays a strong association with a particular environmental variable (for example SSTwint) it is possible this is a direct correlation and driven by physiology, whereas for others, it could be that a species' distribution is indirectly determined by their dependence on resources that are restricted by certain ranges of that environmental variable.

Fishes are the most speciose group of vertebrates on the planet and have accessed, on a global scale, a broad range of environments and resources available in the world's oceans. Reef fish species also occupy many of the major feeding guilds observed in terrestrial systems, for example herbivores, carnivores, browsers and omnivores, while also accessing feeding modes unique to marine systems (e.g. planktivores). As with other ecological systems, fish species also vary in their degree of diet specialisation, from generalists to specialists. With this in mind, I can predict that the distribution of reef fishes and their associations with environmental variables will vary according to their diet guild, either directly through dietary specialisation dependent on metabolic constraints or indirectly through a prey/food item's distribution and habitat use.

In the previous chapter, I demonstrated a quantitative classification of fishes into eight diet guilds within coastal, rocky reef systems of New Zealand dependant on the broad scale food items they consume. These guilds varied in the specificity of the diet and also in the number of species affiliated with each guild. Here, I developed predictive spatial models of the diet diversity for these fishes around coastal New Zealand to explore how spatial patterns in species richness of reef fishes, and the relationships with environmental and geographic variables, is mediated by diet and food resource specialisation. First, I modelled 'average diet diversity' and 'variation in diet diversity' using environmental and geographic

variables at a fine, 1km scale. I was interested in whether the diet diversity of fishes decreased proportionately with the number of species predicted or whether diet diversity decreased with species richness. I then predicted the species richness distributions for three of the individual diet guilds based on the classification method from Chapter 3. These guilds were selected as the invertivores were the most speciose guild, herbivores as a guild of note due to metabolic constraints in temperate waters, while the piscivore/benthic invertivore guild was selected as an opposite to the herbivore guild. With this analysis, I examined whether the guilds discussed showed similar spatial distributions and whether the guilds emulated the overarching species richness latitudinal gradient from Chapter 2. In particular, I expected that the metabolic demands of digestion in herbivores would directly restrict the herbivore guild to northern waters with warmer sea-surface temperatures. The invertebrate consumers, being the most speciose guild, I expected to follow the overall species richness gradient illustrated in Chapter 2, losing species at higher latitudes with both indirect and direct processes, while the piscivore/invertivore guild may indirectly follow the distribution of their prey items.

Specifically, this research aims to:

- Model the 'average' and 'variation in' diet diversity (based on broad food items consumed) of New Zealand rocky reef fishes using environmental and geographic variables and examine which variables are most correlated with diet diversity.
- Examine whether diet diversity decreases proportionately with species diversity, and identify any differences in the environmental variables associated with diet diversity and species diversity.
- Predict and map the species richness of the 'herbivore', 'invertivore' and 'piscivore/benthic invertivore' diet guilds to identify any difference in the species richness patterns for these guilds.
- Examine whether species richness patterns for the three feeding guilds have different associations with environmental or geographic variables.

## 4.2 Materials and Methods

### *Collection of data and predictor variables (see previous chapters).*

Data on observed fish species were collected over an 18-year period (Nov 1986-Dec 2004) during 467 SCUBA dives around the coast of New Zealand. Although 212 species were observed, only 158 species were retained in the final data set; species that were pelagic, cryptic or soft-sediment dwellers were excluded because they were not consistently recorded (Smith et al., 2013).

I compiled data on the diets of each species according to the presence or absence of each of the following nine broad food-item categories: algae, plankton, parasites, and microbenthic invertebrates (<1mm), meso-benthic invertebrates (0-20mm), macro-benthic invertebrates (>20mm), small fish, medium/large fish, and scavengers (dead animal material). I sourced diet information from published books (Francis, 1996; Roberts et al, 2015) and primary literature (Russell, 1983; Thompson, 1981). For species for which I was unable to find any data, I sought expert opinion (Clinton Duffy, pers. comm.). A matrix of dissimilarities was built using hierarchical food-item similarities for each pair of species using a Gamma+ dissimilarity measure (Somerfield and Clarke, 1995) in Primer v7 (see Chapter 2). I used this pair-wise dietary dissimilarity matrix to calculate 'average diet diversity' (AveDD) and 'variation in diet diversity' (VarDD) for the assemblages found at each site (see section 2.4). I modelled five different response variables calculated at individual site level using environmental variables. The response variables were: average diet diversity (AveDD), variation in diet diversity (VarDD) and species richness within three diet guilds 'herbivores', 'invertivores' and 'piscivore/benthic invertivores' (see Chapter 3), as measures of reef fish diversity.

### *Species richness of Diet Guilds*

I predicted the species richness of three of the eight diet guilds from Chapter 3 (herbivores, invertivores and piscivore/benthic invertivores) using boosted regression trees (using the *dismo* package in R) (see section 2.5) and mapped these values onto the New Zealand coastline.

### *Average and Variation in Diet Diversity*

I used two measures to examine patterns in diet diversity of site-level assemblages; ‘average of diet diversity’ (AveDD) and variation of diet diversity (VarDD), calculated in PRIMER v7. I calculated both measures using a distance matrix based on pairwise between species measures of food items consumed within their diet. The path length between classes (the largest distance) is set to 100 with the steps between the different levels of the tree weighted from the hierarchical food items (Warwick and Clarke, 1995). For the assemblage of fish species found at each site, AveDD and VarDD measured the average and variation of the dietary dissimilarities across each pair of species. High AveDD indicates species observed consumed dissimilar food items dependant on the hierarchical classification. High VarDD means we found multiple species that consumed similar food items (clustered) in the hierarchical classification. We used these values to make predictions using boosted regression trees and mapped these predictions onto the New Zealand coastline. We also used the TAXDTEST procedure in PRIMER v7 (Clarke and Gorley, 2006) to produce funnel plots of average and variation in diet diversity of each site sampled compared to the number of species found per site, with 95% bounds made from calculating AveDD and VarDD under the null model of taking random samples of species.

### *Boosted regression tree models*

I used boosted regression trees (BRTs; using the *dismo* package for R) to model species richness of diet guilds, (see section 2.3) the average dietary distinctness and variation in dietary distinctness of rocky reef fish assemblages (see section 2.4). BRT models were fitted using a Gaussian error distribution. VarDD was square-root transformed prior to analysis to remove skewness. To control the number of trees in each BRT model and thus avoid over-fitting, a ten-fold cross-validation procedure (Elith et al, 2008) was used to randomly assign the data to one of ten folds. Geographically clustered sites (within c. 1km) were always assigned to the same fold to improve the independence of the test data. This allowed the algorithm and the final number of trees to be chosen based on minimising the deviance for withheld data. The individual trees were constrained to complexity of 5 (i.e. the depth of the trees), and by a learning rate (shrinkage) of 0.002 (Elith et al., 2008).

Three categories of predictor variables were available for the model: environmental, geographic, and dive-specific with 15 predictor variables in total (see Table 1). The environmental variables were developed by scientists as part of the New Zealand Marine Environment Classification (NZMEC) with values on a 1 km grid. The NZMEC provides environmental and geographical frameworks using several spatial data layers that describe the physical environment (Snelder et al., 2005). The geographical variables were developed for the same grid by Smith et al. (2013). The dive specific variables were taken during the sampling, and were used in the models to control for differences in the scope and duration of the surveys, and to assign standardised values for prediction. I found substantial correlation of the environmental variables 'chla2', 'suspended particulate matter' and 'dissolved organic matter'. To avoid multi-collinearity, I created a principal component analysis of these variables which resulted in two axes representing 'turbidity'; 'turb1' (PCA axis 1) and 'turb2' (PCA axis 2) as variables in the model (I found visibility to be linearly related to turbidity). I predicted visibility using 'turb 1' and the resulting variable 'visanom' (visibility anomaly) was taken as the residuals from this model. 'Visanom' represents the difference in visibility on each dive, relative to expectation for that geographical location. These predictions were then mapped onto the New Zealand coastline using the *sp* and *raster* packages in R at the 1km scale of the original predictor variables of the NZMEC. Predictions are shown only for grid cells that are known to contain rocky reef (see Smith et al. 2013 for further details).

#### 4.3 Results

The model of average dietary distinctness (AveDD) explained 77% of the deviance for withheld data obtained by fitting 1560 trees (Figure 4.1). The variables that were most important were turbidity (Turb1, PCA axis 1) (33.8%), fetch (12.5%), salinity (9.9%), winter time sea-surface temperature (SSTwint) (7.7%), and visibility anomaly (6.6%) (Figure 4.2). AveDD was predicted to be high at very low values of turbidity, low at mid-range turbidity, and average in high turbidity environments. Average fetch and SSTwint were positively associated with AveDD, whereas sea-bed salinity was negatively associated with AveDD. Visibility anomaly (6.6%) sees a positive relationship with increasing clarity of water and distinct diet guilds found. Sea-surface temperature gradient (6.6%) predicted a decrease in average diet diversity with a decreasing temperature gradient. Increasing sea-surface

temperature anomaly (6.4%) and Turb2 (PCA axis 2) (4%) had an opposite effect with decreasing average dietary diversity. Increasing sea-surface temperature annual amplitude and duration of dive both increased diet diversity. The deeper the minimum dive depth (2.3%) the greater the diet diversity predicted. The two remaining variables contributed less than 2% of total deviance to the model.

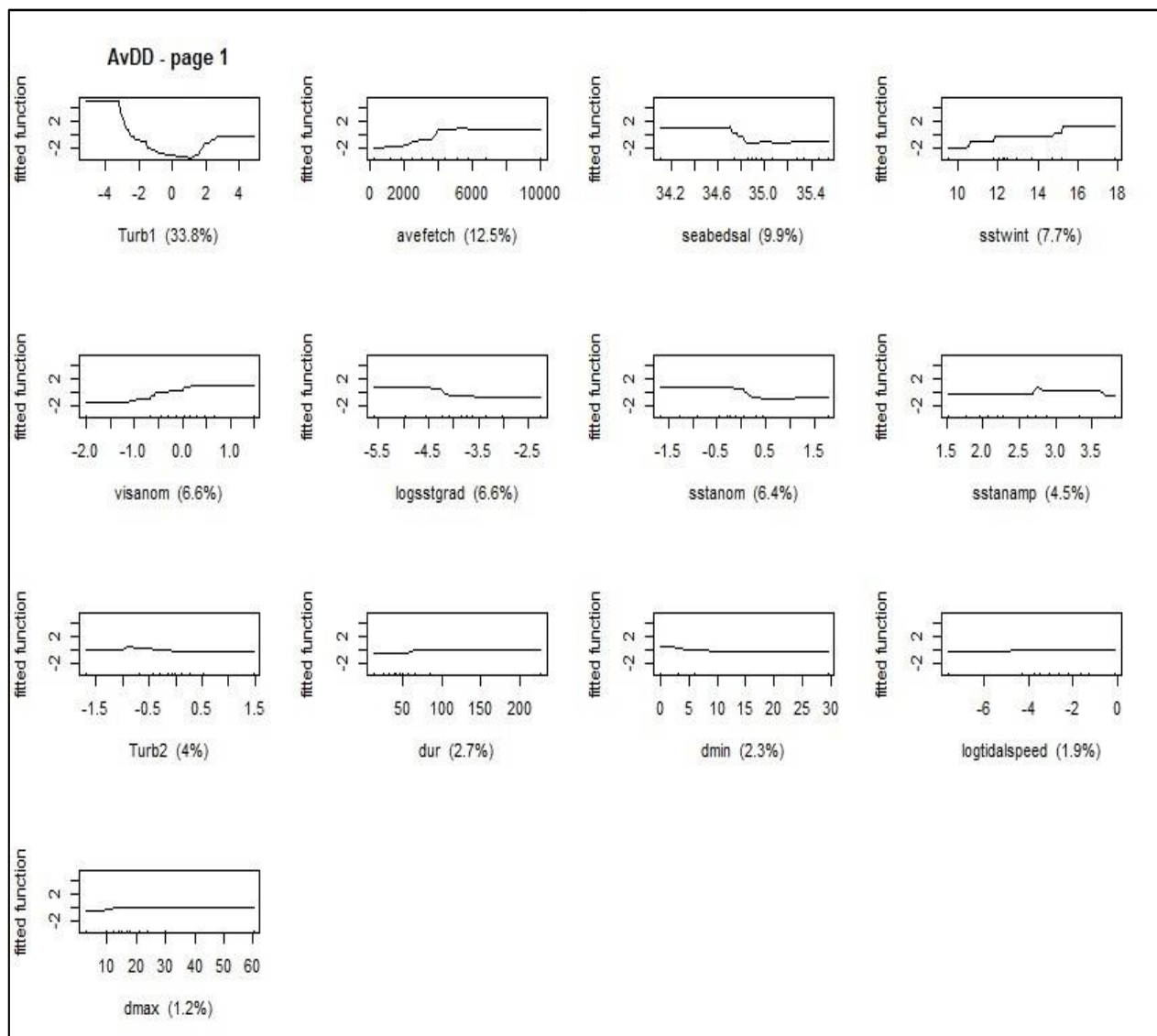


Figure 4.1: Influence of individual predictor variables on response variable of average diet diversity including the combined variable of 'Turb1 and Turb2' and the visibility anomaly 'Visanom'. The y axis for each plot represents the marginal effects of a particular predictor variable on the response variable. It is calculated by comparing predictions across the range of the predictor variable in question, while holding all other predictor variables constant at their median values.

Figure 4.2 shows the predicted AveDD mapped to the NZ coastline. Higher dietary diversity (yellow) is predicted for the Kermadec and the Poor Knights Islands than is expected to be found around the rest of the NZ coastline.

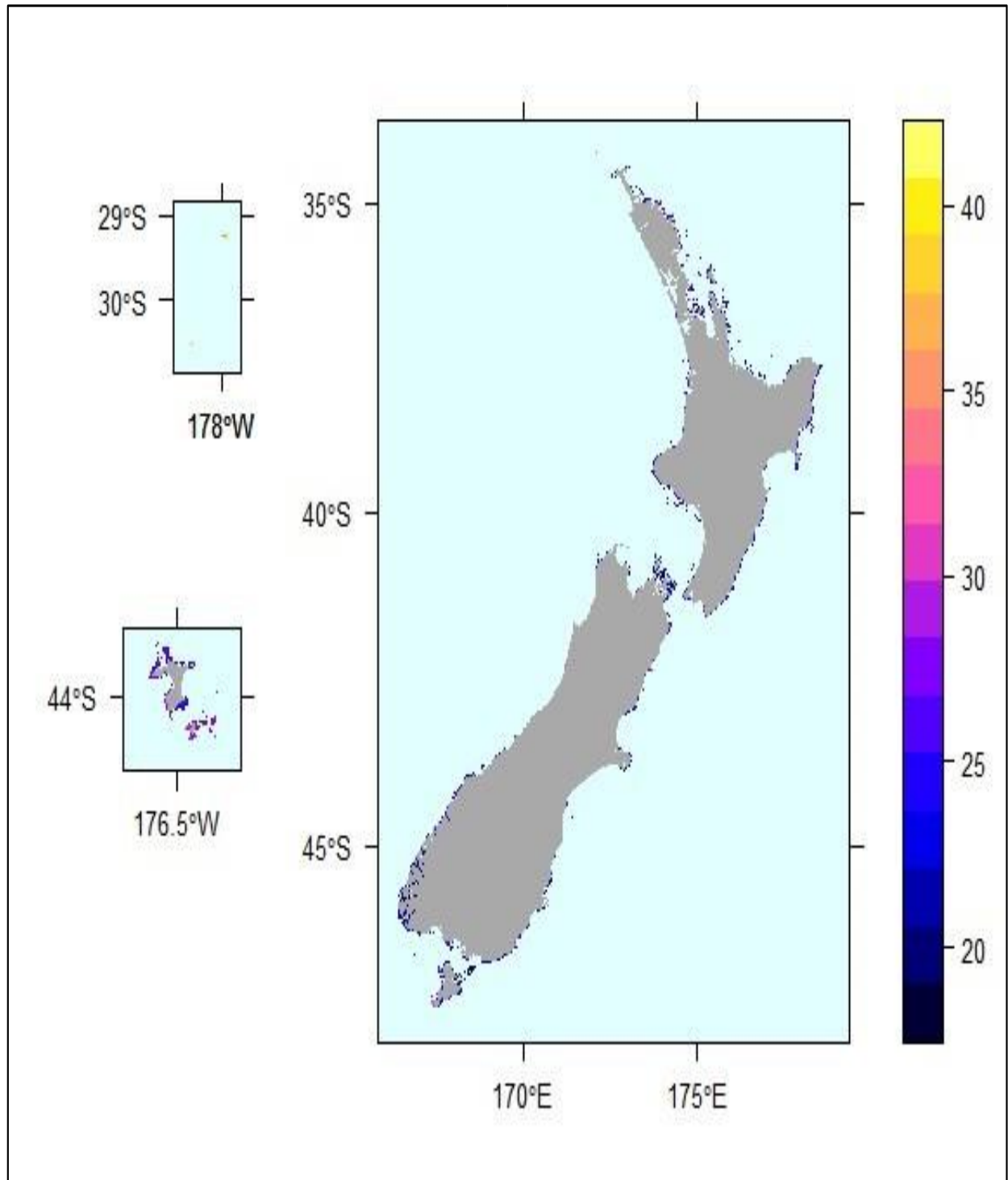


Figure 4.2: Geographic map of predicted average diet diversity of New Zealand rocky reef fish. Key indicates predicted diversity of diets found in each region/area. Insets show the Kermadec Islands (top left) and Chatham Islands (bottom left).

The model of VarDD explained 77% of the deviance for withheld data, obtained by fitting 1640 trees. In Figure 4.4 I identified the variables that were most correlated (Figure 4.3) with the variation in reef fish diet diversity as fetch (17.8%), turbidity (PCA axis 1) (16.7%), sea surface temperature gradient (14.5%), visanom (7.5%) and sea surface temperature anomaly (7.4%). Exposure significantly increased the variation in diet diversity from approximately 2000m from shore. Increasing turbidity on both PCA axis 1 and 2 (6.6%) significantly decreased the variation in diet diversity with a moderate return in higher turbidity waters. This relationship was also reflected in visibility anomaly variable increasing the diversity of diet. Decreasing sea-surface temperature gradient also decreases the variation in diet diversity, however, increasing winter time sea-surface temperature (6.8%) increases the variation in diet diversity. Elevated levels of sea-bed salinity from over 34.8psu decreased variation in diet diversity. Shallower minimum dive depths show greater variation in diet diversity of fish species. Increasing sea surface temperature annual amplitude (4%) and dive duration (3.5%) over 50 minutes also increased the variation in diet diversity. The remaining two variables each made up less than 2.2% of the total deviance of the model.

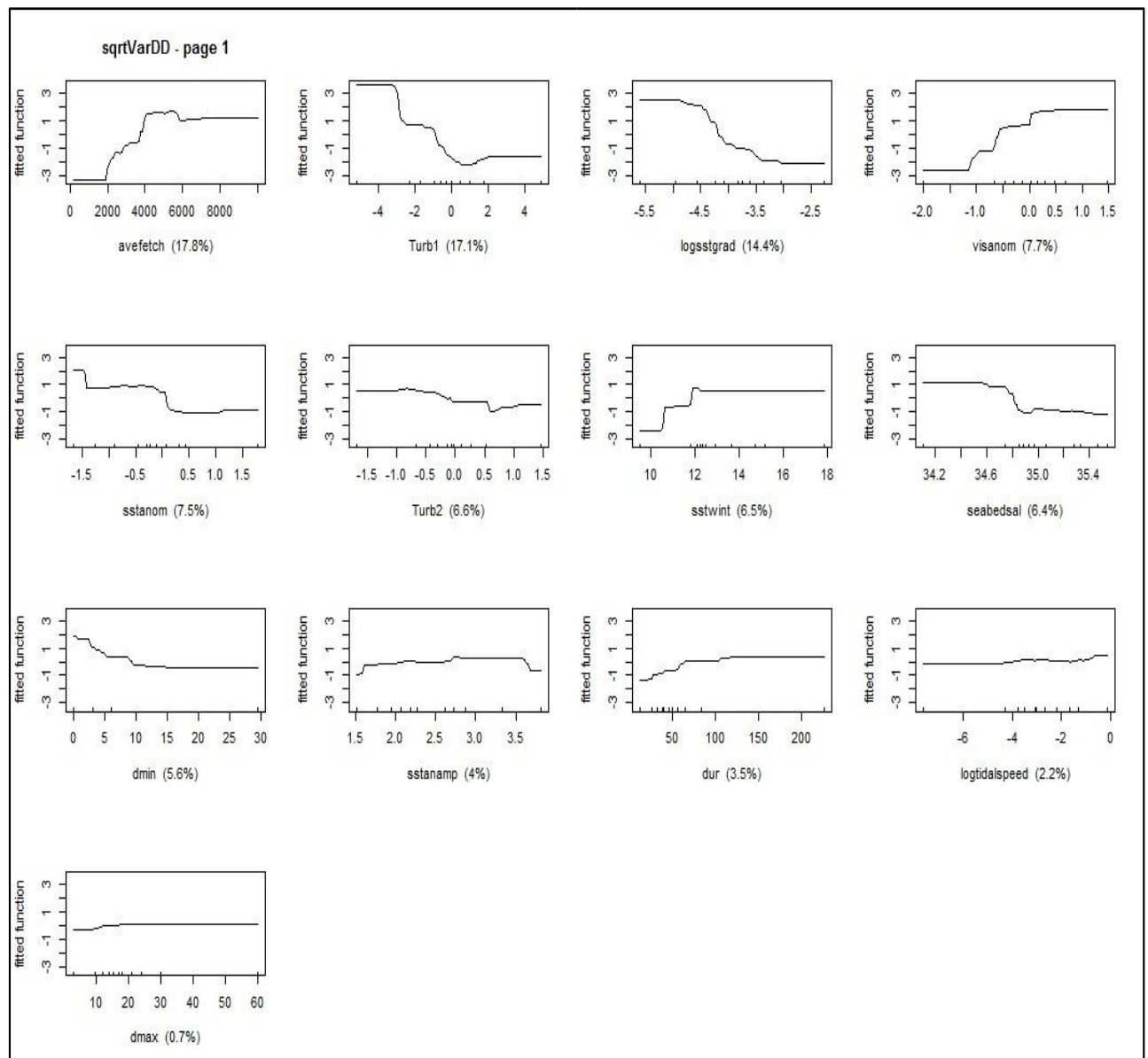


Figure 4.3: Influence of individual predictor variables on response variable of variation in diet diversity including the combined variable of 'turb1 and turb2' and the visibility anomaly 'visanom'. The y axis for each plot represents the marginal effects of a particular predictor variable on the response variable. It is calculated by comparing predictions across the range of the predictor variable in question, while holding all other predictor variables constant at their median values.

Figure 4.4 shows the variation in diet diversity predictions mapped to the NZ coastline. High VarDD is observed in the Kermadec and Poor Knights Islands with moderate variation in predicted dietary distinctness in the Chatham Islands, which remains relatively stable around the rest of the NZ coastline.

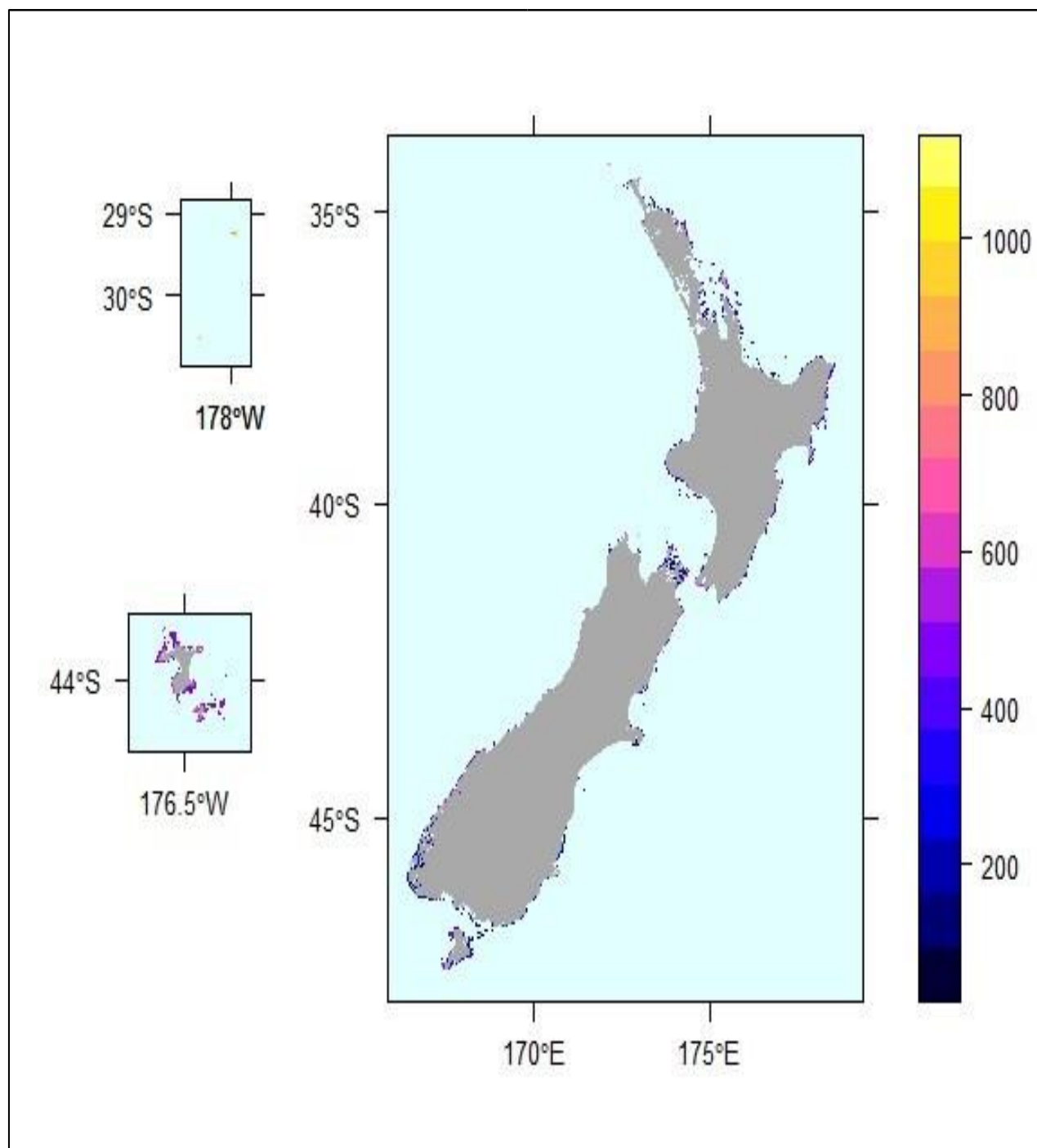


Figure 4.4: Geographic map of predicted variation in diet diversity of New Zealand rocky reef fish species. Key indicates predicted variation in food items consumed found in each region/area. Insets show the Kermadec Islands (top left) and Chatham Islands (bottom left).

### *Species Richness of Diet Guilds*

I modelled the distribution of fishes described as ‘herbivores’ (see Chapter 3) on coastal rocky reef areas in New Zealand. The model explained 85% of the deviance for withheld

data obtained by fitting 1440 trees. The environmental and geographic variables identified that were most correlated (Figure 4.5) with the presence of herbivore species as 'winter time sea-surface temperature' (54.1%), 'sea-bed salinity' (13.4%), 'minimum dive depth' (8.9%), 'average fetch' (5.0%) and 'maximum dive depth' (4.5%).

Increase of sea-surface temperature was associated with an increase of herbivore species found. At around 14-16°C a steep increase is observed. Increasing sea-bed salinity over 35.0psu is also correlated with increased herbivorous species predicted. Also observed is an increase of herbivorous species found in very shallow waters (<5m), interestingly this decreases between 5-30m but increases again over 30m. Average fetch or 'distance to land' has a positive correlation with herbivorous species after 2000m from shore. This positive influence is also observed in the 'duration of dive' variable (3.2%), the longer the dive the more herbivores I predicted would be observed. Increasing amounts of particulate, organic matter and chlorophyll in the water, (turbidity PCA axis 1), saw a decrease in herbivores (2.4%). With increasing 'sea surface to temperature anomaly amplification' (2.1%), a positive correlation with herbivorous species was observed. Decreasing 'log tidal speed' (2.0%), 'log of sea surface temperature gradient' (1.8%), 'turb 2' (1.0%) and 'sea-surface temperature anomaly' (1.0%) had a small negative effect on predicted herbivorous species with 'visanom' barely perceptible at (0.4%).

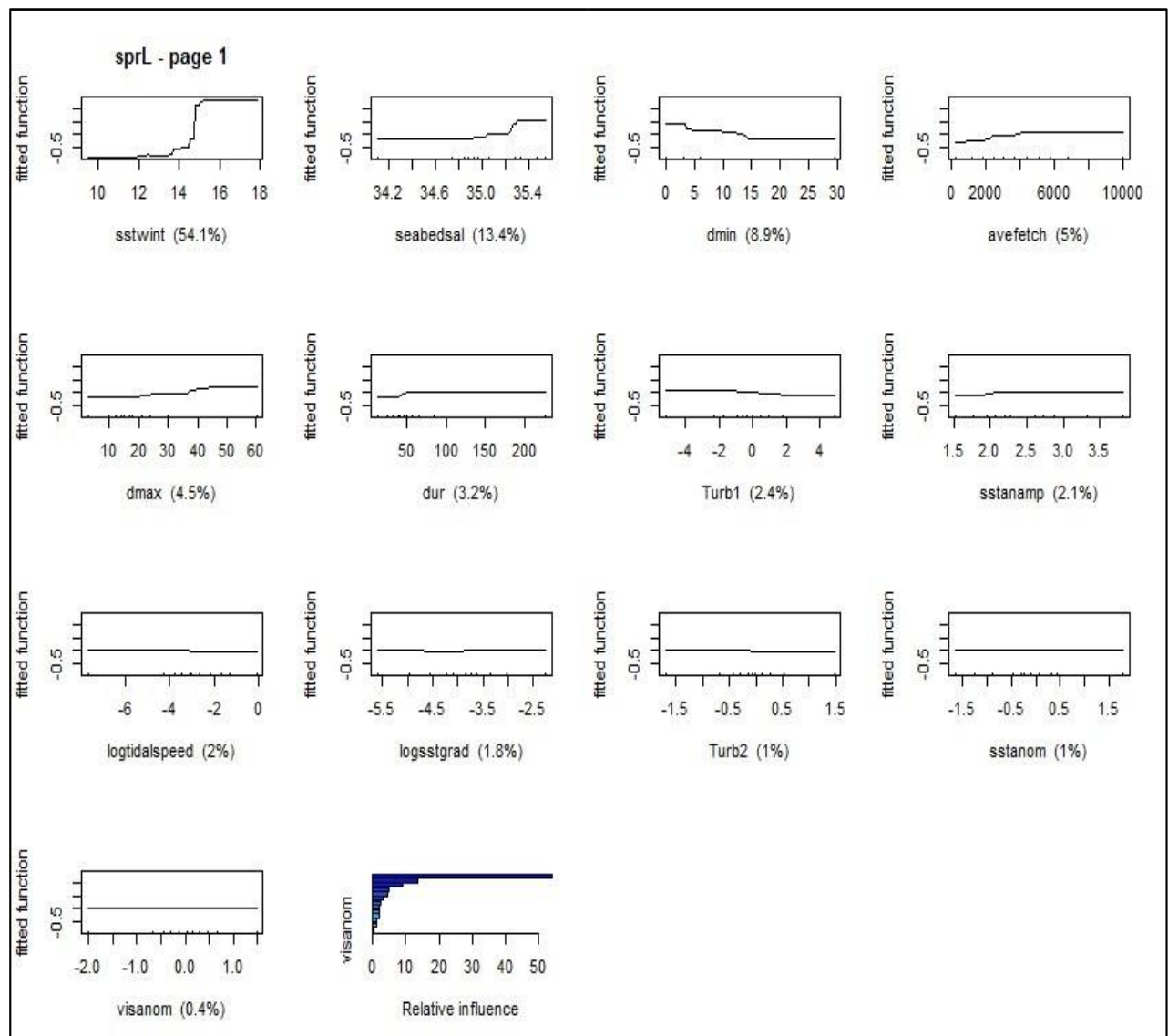


Figure 4.5: Influence of individual predictor variables on response variable of species richness of Herbivores, including the combined variable of 'turb1 and turb2' and the visibility anomaly 'visanom'. The y axis for each plot represents the marginal effects of a particular predictor variable on the response variable. It is calculated by comparing predictions across the range of the predictor variable in question, while holding all other predictor variables constant at their median values.

Figure 4.6 illustrates the predicted distribution of herbivorous species mapped to the NZ coastline. The predicted presence of more than three species (yellow) is seen in Kermadec Islands and the far north-east of the North Island. The Hauraki Gulf and the Poor Knights Islands predict 2 to 3 species of herbivores. Herbivore species are predicted at all sites around the coastline except the south-east of the South Island.

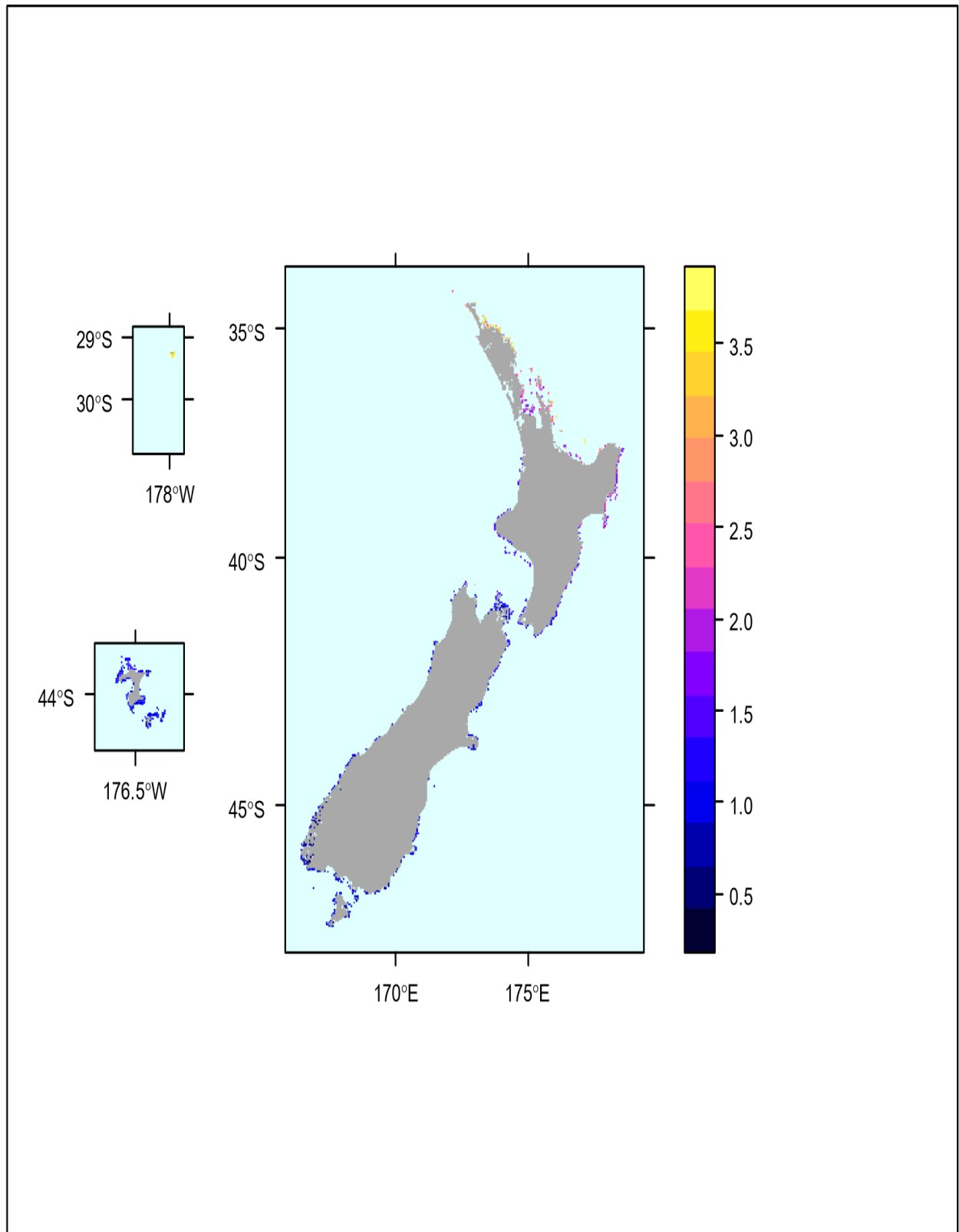


Figure 4.6: Geographic map of predicted distribution of herbivorous New Zealand rocky reef fish. Key indicates predicted abundance of herbivorous species found in each region/area. Insets show the Kermadec Islands (top left) and Chatham Islands (bottom left).

The model explained 89% of the deviance for withheld data obtained by fitting 2000 trees. In Figure 4.7 I identified the environmental, geographic and dive-specific variables that were most correlated with the variation in reef fish taxonomic diversity as 'winter time sea-surface temperature' (51.5%), 'turb 1' (9.6%), 'sea bed salinity' (9.5%), 'maximum depth of dive' (8.4%), 'duration' (4.5%). Increasing SSTwint (from 14°C) significantly increases the presence of invertivore species. Increasing turbidity (PCA axis 1) decreases the species richness of invertivores. Increasing seabed salinity (over 35.0psu), maximum dive depths (over 10m) and duration of dive (more than 50 minutes) all substantially increased the predicted presence of invertebrate consumers. Decreasing sea-surface temperature gradient (3.7%) and decreasing tidal speed (3.6%) both reduced the presence of invertebrate consumer species. Increasing clarity of water explained by the variable 'visanom' (2.4%) and increasing exposure (2.1%) slightly increases the presence of invertivores. The remaining variables contributed less than 2% of the deviance in the model.

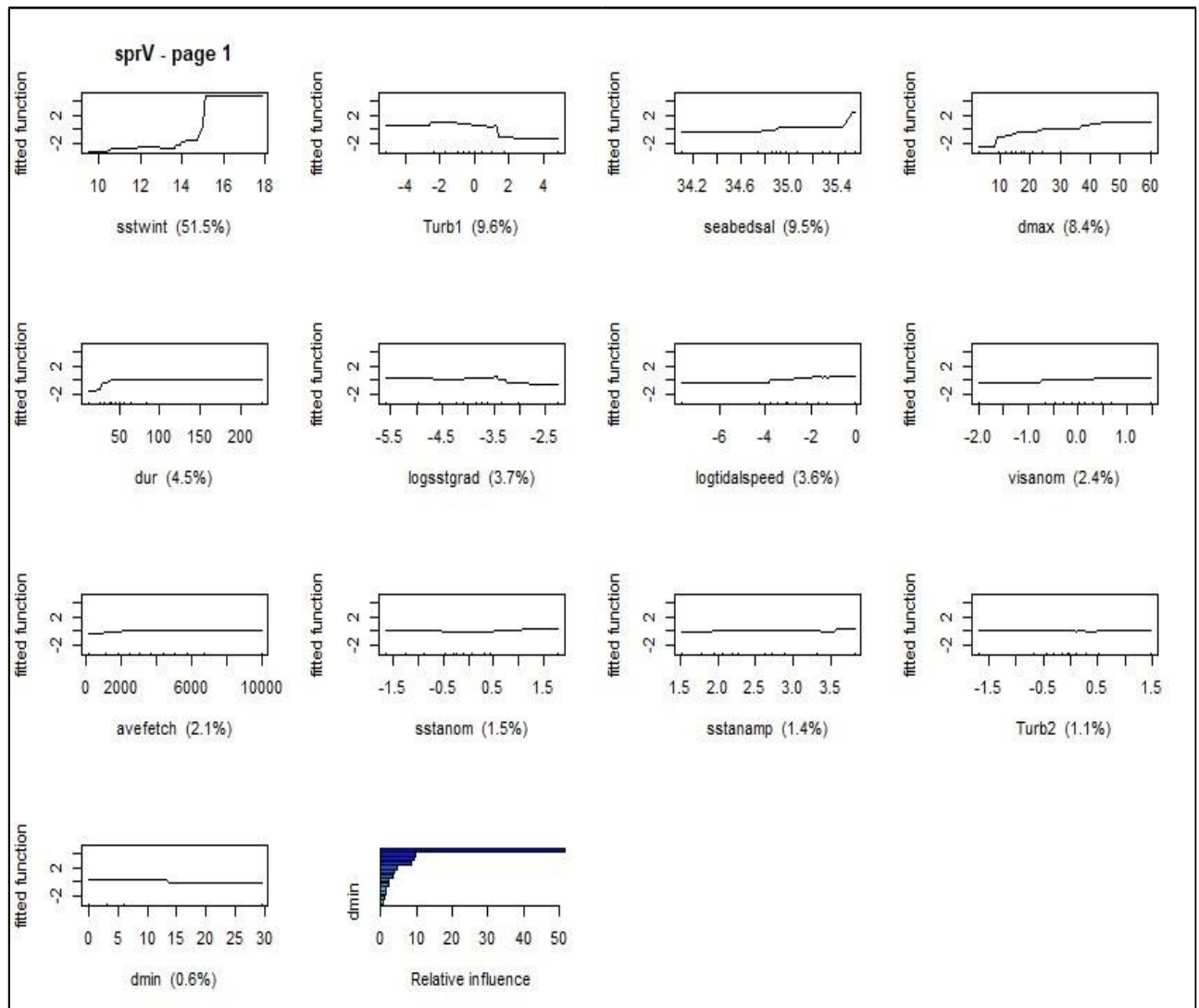


Figure 4.7: Influence of individual predictor variables on response variable of species richness of invertebrate consumers, including the combined variable of 'Turb1 and Turb2' and the visibility anomaly 'visanom'. The y axis for each plot represents the marginal effects of a particular predictor variable on the response variable. It is calculated by comparing predictions across the range of the predictor variable in question, while holding all other predictor variables constant at their median values.

Figure 4.8 maps the predicted distribution of invertebrate consumer species mapped to the NZ coastline. The predicted presence of 16 or more invertivore species (yellow) is seen in the Kermadec and Poor Knights Islands, the far north-east of the North Island and the Coromandel Peninsula. The model predicts more than eight invertebrate consumer species at all sites around the NZ coastline.

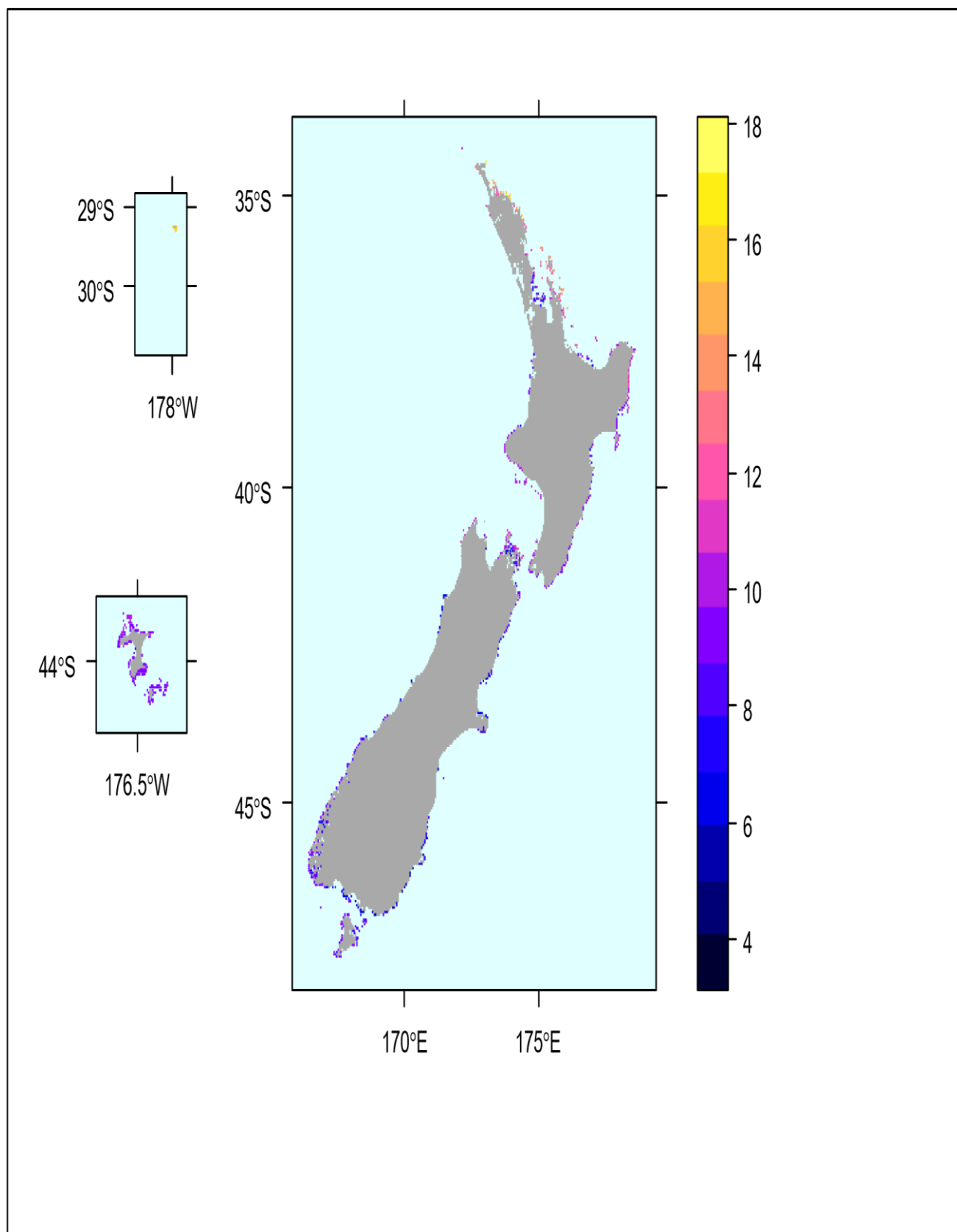


Figure 4.8: Geographic map of predicted distribution of New Zealand rocky reef fish invertivore species. Key indicates how many invertivore species predicted to be found in each region/area. Insets show the Kermadec Islands (top left) and Chatham Islands (bottom left).

The model explained 75% of the deviance for withheld data obtained by fitting 1515 trees. In Figure 4.9, I identified the environmental, geographic and dive-specific variables that were most correlated with the variation in piscivore/benthic invertivores as 'turb 1' (27.8%), 'winter time sea-surface temperature' (20.1%), 'minimum depth of dive' (8.1%), 'sea-surface temperature anomaly' (7.8%), and 'average fetch' (7.7%). Increasing turbidity (PCA axis 1) significantly decreased the predicted presence of piscivore consumer species while increasing winter sea-surface temperature (from 14-15C) significantly increases the presence of piscivore species. Interestingly, the deeper the minimum depth of the dive the lower the predicted presence of fish and benthic invertebrate consumer species. Increasing sea-surface temperature anomaly also decreased the number of species predicted whereas increased exposure from 2000m and dives lasting longer than 50mins (with another stepped increase at 100mins; accounting for 7.7% of the deviance) increased the predicted presence of piscivore/benthic invertivores. Decreasing sea-surface temperature gradient (5.5%) and tidal speed (4.3%) both decrease the species richness of piscivores. Increasing visibility (3.7%), sea-bed salinity (3.5%) and maximum dive depth (2.6%) all improved the chance of finding fish and benthic invertebrate consumer species. The remaining two variables contributed less than 1% each to the total deviance.

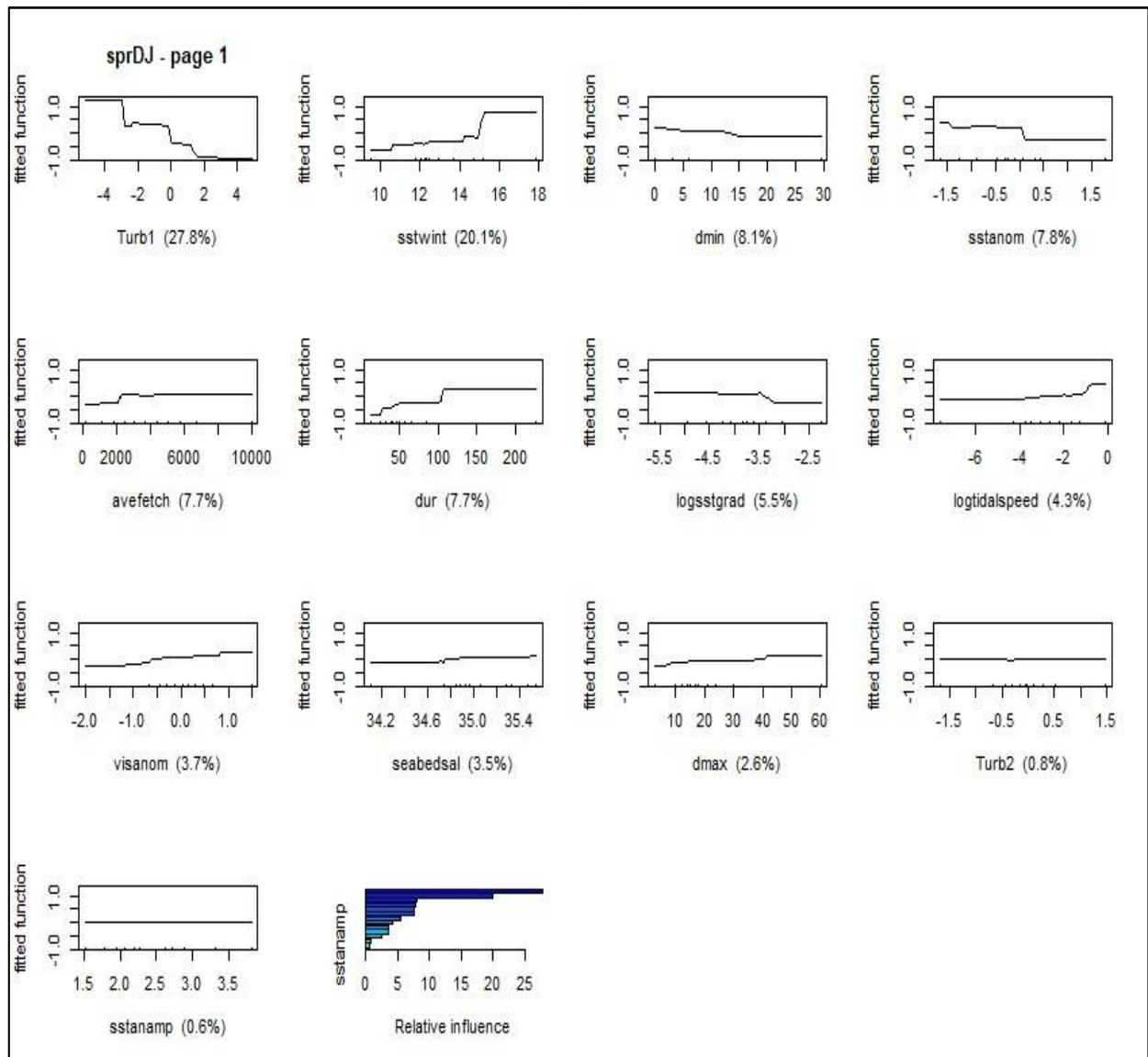


Figure 4.9: Influence of individual predictor variables on response variable of species richness of piscivore/benthic invertivores, including the combined variable of 'turb 1 and turb 2' and the visibility anomaly 'visanom'. The y axis for each plot represents the marginal effects of a particular predictor variable on the response variable. It is calculated by comparing predictions across the range of the predictor variable in question, while holding all other predictor variables constant at their median values.

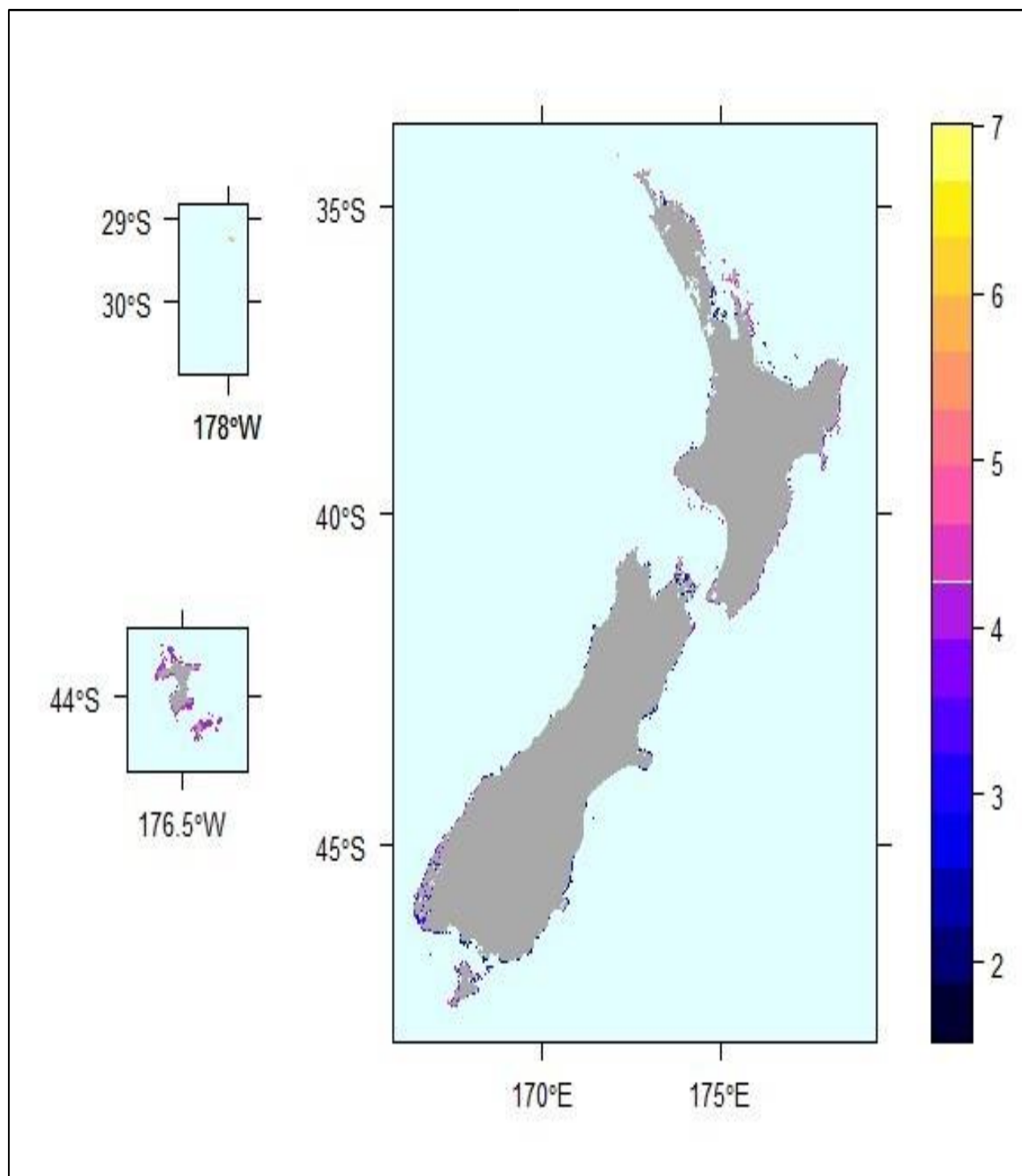


Figure 4.10: Geographic map of predicted distribution of New Zealand rocky reef fish species that consume fish and benthic invertebrates. Key indicates how many piscivore/benthic invertivore species are predicted to be found in each region/area. Insets show the Kermadec Islands (top left) and Chatham Islands (bottom left).

Figure 4.10 maps the predicted distribution of piscivore/benthic invertivore species mapped to the NZ coastline. The predicted presence of 6 or more piscivore consumer

species (yellow) is seen in the Kermadec Islands. The Poor Knights Islands, Chatham Islands and most of the North Island (except the Hauraki Gulf) show moderate species richness (4-5 species). The model predicts more than three fish/benthic invertebrate consumer species at all sites around the NZ coastline.

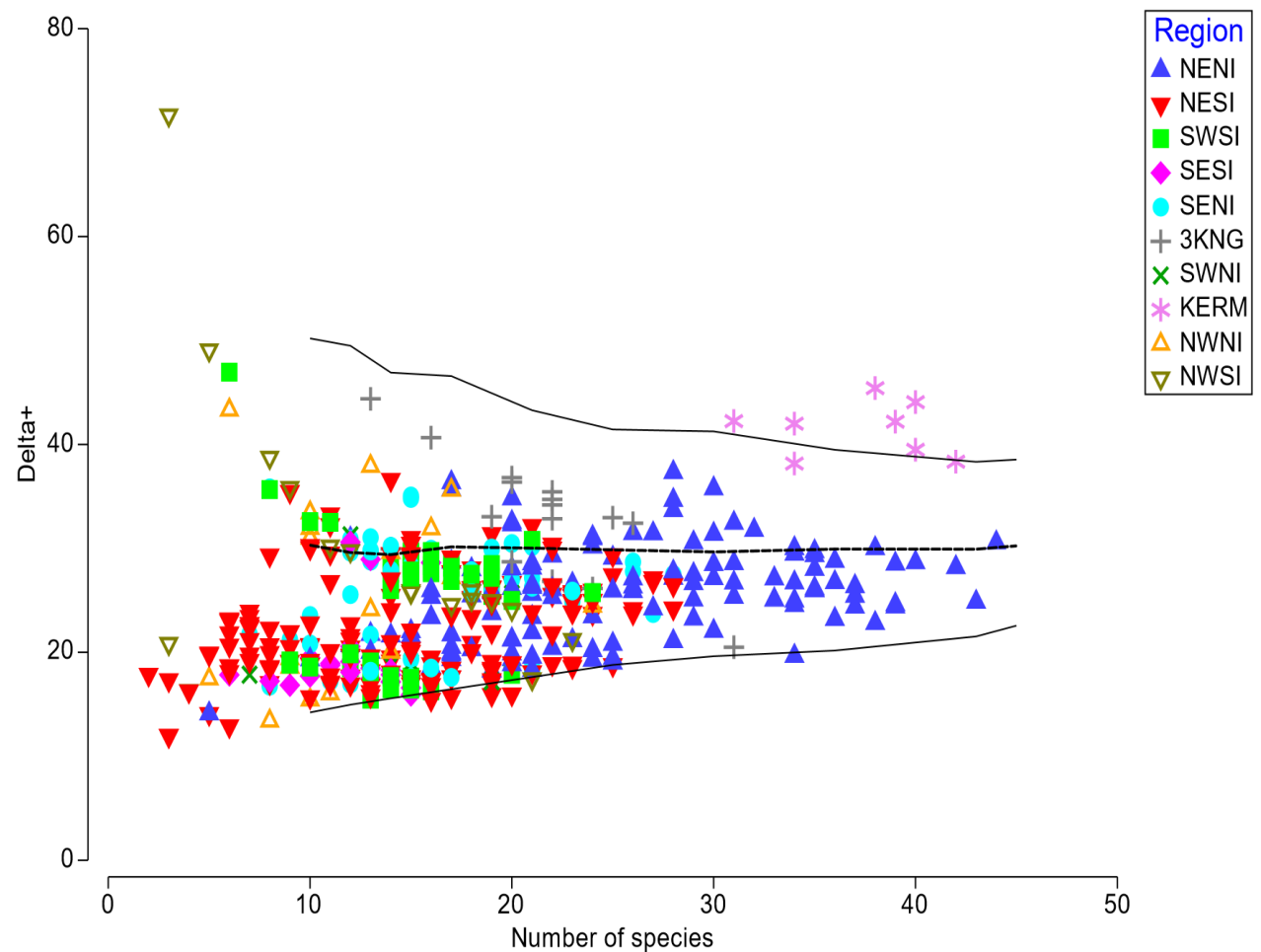


Figure 4.11: : Funnel plots of average diet diversity of the food-items consumed by fish species found at each site in relation to the number of fish species found at each site including a 95% contour. NENI-North east, North Island. NESI-North east, North Island. SWSI-South west, South Island. SESI-South east, South Island. SENI-South east, North Island. 3KNG- The Three King Islands. SWNI-south west, North Island. KERM-The Kermadec Islands. NWNI-North west, North Island. NWSI-North west, South Island.

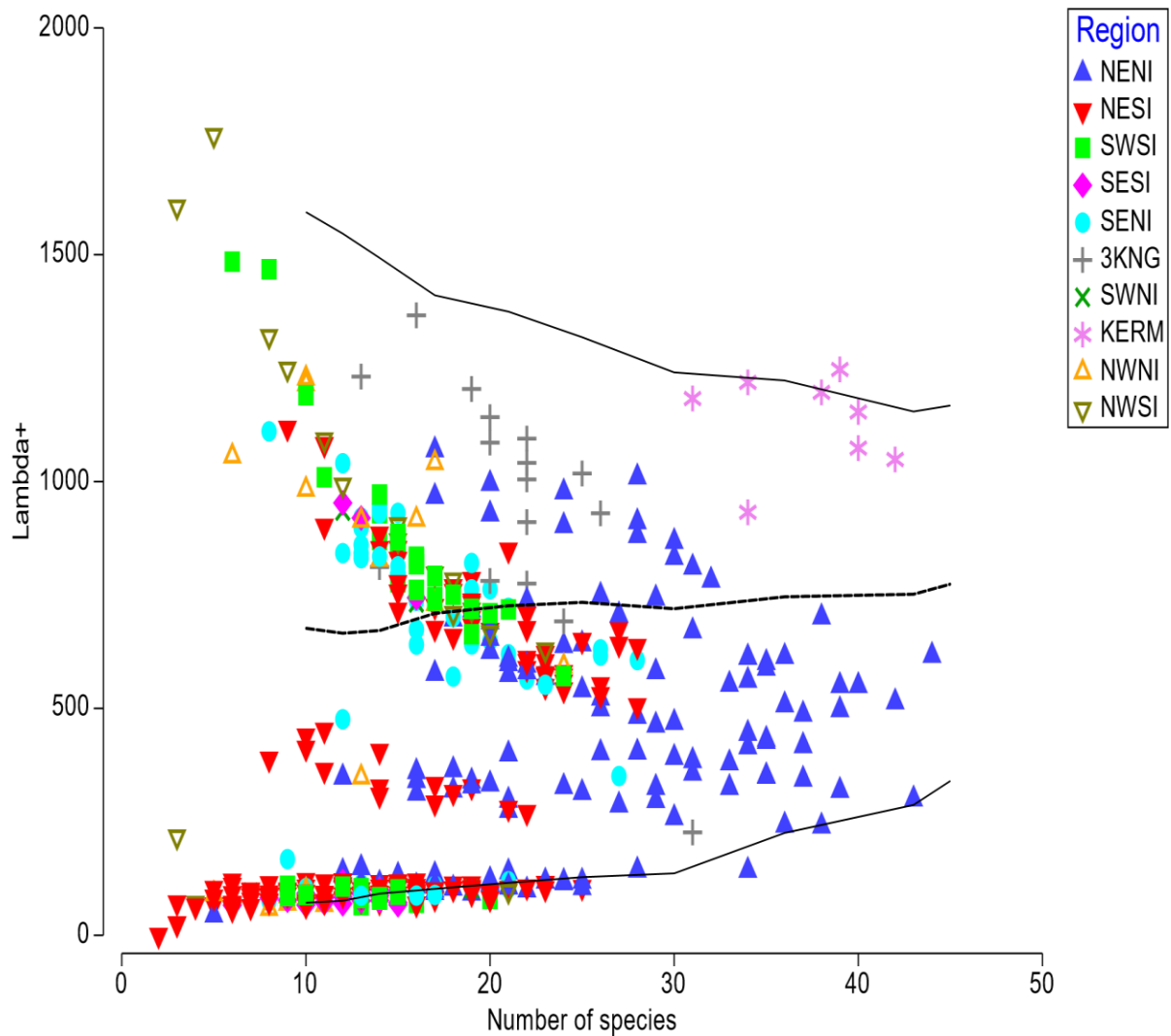


Figure 4.12: Funnel plots of variation in diet diversity (square-rooted) of the food-items consumed by fish species found at each site in relation to the number of fish species found at each site including a 95% contour. NENI-North east, North Island. NESI-North east, North Island. SWSI-South west, South Island. SESI-South east, South Island. SENI-South east, North Island. 3KNG- The Three King Islands. SWNI-south west, North Island. KERM-The Kermadec Islands. NWN-North west, North Island. NWSI-North west, South Island.

The funnel plot of AveDD (Figure 4.11) shows that several sites in the Kermadec Islands and a site in the south west of the South Island surpass the upper 95% contour of expected AveDD, although a majority of the sites are concentrated in the lower half of the contour. This indicates that AveDD is lower than expected given the number of species observed. The funnel plot of VarDD indicates that a site in both the Kermadec Islands and the south west of the South Island surpassing the upper 95% contour (Figure 4.12) which indicates a clustering in the range of food items consumed the by the species at these sites.

#### 4.4 Discussion

I developed predictive models of New Zealand (NZ) rocky reef fishes to explore how spatial patterns in diet diversity were related to environmental and geographic variables. I modelled geographic diet diversity of fishes based on nine broad food item categories in shallow, subtidal, rocky reef habitats to compare the indices of average diet diversity (AveDD), variation in diet diversity (VarDD), and the species richness within the diet guilds of herbivore, invertivore and piscivore/benthic invertivore consumers (as outlined in Chapter 3), using environmental, geographic and dive specific variables. Additionally, I isolated the environmental variables correlated with diet diversity at smaller, regional scales. Overall, I found that diet diversity and species richness did not follow the same spatial patterns, suggesting that the availability of food resources may be an important driver of species distributions around coastal New Zealand. However, some regions of NZ were found to deviate from the overall pattern. Furthermore, the trend varied slightly among the three diet guilds investigated. Below I synthesise major insights that the analysis provides in to diet diversity of fishes around New Zealand and the role that diet plays in the pattern of species richness of New Zealand's fishes.

The models showed that low turbidity was the most important predictor variable for high AveDD. Interestingly, higher levels of turbidity see a small recovery of diversity. Balata et al, (2007) discusses a loss of higher taxonomic levels of benthic marine fish species in response to disturbance. This loss of higher taxa in response high turbidity (turbidity gradient) is also considered by Pearson and Rosenberg (1978) and is discussed in terms of 'organic enrichment' in nearshore benthic environments. A loss of diversity of all biota is expected in disturbed environments (Swartz, 1972) contributing to an overall decrease of diet diversity in reef fish communities. This turbidity gradient is reflected in the geographic map of AveDD, with the Kermadec and to a lesser degree the Poor Knights Islands both predicting greater than expected diet diversity. Increasing exposure increased diversity of diets predicted and in the Kermadec Islands may be indicative of speciation in isolated islands (MacArthur and Wilson, 1967), however this probably not the case at the Poor Knights Islands. Lower salinity levels and warmer water temperatures both contributed to the diversity of diets predicted. This relationship with salinity and water temperature been

previously observed in the estuarine fish species *Acanthopagrus butcheri* (black bream) where higher and more variable salinities saw a restriction in the range of potential prey and therefore a restricted diet composition of the fish community (Chuwen et al, 2007). Tropical waters are known to be more ecologically diverse (Hillebrand, 2004a) and the models seem to support this theory with predicted diet diversity highest at sites with the lowest latitudes.

Variation in diet diversity (VarDD) measures the degree of unevenness in the similarities of the diets among assemblages of fishes. Increasing fetch (exposure) is the most important predictor variable for high VarDD. Again, the Kermadec and Poor Knights Islands show a much higher than expected variation in diet diversity, meaning that several species have very similar diets, but there are also a several species that have different diets from the other co-occurring species. Both sites are protected by no-take marine reserves and their isolation may also alleviate human impacts at these sites as marine extinctions at all levels can be attributed to a) exploitation (55%) and b) habitat loss/degradation (37%) (Dulvy et al. 2003). Turbidity is also an important predictor variable for variation in diet diversity of reef fishes. As discussed with AveDD, reduced taxa inhabiting disturbed environments will limit variation in diet diversity, which will limit availability of food items to consume. A reduced sea surface temperature gradient (i.e. smaller fluctuations in the overall temperature experienced at any particular site) also diminished the variation in diet. This evenness of species that consume dissimilar food items could be explained by strong competition of closely related species limiting their co-existence resulting in a broad spread of divergent species filling unrelated specific diet niches (Darwin, 1859; Cavender-Barnes et al, 2009).

The spatial distribution of herbivores is of particular interest, due to metabolic constraints of an algal diet in fish species habituating temperate regions (Jones & Andrew, 1990). Unsurprisingly, I found winter sea surface temperature to be the highest contributing predictor variable, accounting for 54% of the explained deviance (slightly more than invertivore at 51% and substantially more than piscivore/invertivores at 20%).

Herbivorous species were concentrated in the north east of the North Island and the Kermadec Islands, and declined with latitude, reflecting the patterns found for overall species richness in Chapter 2. Increasing salinity and shallower minimum dive depths also contributed to increased herbivorous fish species. It could be that shallower waters and subtidal areas are more structurally complex, leading to greater habitat heterogeneity although some algal species are specialised to shallow depth as photosynthesis is limited by depth (Barranguet, 1998). Intensity of fish grazing appears to be more locally intense in these heterogeneous areas (Hay, 1981; Choat, 1982). It is worth noting that herbivorous species in temperate waters tend to be generalist feeders in terms of algal species consumed (Horn et al, 1982; Jones & Norman, 1986), although some species (for example

*Odax pullus*) exhibit selective preferences for particular algal taxa (Jones and Andrew, 1990).

The orders of Fucales and Laminariales algae dominate north-eastern NZ coastal reef areas (Schiel, 1988). Species of algae from these orders are thought to be generally intolerant of low salinities (Schiel & Foster, 1986), and are rarely found in estuarine environments (Mathieson and Fraclick, 1973). It appears that, on a broader scale, herbivorous fishes are latitudinally concentrated in regions of warmer water due to the physiological and metabolic constraints of colder waters, as well as locally distributed in open coast reef areas that have higher levels of salinity and are complex and heterogenic in structure.

The diet guild of invertivores (Chapter 3) also reflected the latitudinal spatial distribution seen in overall total species richness in Chapter 2. Predominantly affected by warmer water temperature (>15C), which made up 51.5% of the overall deviance of the withheld data in the model. The Kermadec Islands and the north east of the North Island recorded a higher than expected number of invertebrate consumer species with moderate numbers of invertivore species expected throughout the rest of the North Island, Marlborough Sounds and the Chatham Islands. Previous research has observed higher speciation rates at lower latitudes with multiple explanations for this latitudinal diversity gradient (Hillebrand, 2004a; MacArthur and Wilson, 1967), however new research (Rabosky

et al, 2018) inverses this latitudinal gradient of speciation. The invertivore diet guild (see chapter 3) was the most speciose of all guilds in the analysis (approximately 25% of the overall species analysed) and mechanisms linking these fish species other than shared diet is complicated to address. Similarity in resource partitioning may be attributable to ecological and phenotypic similarity of species with a recent shared ancestry (Cavender-Bares et al, 2009), common in lower latitudes due to recent speciation. Additionally, the species richness of invertivores decreased with turbidity and increased with salinity (Figure 4.6). The models suggest that some fish species may be excluded from highly turbid conditions (Bellwood et al, 2003). Cyrus and Blaber (1992) found salinity and turbidity to have significant influence on fish species distributions in tropical estuarine environments however research specifically on invertebrate consumer species in marine habitats is depauperate.

Piscivores/benthic invertivores was the second most speciose diet guild identified in Chapter 3. Increased turbidity and SSTwint was the strongest predictor of species richness in this guild. The correlation between the overall species richness distribution from Chapter 2 is less apparent for the piscivore/benthic invertivore consumers than herbivore or invertivore guilds. The isolated Kermadec Islands again showed higher than expected number of species from this guild. The rest of the North Island (except the Auckland region) as well as the Chatham Islands showed a moderate number of species. There still seems to be a latitudinal gradient to the species distribution of the piscivore/benthic invertivore guild but without the concentration of species in the north-east of the North Island (Figure 4.10). As previously discussed, turbidity has an adverse effect on diversity of taxa at all levels in the context of both predator and prey species. The harbours around Auckland appear to illustrate the inverse association of diversity with turbidity. As NZ's largest city, disturbance comes from a number of sources (anthropogenic - such as sewage outlets and run-off) (Ellis et al, 2000) as well as wind/wave disturbance (Bell et al, 2008). The richness and distribution of the piscivore/benthic invertivore guild seem to be predominantly driven by localised environmental processes.

## 4.5 Conclusion

Patterns in the diversity of diets in NZ rocky reef fish species are complicated and multifaceted. At broad spatio-temporal scales, biogeographical processes such as isolation and speciation are thought to influence species distributions and richness (MacArthur & Wilson 1967; Cavender-Barnes et al., 2009). At regional scales, environmental variables and their influence on available resources can act as filters, driving species diversity (Ricklefs, 2004; Cavender-Barnes, 2009) while species interactions within communities and spatial heterogeneity are thought to be the main mechanisms in small spatial scales of habitats (Davies et al, 2005). High average diet diversity and variation in diet diversity at the isolated Kermadec Islands and Poor Knights Islands seem to be correlated with local environmental conditions (from the predictions of turbidity and fetch) as there is no general declining diet diversity gradient (north to south) with these variables, which would indicate broader scale processes. The species richness of the three diet guilds show variations in latitudinal gradients in their geographic distributions. The diversity of two of the three diet guilds (herbivores and invertivores) show similar patterns to the overall species richness gradient seen in Chapter 2, being driven by the environmental variables of SST<sub>wint</sub>, turbidity and salinity with warmer water temperatures indicative of biogeographical processes on a regional scale, whereas salinity and turbidity possibly work on more localised scales. The diversity of the piscivore-benthic invertivore guild showed far less correlation with SST<sub>wint</sub> but a stronger relationship with turbidity. In conclusion, I find that the food items that species consume can play a significant role in species distributions, driven by environmental variables at both regional and local scales.

## Chapter 5

### **General Discussion and overall chapter synthesis**

In this General Discussion, I review the major findings of each chapter and synthesise the results. I discuss the findings of my research in the context of the broader literature and offer some future directions for further research on reef fishes in New Zealand and the use of multiple indices to measure species richness patterns.

#### **5.1 Chapter 2 conclusions**

Chapter 2 models coastal rocky reef fish species richness, average taxonomic distinctness and variation in taxonomic distinctness. I was interested in testing whether global latitudinal gradients (Hillebrand, 2004a&b; Gaston 1996) in species richness (where lower latitudes have high species richness declining toward higher latitudes) are present on a national scale in New Zealand (NZ). I also considered whether measures of taxonomic diversity and variation also reflected this latitudinal gradient of species diversity. To test these ideas, I addressed species richness as the basic index of diversity in this chapter. Our analysis of species richness supported latitudinal gradients of diversity based on environmental predictor variables that strongly correlated with latitude (such as wintertime sea-surface temperature), but also other more local processes, such as isolation (average fetch and turbidity). I found Fiordland and the Marlborough Sounds to have higher than predicted levels of taxonomic distinctness as well as unevenly clustered taxonomic groups within these regions, this suggests that fine-scale local environmental processes, and potentially food resources, are important in driving taxonomic diversity patterns.

#### **5.2 Chapter 3 conclusions**

One of the hypotheses from Chapter 2 was whether diet or use of resources inform patterns of species richness. Here, I address one of the questions resulting from the Chapter 2 analysis; can I quantitatively describe the use of food resources of each of the study species. I intended to provide an objective method for categorising groups of fishes that shared a similar diet, using these relationships to understand how resource partitioning and food item availability might determine species distributions and ultimately impact overall patterns of species richness. Using a quantitative (based on diet items recorded

from the literature) rather than qualitative analysis of diet is not new, it is however innovative over so many species. Comparisons of diet across multiple species in a robust, multivariate framework divulges relationships that were not initially apparent. Disregarding taxonomic similarities and subjective expert analysis I was able to ascertain similarities in the diet of species based purely on quantitative analysis. This analysis yielded eight diet guilds. I hypothesised that these diet guilds may be differently influenced, and limited, by available food resources around NZ affecting their distributions. In addition, I presented a proof of concept that this methodology can objectively distinguish diet guilds that were intuitive in nature (herbivores) and also guilds that were previously unanticipated (such as *Ostracion cubicus* and *Notothenia angustata*). This analysis furthers our understanding of the food resource requirements of NZ's rocky reef fishes.

### 5.3 Chapter 4 conclusions

Chapter 4 explores one of the hypotheses proposed from Chapter 2, whether a species use of food resources (diet) affects patterns of species richness. By utilising the quantitative analysis approach from Chapter 3 I was able to model 1) the species richness of three of the eight diet guilds, and 2) the dietary distinctness between species and variation in that distinctness (the latter was across all species). I then employed this new analysis of hierarchical similarities based on diet based on the same multivariate method I employed to quantify taxonomic distinctness and variation in Chapter 2. I wanted to understand how diet and food resources consumed on NZ's rocky reefs affected patterns of species richness with reference to resource availability and the role of local environments. I found that herbivores were directly restricted in their range by environmental factors such as a minimum temperature tolerance. For the piscivore/benthic invertebrate consumers I found that food resources likely played a role in determining the patterns of species richness as the variable of turbidity was the most important. I found that spatial variations in patterns of species richness for these guilds reflected the overall latitudinal species richness gradient, which correlated with predictor variables of sea-surface temperature and fetch. I also found strong correlations across the three diet guilds analysed (herbivores, invertivores, and piscivore/benthic invertivores) with the variables of turbidity and salinity, which seem to reflect local-scale processes high turbidity and low salinity decreased the species observed in a

particular area. Overall, I concluded that patterns of species richness may be determined by both direct and indirect processes that affect species distributions, whether prey or predator, physiological and metabolic constraints or environmental drivers that occur at both broad and fine spatial scales.

#### *5.4 General Discussion*

Diversity has traditionally been measured in terms of species richness (Gaston, 1996). However, species richness used as an index in isolation does little to explain underlying relationships between an individual species and its environment nor does it build an understanding of inter-species partitioning within that habitat (Villegger et al, 2017). Species richness gradients, of increasing species number towards lower latitudes are seen in many taxonomic groups (birds –Blackburn and Gaston, 1996; mammals – Kaufman, 1995), but there are exceptions such as aphids (Dixon et al, 1987) and marine amphipods (Barnard, 1991). By using indices of diversity that also reflect the functionality of a species (such as resource use) as well as quantifying taxonomic dis/similarities I can build a greater understanding of the processes by which an assemblage functions, its resilience and the ecological and geographical drivers of an assemblage’s diversity (Clarke and Warwick, 1998; Faith, 1992). In a previous analysis of fish species richness patterns around coastal NZ (Leathwick et al, 2006) found higher species richness at depth and in areas of high primary productivity found in mixing bodies of water. In my research, I compare multiple indices so that I may ascertain why a specific species is found in a particular area, predict where else they may be found correlated with similar environmental variables, and the indirect and direct processes that underlie that environment resulting in specific species’ assemblages.

This research provides an innovative quantitative diet analysis of 158 New Zealand rocky reef fish species utilising broad food item categories to produce distinct diet guilds based on multivariate, hierarchical analysis of similarities of diet. Along with these diet guilds, I analysed the taxonomic distinctness and the evenness/unevenness in taxonomic similarities of fish in coastal regions around New Zealand. By comparing taxonomic relationships within regions and the overall species richness distributions as indices of diversity, a more subtle understanding of the assemblage composition is revealed. Moreover, by comparing species distributions based on quantitative diet analysis I add yet another

measure of diversity to my research. Figure 5.1 compares all the indices I have measured in the previous three chapters.

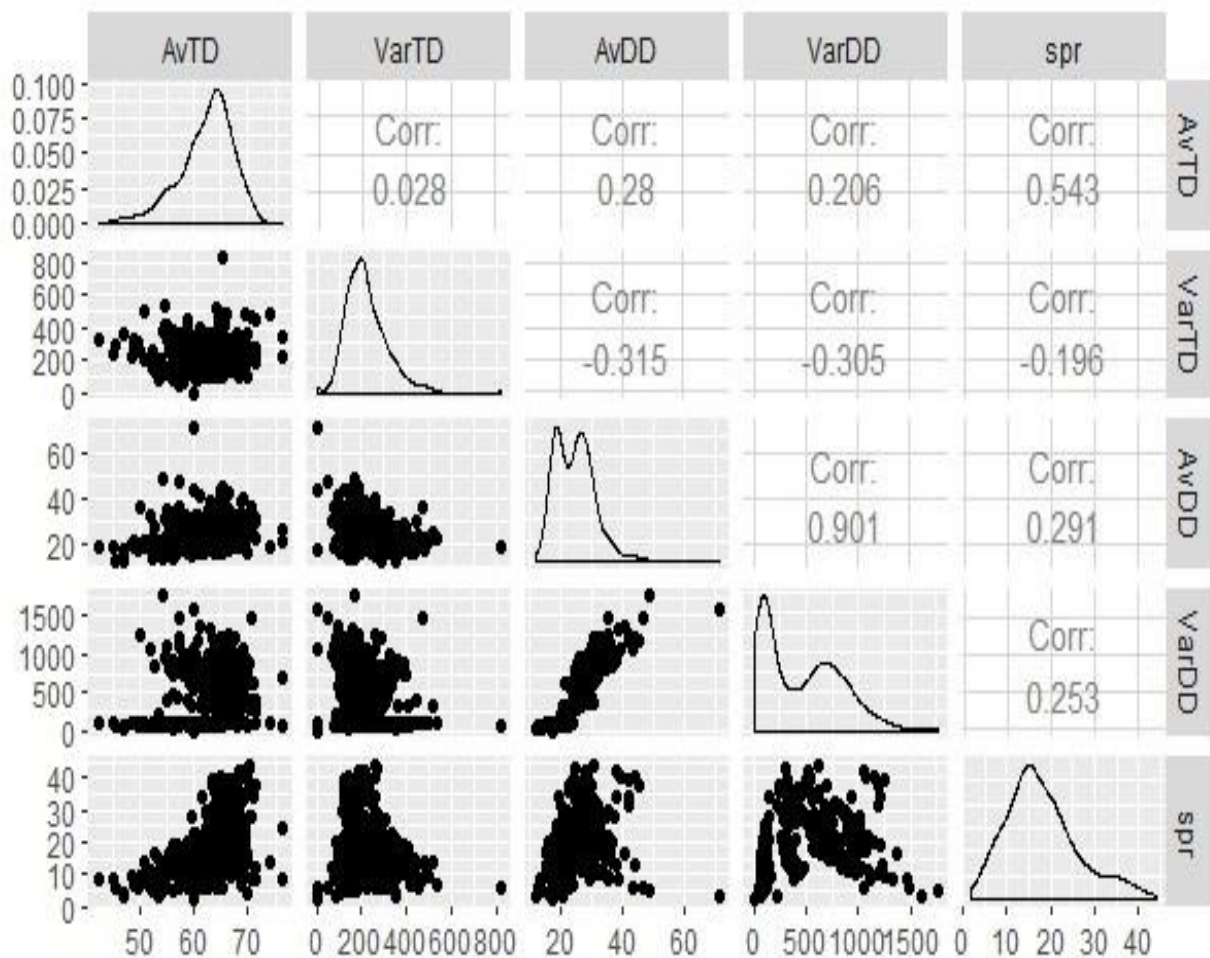


Figure 5.1: Pairs plots of the correlations between average taxonomic distinctness, variation in taxonomic distinctness, species richness, average diet diversity and variation in diet diversity across 467 sites in New Zealand.

In Figure 5.1, a strong correlation (0.901) is observed between AveDD and VarDD which may indicate overlapping ecological drivers behind these variables. AveDD and VarDD scale with each other, which means that locations with species that consume from multiple guilds were also closely related guilds. Diet diversity is not highly correlated with species richness, especially in locations with high diet diversity, which means that species richness patterns around New Zealand may not be primarily driven by food item availability. Instead, a direct relationship with other environmental factors (i.e. not mediated by their reliance on certain food resources) may be more important in determining patterns of

species richness. The other indices seem to be heterogeneous in their relationships which shows that using multiple indices of diversity can help illuminate different underlying specific environmental drivers found in both local and regional processes and therefore both indirect and direct processes that dictate species richness and their distributions.

### *5.5 Future directions*

This research utilised an observational historical dataset which was not collected with traditional sampling methods. There are limitations with non-standardised data collected over long periods of time, however, I strove to alleviate this with the types of statistical analyses used (BRTs and TAXDTEST). This research illustrates ways by which new quantitative methodologies are employed to extract meaningful analysis from pre-existing data. I also data mined over 50 years of diet and feeding mode data available in the current literature for NZ fish species. Utilising pre-existing research and data shows the new possibilities for quantitative analysis to understand new ideas in food availability and resource use in fish assemblages based on environmental drivers and inherent physiology.

Several future research avenues are highlighted by this research. These models, based on easily acquired environmental and geographic variables and the resulting predictive spatial distributions have pinpointed regions worthy of further study. Further research into resource partitioning of the eight diet guilds at the Kermadec Islands, Fiordland, Marlborough Sounds and Poor Knights Islands may be of some interest due to their unusual status as being not only species rich within specific diet guilds but also taxonomically distinct and variable. Investigating the patterns in species richness of the other five diet guilds may also be complementary to this work.

Applications of this quantitative method of diet analysis utilised in Chapter 3 may also be trialled in other habitats and with other species to confirm its robustness. Analysing habitats in terms of diet/resource partitioning and well as other functional traits (e.g. fin size, gape size) is becoming common place in ecology (Villegger, 2008), therefore further research into how fish diet guilds (e.g. invertivores, piscivores) interact with specific environmental variables on smaller spatial scales may be a credible research pursuit.

## References

- Akin, S., Buhan, E., Winemiller, K. O., & Yilmaz, H. (2005). Fish assemblage structure of Koycegiz Lagoon–Estuary, Turkey: Spatial and temporal distribution patterns in relation to environmental variation. *Estuarine, Coastal and Shelf Science*, 64(4), 671-684.
- Anderson, M. J., & Millar, R. B. (2004). Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand. *Journal of Experimental Marine Biology and Ecology*, 305(2), 191-221.
- Andriashev, A. P. (1953). Ancient deep-water and secondary deep-water fishes and their importance in a zoogeographical analysis. *Notes on special problems in ichthyology*.
- Balata, D., Piazzì, L., & Benedetti-Cecchi, L. (2007). Sediment disturbance and loss of beta diversity on subtidal rocky reefs. *Ecology*, 88(10), 2455-2461.
- Barnard, J. L. (1991). Amphipodological agreement with Platnick. *Journal of Natural History* 25, 1675-76.
- Barranguet, C., Kromkamp, J., & Peene, J. (1998). Factors controlling primary production and photosynthetic characteristics of intertidal microphytobenthos. *Marine Ecology Progress Series*, 173, 117-126.
- Behrens, M. D., & Lafferty, K. D. (2007). Temperature and diet effects on omnivorous fish performance: implications for the latitudinal diversity gradient in herbivorous fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 64(6), 867-873.
- Bell, S. S., Fonseca, M. S., & Kenworthy, W. J. (2008). Dynamics of a subtropical seagrass landscape: links between disturbance and mobile seed banks. *Landscape Ecology*, 23(1), 67-74.
- Bellwood, D. R., Wainwright, P. C., Fulton, C. J., & Hoey, A. (2002). Assembly rules and functional groups at global biogeographical scales. *Functional Ecology*, 16(5), 557-562.
- Bellwood, D. R., Hoey, A. S., & Choat, J. H. (2003). Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology letters*, 6(4), 281-285.
- Bernard, E., & Fenton, M. B. (2002). Species diversity of bats (Mammalia: Chiroptera) in forest fragments, primary forests, and savannas in central Amazonia, Brazil. *Canadian Journal of Zoology*, 80(6), 1124-1140.
- Blackburn, T. M., & Gaston, K. J. (1996). Spatial patterns in the geographic range sizes of bird species in the New World. *Phil. Trans. R. Soc. Lond. B*, 351(1342), 897-912.
- Budd, A. F., & Pandolfi, J. M. (2010). Evolutionary novelty is concentrated at the edge of coral species distributions. *Science*, 328(5985), 1558-1561.
- Bonato, K. O., Delariva, R. L., & da Silva, J. C. (2012). Diet and trophic guilds of fish assemblages in two streams with different anthropic impacts in the northwest of Paraná, Brazil. *Zoologia*, 29(1).
- Cavender-Bares, J., Kozak, K. H., Fine, P. V., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology letters*, 12(7), 693-715.
- Chase, J. M., & Leibold, M. A. (2003). *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press.
- Choat, J. H. (1982). Fish feeding and the structure of benthic communities in temperate waters. *Annual review of ecology and systematics*, 13(1), 423-449.
- Choat, J. H., & Ayling, A. M. (1987). The relationship between habitat structure and fish faunas on New Zealand reefs. *Journal of experimental marine biology and ecology*, 110(3), 257-284.
- Choat, J. H., & Bellwood, D. R. (1991). Reef fishes: their history and evolution. In *The ecology of fishes on coral reefs* (pp. 39-66).
- Chuwen, B. M., Platell, M. E., & Potter, I. C. (2007). Dietary compositions of the sparid *Acanthopagrus butcheri* in three normally closed and variably hypersaline estuaries differ markedly. *Environmental Biology of Fishes*, 80(4), 363.
- Clarke, K. R., & Gorley, R. N. (2006). *Primer-E, Plymouth*. Clarke, K. R., Somerfield, P. J., & Gorley, R. N. (2008). Testing of null hypotheses in exploratory community analyses:

- similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology*, 366(1-2), 56-69.
- Clarke, K. R., & Warwick, R. M. (1998). A taxonomic distinctness index and its statistical properties. *Journal of applied ecology*, 35(4), 523-531.
- Colman, D. R., Toolson, E. C., & Takacs-Vesbach, C. D. (2012). Do diet and taxonomy influence insect gut bacterial communities? *Molecular Ecology*, 21(20), 5124-5137.
- Crawley, M. J. (2013). *The R book*. Retrieved from Massey University Library Catalogue.
- Clarke, K. R., & Warwick, R. M. (2001). A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine ecology Progress series*, 216, 265-278.
- Eggleton, P. (1994). Termites live in a pear-shaped world: a response to Platnick. *Journal of Natural History* 28, 318-30.
- Cyrus, D. P., & Blaber, S. J. M. (1992). Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. *Estuarine Coastal and Shelf Science*, 35, 545-563.
- Davies, K. F., Chesson, P., Harrison, S., Inouye, B. D., Melbourne, B. A., & Rice, K. J. (2005). Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. *Ecology*, 86(6), 1602-1610.
- Darwin, C. (1859). On the origin of species by means of natural selection. *Murray, London*.
- Davis, J. H. (1940). The ecology and geologic role of mangroves in Florida. *Publications of the Carnegie Institution of Washington*, (517), 303-412.
- Dawbin, W. H. (1956). *Whale marking in South Pacific waters*.
- Dawbin, W. H. (1966). The seasonal migratory cycle of humpback whales. *Whales, dolphins and porpoises. University of California Press, Berkeley*, 145-170.
- Diaz, S., & Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in ecology & evolution*, 16(11), 646-655.
- Dixon, A. F. G., Kindlmann, P., Leps, J., & Holman, J. (1987). Why there are so few species of aphids, especially in the tropics. *The American Naturalist*, 129(4), 580-592.
- Dobzhansky, T. (1950). Evolution in the tropics. *American Scientist*, 38(2), 209-221.
- Dulvy, N. K., Sadovy, Y., & Reynolds, J. D. (2003). Extinction vulnerability in marine populations. *Fish and fisheries*, 4(1), 25-64.
- Eken, G., Bennun, L., Brooks, T. M., Darwall, W., Fishpool, L. D. C., Foster, M., Knox, D., Langhammer, P., Matiku, P., Radford, E., Salaman, P., Sechrest, W., Smith, M. L., Spector, S. & Tordoff, A. (2004). *Key Biodiversity Areas as Site Conservation Targets*. *BioScience*, 54(12), 1110-1118.
- Elith, J., Graham, C. H., Anderson, R. P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. McC., Peterson, A. T., Phillips, S. J., Richardson, K. S., Scachetti-Pereira, R., Schapire, R. E., Soberon, J., Williams, S., Wisz, M. S. & Zimmerman, N. E. (2006). Novel methods improve prediction of species distributions from occurrence data. *Ecography*, 29, 129-151.
- Elith, J., Leathwick, J. R. & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, 77, 802-813.
- Elith, J. & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution and Systematics*, 40, 677-697.
- Ellis, J. I., Schneider, D. C., & Thrush, S. F. (2000). Detecting anthropogenic disturbance in an environment with multiple gradients of physical disturbance, Manukau Harbour, New Zealand. In *Island, Ocean and Deep-Sea Biology* (pp. 379-391). Springer, Dordrecht.
- Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological conservation*, 61(1), 1-10.

- Faith, D. P. & Walker, P. A. (1996). Environmental diversity: on the best possible use of surrogate data for
- Fauchald, K., & Jumars, P. A. (1979). The diet of worms: a study of polychaete feeding guilds.
- Fletcher, D., MacKenzie, D., & Villouta, E. (2005). Modelling skewed data with many zeros: a simple approach combining ordinary and logistic regression. *Environmental and ecological statistics*, 12(1), 45-54.
- Floeter, S. R., Behrens, M. D., Ferreira, C. E. L., Paddock, M. J., & Horn, M. H. (2005). Geographical gradients of marine herbivorous fishes: patterns and processes. *Marine Biology*, 147(6), 1435-1447.
- Floeter, S. R., Ferreira, C. E. L., Dominici-Arosemena, A., & Zalmon, I. R. (2004). Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. *Journal of Fish Biology*, 64(6), 1680-1699.
- Fralick RA, Mathieson AC (1973) Ecological studies of *Codium fragile* in New England, USA. *Marine Biology* 19. 127–132
- Francis, M. (1996). *Coastal fishes of New Zealand: an identification guide* (p. 72). Auckland: Reed.
- Francis, M. P. (1996). Geographic distribution of marine reef fishes in the New Zealand region. *New Zealand Journal of Marine and Freshwater Research*, 30(1), 35-55.
- Gaston, K. J. (1996). Biodiversity-latitudinal gradients. *Progress in Physical Geography*, 20(4), 466-476.
- Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology letters*, 4(4), 379-391.
- Gray, J. S. (2002). Species richness of marine soft sediments. *Marine Ecology Progress Series*, 244, 285-297.
- Greenberg, R., Bichier, P., & Sterling, J. (1997). Bird populations in rustic and planted shade coffee plantations of eastern Chiapas, Mexico. *Biotropica*, 29(4), 501-514.
- Guerrero, I., Morales, M. B., Oñate, J. J., Aavik, T., Bengtsson, J., Berendse, F. & Fischer, C. (2011). Taxonomic and functional diversity of farmland bird communities across Europe: effects of biogeography and agricultural intensification. *Biodiversity and conservation*, 20(14), 3663-3681.
- Hay, M. E. (1981). Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquatic botany*, 11, 97-109.
- Hillebrand, H. (2004a). On the generality of the latitudinal diversity gradient. *The American Naturalist*, 163(2), 192-211.
- Hillebrand, H. (2004b). Strength, slope and variability of marine latitudinal gradients. *Marine Ecology Progress Series*, 273, 251-267.
- Horn, M. H., Murray, S. N., & Edwards, T. W. (1982). Dietary selectivity in the field and food preferences in the laboratory for two herbivorous fishes (*Cebidichthys violaceus* and *Xiphister mucosus*) from a temperate intertidal zone. *Marine Biology*, 67(3), 237-246.
- Jones, G. P. (1988). Ecology of rocky reef fish of north-eastern New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research*, 22(3), 445-462.
- Jones, G. P., & Andrew, N. L. (1990). Herbivory and patch dynamics on rocky reefs in temperate Australasia: the roles of fish and sea urchins. *Australian Journal of Ecology*, 15(4), 505-520.
- Jones, G. P., & Norman, M. D. (1986). Feeding selectivity in relation to territory size in a herbivorous reef fish. *Oecologia*, 68(4), 549-556.
- Leathwick, J. R., Elith, J., Francis, M. P., Hastie, T., & Taylor, P. (2006). Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. *Marine Ecology Progress Series*, 321, 267-281.
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press.
- Mathieson, A. C., & Fralick, R. A. (1973). Benthic algae and vascular plants of the lower Merrimack River and adjacent shoreline. *Rhodora*, 75(801), 52-64.

- Micheli, F., & Halpern, B. S. (2005). Low functional redundancy in coastal marine assemblages. *Ecology Letters*, 8(4), 391-400.
- Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., ... & McCain, C. M. (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, 10(4), 315-331.
- Mouillot, D., Gaillard, S., Aliaume, C., Verlaque, M., Belsher, T., Troussellier, M., & Do Chi, T. (2005). Ability of taxonomic diversity indices to discriminate coastal lagoon environments based on macrophyte communities. *Ecological Indicators*, 5(1), 1-17.
- Novakowski, G. C., Hahn, N. S., & Fugi, R. (2008). Diet seasonality and food overlap of the fish assemblage in a pantanal pond. *Neotropical Ichthyology*, 6(4), 567-576.
- Oberdorff, T., Guégan, J. F., & Hugueny, B. (1995). Global scale patterns of fish species richness in rivers. *Ecography*, 18(4), 345-352.
- Pearson, T. H., & Rosenberg, R. (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.*, 16, 229-311.
- Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5(3), 402-411.
- Platell, M. E., & Potter, I. C. (2001). Partitioning of food resources amongst 18 abundant benthic carnivorous fish species in marine waters on the lower west coast of Australia. *Journal of Experimental Marine Biology and Ecology*, 261(1), 31-54.
- Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., & Alfaro, M. E. (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 1.
- Ricklefs, R. E. (1987). Community diversity: relative roles of local and regional processes. *Science*, 235(4785),
- Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, 7(1), 1-15.
- Roberts, C., Stewart, A. L., & Struthers, C. D. (Eds.). (2015). *The Fishes of New Zealand*. Te Papa Press.
- Rohde, K. (1992). Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, 514-527.
- Root, R. B. (1967). The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological monographs*, 37(4), 317-350.
- Roberts, C. M. (1995). Effects of fishing on the ecosystem structure of coral reefs. *Conservation biology*, 9(5), 988-995.
- Russell, B. C. (1977). Population and standing crop estimates for rocky reef fishes of North-Eastern New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 11(1), 23-36.
- Russell, B. C. (1983). The food and feeding habits of rocky reef fish of north-eastern New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 17(2), 121-145.
- Sale, P. F. (1977). Maintenance of high diversity in coral reef fish communities. *The American Naturalist*, 111(978), 337-359.
- Schiel, D. R., & Foster, M. S. (1986). The structure of subtidal algal stands in temperate waters. *Oceanography and Marine Biology*, 24, 265-307.
- Schiel, D. R. (1988). Algal interactions on shallow subtidal reefs in northern New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research*, 22(3), 481-489.
- Shannon, C. E. (1949). *The Mathematical Theory of Communication*. By CE Shannon and Warren Weaver. Urbana.
- Simberloff, D., & Dayan, T. (1991). The guild concept and the structure of ecological communities. *Annual review of ecology and systematics*, 22(1), 115-143.
- Soininen, J., McDonald, R., & Hillebrand, H. (2007). The distance decay of similarity in ecological communities. *Ecography*, 30(1), 3-12.

- Smith, A. N., Duffy, C. A. J., & Leathwick, J. R. (2013). *Predicting the distribution and relative abundance of fishes on shallow subtidal reefs around New Zealand*. Publishing Team, Department of Conservation.
- Snelder, T. H., Leathwick, J. R., Dey, K. L., Rowden, A. A., Weatherhead, M. A., Fenwick, G. D., ... & Hewitt, J. E. (2007). Development of an ecologic marine classification in the New Zealand region. *Environmental Management*, 39(1), 12-29.
- Snelder, T., Leathwick, J., Dey, K., Weatherhead, M., Fenwick, G., Francis, M., & Hume, T. (2005). The New Zealand marine environment classification. *Wellington, Ministry for the Environment*.
- Somerfield, P. J., & Clarke, K. R. (1995). Taxonomic levels, in marine community studies, revisited. *Marine Ecology Progress Series*, 127, 113-119.
- Somerfield, P. J., & Clarke, K. R. (2013). Inverse analysis in non-parametric multivariate analyses: distinguishing groups of associated species which covary coherently across samples. *Journal of Experimental Marine Biology and Ecology*, 449, 261-273.
- Spellerberg, I. F. (1991). Biogeographical basis of conservation. *The scientific management of temperate communities for conservation*. 293-322.
- Spellerberg, I. F., & Fedor, P. J. (2003). A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the ‘Shannon–Wiener’ Index. *Global ecology and biogeography*, 12(3), 177-179.
- Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., ... & Becerro, M. A. (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature*, 501(7468), 539.
- Swartz, R. C. (1972). Biological criteria of environmental change in the Chesapeake Bay. *Chesapeake Science*, 13, S17-S41.
- Terlizzi, A., Scuderi, D., Fraschetti, S., & Anderson, M. J. (2005). Quantifying effects of pollution on biodiversity: a case study of highly diverse molluscan assemblages in the Mediterranean. *Marine Biology*, 148(2), 293-305.
- Thiollay, J. M. (1990). Comparative diversity of temperate and tropical forest bird communities: the influence of habitat heterogeneity. *Acta Oecologica*, 11(6), 887-911.
- Thompson, S. (1981). *Fish of the marine reserve: a guide to the identification and biology of common coastal fish of north-eastern New Zealand*. Leigh Laboratory, University of Auckland.
- Toft, C. A. (1981). Feeding ecology of Panamanian litter anurans: patterns in diet and foraging mode. *Journal of Herpetology*, 139-144.
- Tolimieri, N., & Anderson, M. J. (2010). Taxonomic distinctness of demersal fishes of the California current: moving beyond simple measures of diversity for marine ecosystem-based management. *PLoS One*, 5(5), e10653.
- Trip, E. D., Clements, K. D., Raubenheimer, D., & Choat, J. H. (2014). Temperature-related variation in growth rate, size, maturation and life span in a marine herbivorous fish over a latitudinal gradient. *Journal of animal ecology*, 83(4), 866-875.
- Vane-Wright, R. I., Humphries, C. J., & Williams, P. H. (1991). What to protect?—Systematics and the agony of choice. *Biological conservation*, 55(3), 235-254.
- Villéger, S., Mason, N. W., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), 2290-2301.
- Villéger, S., Brosse, S., Mouchet, M., Mouillot, D., & Vanni, M. J. (2017). Functional ecology of fish: current approaches and future challenges. *Aquatic Sciences*, 79(4), 783-801.
- Warwick, R. M., & Clarke, K. R. (1995). New ‘biodiversity’ measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series*, 129, 301-305.
- Webb, C. O., Ackerly, D. D., McPeck, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual review of ecology and systematics*, 33(1), 475-505.

- Willig, M. R., Kaufman, D. M., & Stevens, R. D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 273-309.
- Wright, J. P., Naeem, S., Hector, A., Lehman, C., Reich, P. B., Schmid, B., & Tilman, D. (2006). Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters*, 9(2), 111-120.
- Zintzen, V., Anderson, M. J., Roberts, C. D., & Diebel, C. E. (2011). Increasing variation in taxonomic distinctness reveals clusters of specialists in the deep sea. *Ecography*, 34(2), 306-317.
- Zurell, D., Zimmermann, N. E., Sattler, T., Nobis, M. P., & Schröder, B. (2016). Effects of functional traits on the prediction accuracy of species richness models. *Diversity and Distributions*, 22(8), 905-917.



Aul.chi	Aulostomidae	Aulostomus chinensis	4.2	0	0	0	0	0	1	2	0	0
Hip.abd	Syngnathidae	Hippocampus abdominalis	3.4	0	0	0	1	1	2	1	0	0
Sti.mac	Syngnathidae	Stigmatopora macropterygia	3.5	0	0	2	1	1	1	0	0	0
Sol.spi	Syngnathidae	Solegnathus spinosissimus	3.5	0	0	2	1	1	1	0	0	0
Pte.vol	Scorpaenidae	Pterois volitans	4.4	0	0	0	0	1	1	2	1	0
Hel.per	Sebastidae	Helicolenus percoides	4	0	0	0	0	0	2	1	0	0
Sco.car	Scorpaenidae	Scorpaena cardinalis	3.5	0	0	0	0	0	1	2	1	0
Sco.coo	Scorpaenidae	Scorpaena cookii	3.5	0	0	0	0	1	2	1	0	0
Sco.pap	Scorpaenidae	Scorpaena papillosa	4	0	0	0	0	1	2	1	0	0
Sco.sca	Scorpaenidae	Scorpaenodes scaber	3.6	0	0	0	0	1	2	1	0	0
Con.leu	Congiopodidae	Congiopodus leucopaecilus	3.3	0	0	0	0	1	2	0	0	0
Aca.cin	Serranidae	Acanthistius cinctus	4.1	0	0	0	0	0	0	2	1	0
Aul.tem	Serranidae/Gramn	Aulacocephalus temmincki	4	0	0	0	0	1	2	0	0	0
Cal.aus	Callanthiidae	Callanthias australis	3.1	0	0	2	1	1	1	0	0	0
Cae.lep	Serranidae	Caesioperca lepidoptera	3.1	0	0	2	1	1	1	0	0	0
Cap.lon	Serranidae	Caprodon longimanus	3.9	0	0	2	1	1	1	0	0	0
Epi.dae	Serranidae	Epinephelus daemeli	4	0	0	0	0	1	2	1	1	0
Hyp.hun	Serranidae	Hypoplectrodes huntii	4.1	0	0	0	0	0	2	1	0	0
Hyp.spA	Serranidae	Hypoplectrodes coronatus	3.6	0	0	0	0	1	2	0	0	0
Hyp.spB	Serranidae	Hypoplectrodes dimidiatus	3.6	0	0	0	0	2	1	0	0	0
Tra.mac	Serranidae	Trachypoma macracanthus	3.5	0	0	0	0	0	2	1	0	0
Apo.doe	Apogonidae	Apogon doederleini	3.6	0	0	0	0	0	2	0	0	0
Dec.koh	Carangidae	Decapterus koheru	3.4	0	0	2	1	1	1	0	0	0
Dec.mur	Carangidae	Decapterus muroadsi	3.4	0	0	2	1	1	0	0	0	0
Pse.den	Carangidae	Pseudocaranx dentex	3.9	1	0	2	1	1	1	1	0	0
Ser.lal	Carangidae	Seriola lalandi	4.2	0	0	0	0	0	0	2	1	0
Ser.riv	Carangidae	Seriola rivoliana	4.5	0	0	0	0	0	2	1	1	0
Tra.sp.	Carangidae	Trachurus novaezelandiae	3.2	0	0	2	1	1	1	1	0	0
Arr.tru	Arripidae	Arripis trutta	4.1	0	0	2	1	1	1	1	0	0
Arr.xyl	Arripidae	Arripis xylabion	4.4	0	0	2	1	1	1	1	0	0
Pla.rub	Emmelichthyidae	Plagiogeneion rubiginosus	3.4	0	0	2	1	1	1	0	0	0
Pag.aur	Sparidae	Pagrus auratus	3.6	0	0	0	0	1	2	1	1	1
Upe.lin	Mullidae	Upeneichthys lineatus/poros	3.1	0	0	0	0	1	2	0	0	0

Par.cil	Mullidae	Parupeneus ciliatus	3.5	0	0	0	0	2	1	0	0	0
Par.spi	Mullidae	Parupenus spilurus	3.5	0	0	0	0	2	1	0	0	0
Mul.van	Mullidae	Mulloidichthys vanicolensis	3.6	0	0	0	0	2	1	0	0	0
Pem.ads	Pempheridae	Pempheris adspersa	3	0	0	2	0	1	1	0	0	0
Pem.ana	Pempheridae	Pempheris analis	3.4	0	0	2	0	1	1	0	0	0
Aty.lat	Kyphosidae/Micro	Atypichthys latus	3.5	1	1	1	1	2	1	0	0	0
Sco.lin	Kyphosidae/Scorpi	Scorpi lineolata	3.1	0	1	2	1	1	1	0	0	0
Sco.vio	Kyphosidae/Scorpi	Scorpi violaceus	3.1	0	1	2	1	1	1	0	0	0
Kyp.big	Kyphosidae	Kyphosus bigibbus	2	0	2	0	0	0	0	0	0	0
Kyp.syd	Kyphosidae	Kyphosus sydneyanus	2	0	2	0	0	1	0	0	0	0
Gir.cya	Kyphosidae/Girelli	Girella cyanea	2	0	2	1	0	1	1	0	0	0
Gir.tri	Kyphosidae/Girelli	Girella tricuspidata	2.1	1	2	1	1	1	1	0	0	1
Gir.fim	Kyphosidae/Girelli	Girella fimbriata	2	0	2	0	0	0	0	0	0	0
Bat.cul	Kyphosidae/Scorpi	Bathystethus cultratus	3.1	0	0	2	1	1	0	0	0	0
Lab.nit	Kyphosidae/Scorpi	Labracoglossa nitida	3.1	0	0	2	0	1	1	0	0	0
Amp.how	Chaetodontidae	Amphichaetodon howensis	2.8	0	0	0	0	1	2	0	0	0
Fcp fla	Chaetodontidae	Forcipiger flavissimus	3.1	1	0	0	0	1	2	0	0	0
Cir.spl	Cirrhitidae	Notocirrhitus splendens	4	0	0	0	0	1	2	1	0	0
Par.lab	Pentacerotidae	Paristiopterus labiosus	3.3	0	0	0	0	1	2	0	0	0
Zan.ele	Pentacerotidae	Zanclistius elevatus	3.3	0	0	0	0	1	2	0	0	0
Evi.acu	Pentacerotidae	Evistias acutirostris	3.5	0	0	0	0	1	2	0	0	0
Chr.dis	Pomacentridae	Chromis dispilus	3	0	0	2	1	1	0	0	0	0
Chr.hyp	Pomacentridae	Chromis hypsilepis	2.7	0	0	2	1	1	0	0	0	0
Chr.rap	Pomacentridae	Chrysiptera rapanui	2.7	0	0	1	1	1	1	0	0	0
Par.alb	Pomacentridae	Parma alboscaphularis	2	0	2	1	0	1	0	0	0	0
Par.ker	Pomacentridae	Parma kermadecensis	2.7	0	2	0	0	0	0	0	0	0
Ste.fas	Pomacentridae	Stegastes fasciolatus	2.2	0	2	0	0	0	0	0	0	0
Chi.mar	Chironemidae	Chironemus marmoratus	3.7	0	0	0	0	1	2	1	0	0
Apl.arc	Aplodactylidae	Aplodactylus arctidens	2	0	2	0	0	0	0	0	0	0
Apl.eth	Aplodactylidae	Aplodactylus etheridgii	2	0	2	0	0	0	0	0	0	0
Che.eph	Cheilodactylidae	Cheilodactylus ephippium	3.5	0	0	0	1	2	1	0	0	0
Che.fra	Cheilodactylidae	Cheilodactylus francisi	3.2	0	0	0	0	2	1	0	0	0
Che.nig	Cheilodactylidae	Cheilodactylus nigripes	3.1	0	0	0	0	2	1	0	0	0

Che.spe	Cheilodactylidae	Cheilodactylus spectabilis	3.4	0	0	0	2	1	1	0	0	0
Nem.dou	Cheilodactylidae	Nemadactylus douglasii	3.4	0	0	0	1	2	1	0	0	0
Nem.mac	Cheilodactylidae	Nemadactylus macropterus	3.4	0	0	0	1	2	1	0	0	0
Lat.cil	Latridae	Latridopsis ciliaris	3.3	0	0	0	1	2	1	0	0	0
Lat.for	Latridae	Latridopsis forsteri	3.6	0	0	0	0	2	1	1	0	0
Lat.lin	Latridae	Latris lineata	3.7	0	0	1	1	1	2	1	0	0
Men.lin	Latridae	Mendosoma lineatum	3.9	0	0	2	1	1	1	1	0	0
Ald.for	Mugilidae	Aldrichetta forsteri	2.5	0	1	1	2	1	1	0	0	1
Not.cel	Labridae	Notolabrus celidotus	3.4	1	0	1	1	1	2	0	0	0
Not.cin	Labridae	Notolabrus cinctus	3.6	1	0	1	1	1	2	0	0	0
Not.fuc	Labridae	Notolabrus fucicola	3.7	0	0	0	0	1	2	1	0	0
Not.ins	Labridae	Notolabrus inscriptus	3.7	0	0	0	0	0	2	1	0	0
Pse.luc	Labridae	Pseudolabrus luculentus	3.3	1	0	0	1	1	2	0	0	0
Pse.mil	Labridae	Pseudolabrus miles	3.6	1	0	0	1	1	2	0	0	0
Cor.san	Labridae	Coris sandageri	3.6	1	0	0	1	2	1	0	0	0
Cor.pic	Labridae	Coris picta	3.4	1	0	1	1	2	0	0	0	0
Sue.ayl	Labridae	Suezichthys aylingi	3.5	1	0	1	1	2	0	0	0	0
Sue.arq	Labridae	Suezichthys arquatus	3.5	0	0	0	0	2	0	0	0	0
Bod.vul	Labridae	Bodianus unimaculatus	3.6	0	0	0	0	0	2	0	0	0
Bod fla	Labridae	Bodianus flavipinnis	3.5	0	0	0	0	0	2	0	0	0
Ana.cae	Labridae	Anampses caeruleopunctatus	3.4	0	0	0	0	1	2	0	0	0
Ana.ele	Labridae	Anampses elegans	3.5	0	0	0	0	1	2	0	0	0
Tha.amb	Labridae	Thalassoma amblycephalum	3.1	0	0	2	1	1	0	0	0	0
Tha.lut	Labridae	Thalassoma lutescens	3.7	0	0	0	0	1	2	0	0	0
Tha.tri	Labridae	Thalassoma trilobatum	3.8	0	0	0	0	1	2	0	0	0
Oda.cya	Odacidae/Labridae	Odax cyanoallix	2.7	0	2	0	0	0	0	0	0	0
Oda.pul	Odacidae/Labridae	Odax pullus	2.1	0	2	1	0	1	1	0	0	0
Bov.var	Bovichtidae	Bovichtus variegatus	3.6	0	0	0	0	1	2	0	0	0
Not.ang	Nototheniidae	Notothenia angustata	4.2	0	1	0	0	0	2	1	0	0
Par.col	Pinguipedidae	Parapercis colias	3.9	0	0	1	1	1	2	1	1	1
Ble.dor	Tripterygiidae	Blennodon dorsalis	3.4	0	0	0	0	1	2	0	0	0
Bel.les	Tripterygiidae	Bellapiscis lesleyae	3.3	0	0	0	0	2	1	0	0	0
Bel.med	Tripterygiidae	Bellapiscis medius	3.5	0	0	0	0	2	1	0	0	0

Fst.fla	Tripterygiidae	Forsterygion flavonigrum	3.3	0	0	0	2	1	0	0	0	0
For.lap	Tripterygiidae	Forsterygion lapillum	3.3	1	0	0	1	1	2	0	0	0
For.mal	Tripterygiidae	Forsterygion malcolmi	3.4	0	0	0	0	1	2	0	0	0
For.var	Tripterygiidae	Forsterygion varium	3.5	0	0	0	0	1	2	1	0	0
Gil.abd	Tripterygiidae	Gilloblennius abditus	3.2	0	0	0	0	1	2	0	0	0
Gil.tri	Tripterygiidae	Gilloblennius tripennis	3.4	0	0	0	0	1	2	0	0	0
Gra.gym	Tripterygiidae	Forsterygion gymnotum	3.3	0	0	0	0	1	2	0	0	0
Gra.nig	Tripterygiidae	Forsterygion nigripenne	3.3	0	0	0	0	1	2	0	0	0
Gra.cap	Tripterygiidae	Grahamina/Forsterygion capi	3.3	0	0	0	0	1	2	0	0	0
Kar.ste	Tripterygiidae	Karalepis stewarti	3.3	0	0	0	0	1	2	1	0	0
Not.cae	Tripterygiidae	Notoclinops caerulepunctus	3.1	2	0	0	1	1	0	0	0	0
Not.seg	Tripterygiidae	Notoclinops segmentatus	3.3	1	0	0	1	2	0	0	0	0
Not.yal	Tripterygiidae	Notoclinops yaldwyni	3.2	1	0	0	1	2	1	0	0	0
Obl.mar	Tripterygiidae	Forsterygion maryannae	3.3	0	0	2	0	1	1	0	0	0
Rua.dec	Tripterygiidae	Ruanoho decemdigitatus	3.3	0	0	0	0	1	2	0	0	0
Rua.whe	Tripterygiidae	Ruanoho whero	3.3	0	0	0	0	2	1	0	0	0
Ker.tri	Tripterygiidae	Enneapterygius kermadecens	3.1	0	0	0	0	2	1	0	0	0
Cir.alb	Blenniidae	Cirripectes alboapicalis	2	0	2	0	0	0	0	0	0	1
Par.lat	Blenniidae	Parablennius laticlavus	3.4	1	1	0	0	1	2	0	0	0
Pla.tap	Blenniidae	Plagiotremus tapeinosoma	3.8	0	0	0	0	0	0	2	2	0
Gra.rad	Thalasseleotridida	Grahamichthys radiata	3.3	0	0	0	1	2	0	0	0	0
Tha.sp.	Thalasseleotridida	Thalaseleotris adela	3.1	0	0	0	1	2	0	0	0	0
Gob.atr	Gobiidae	Gobiopsis atrata	3.3	0	0	0	2	1	0	0	0	0
Ser.bra	Centrolophidae	Seriola brama	3.7	0	0	1	0	1	2	0	0	0
Par.sca	Monacanthidae	Parika/Meuschenia scaber	3.1	0	1	1	1	1	2	1	1	1
Tha.ana	Monacanthidae	Thamnaconus analis	3.4	0	0	0	0	1	2	0	0	0
Ost.cub	Ostraciidae	Ostracion cubicus	3.4	0	2	0	1	1	1	1	0	0
Can.cal	Tetraodontidae	Canthigaster callisterna	3.1	0	0	0	0	1	2	0	0	0
All.jac	Diodontidae	Allomycterus jaculiferus/pilat	3.6	0	0	0	0	0	2	0	0	0
Cal.all	Callanthiidae	Callanthias allporti	3.4	0	0	2	1	1	0	0	0	0