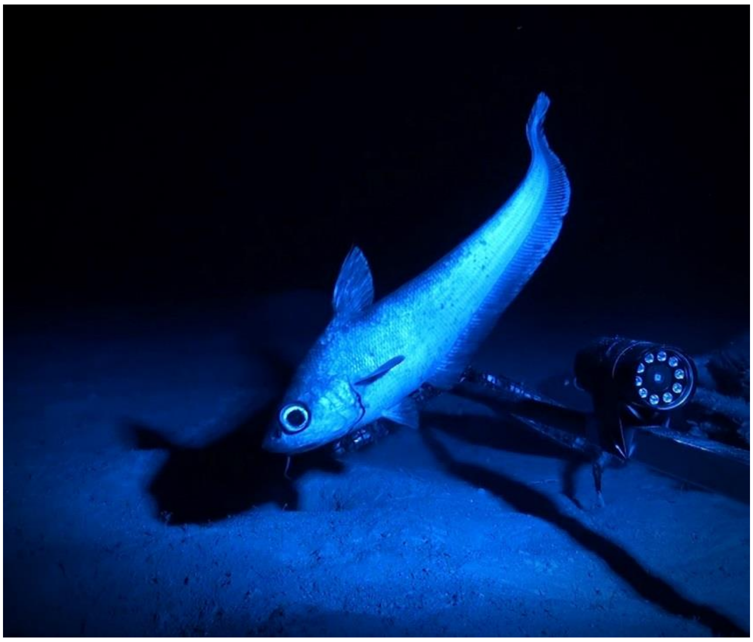
Functional biodiversity of New Zealand's marine fishes *versus* depth and latitude



A thesis presented in partial fulfilment of
the requirements for the degree of
Doctor of Philosophy in Statistics
at Massey University, Auckland,
New Zealand

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June 2020

Thesis Abstract

Understanding patterns and processes governing biodiversity along broad-scale environmental gradients requires an assessment of not only taxonomic richness, but also morphological and functional traits of organisms. The deep sea is the largest habitat on earth and provides many important ecosystem services. Decreases in light, temperature, and trophic resources, along with increases in pressure that occur with greater depth, renders the deep sea one of the most constraining environments for supporting life. However, little is known about how biodiversity, and especially functional biodiversity, changes along the depth gradient. This thesis aimed to fill this gap by using a combination of traits associated with food acquisition and locomotion to quantify and characterise patterns of functional diversity across large-scale depth and latitude gradients and to investigate potential mechanisms driving biodiversity.

First, to identify the major selective forces acting on morphology, I documented patterns of variation in the traits of fishes at broad spatial scales. I found that with increasing depth, fishes, on average, became larger and more elongate, and had a larger oral gape and eye size. With increasing depth, fish morphology shifted towards body shapes that enable energy-efficient undulatory swimming styles and an increased jaw-length *versus* mouth width to aid opportunistic feeding.

Second, I investigated the role of environmental filters *versus* biotic interactions in shaping the functional space of communities along depth and latitude gradients by measuring the intra- and inter-specific richness, dispersion and regularity in functional trait space. I found that functional alpha diversity was unexpectedly high in deep-sea communities, but decreased with increasing latitude, and that competition within and among species shaped the multi-dimensional functional space for fishes at the local alpha diversity level.

Third, I described spatial patterns in functional beta diversity for New Zealand marine fishes *versus* depth and latitude, and delineated functional bioregions. The functional turnover in fish communities was greater across depth than latitude, and latitudinal functional turnover decreased with increasing depth. I surmise that environmental filtering may be the primary driver of broad-scale patterns of beta diversity in the deep sea.

Overall, this thesis contributes new knowledge regarding broad-scale functional biodiversity patterns across depth and latitude *via* the morphological and functional traits of New Zealand's marine fishes. Through the measurement of individual trait variation, and the quantification of functional alpha and beta diversity, this thesis characterised variation in the traits of fishes over large spatial scales, determined the spatial turnover of functional traits, and described the relative importance of environmental versus biotic drivers in shaping the functional space of deep-sea communities. These contributions provide foundational understanding for future research on the functional diversity of marine fishes, biodiversity patterns across the depth gradient, and the monitoring of biodiversity change across New Zealand's latitudinal and depth gradients.

Declaration by Author

The research carried out for my doctoral thesis has been used in whole or in part for this qualification only. The research is my original work, except as indicated by appropriate attribution in the text and/or acknowledgements; quotation marks have been used where required; and I take responsibility for the content and quality of this thesis. I have clearly stated the contribution by others in jointly authored works, which can be found at the end of each chapter. The “Statement of Contribution to Doctoral Thesis Containing Publications (DRC16)’, has been completed for each published article within the thesis, and is included in the electronic copy at the end of each chapter.

Publications during candidature

Peer-reviewed journal articles included in this thesis

Myers, E.M.V., Anderson, M.J., Eme, D., Liggins, L. & Roberts, C.D. (2019) Changes in key traits versus depth and latitude suggest energy-efficient locomotion, opportunistic feeding and light lead to adaptive morphologies of marine fishes. *Journal of Animal Ecology,* **89(2),** 309-322.

https://doi.org/10.1111/1365-2656.13131

Peer-reviewed journal articles ***not*** *included in this thesis*

Eme, D., Anderson, M., **Myers, E**., Roberts, C. & Liggins, L. (2020) Phylogenetic measures reveal eco-evolutionary drivers of biodiversity along a depth gradient. *Ecography,* **43,** 1-14.

https://doi.org/10.1111/ecog.04836

Acknowledgements

Deciding to move back to New Zealand to do this PhD after 16 years in Perth has been one of the best decisions of my life. It has been an amazing journey thanks to the following people and organisations.

Marti, thank you for taking me on for this exciting project. You have been so supportive, kind, and have given me countless amazing opportunities. It has been a privilege to meet and learn from you weekly, and see that brain of yours whizzing away in real time. By fostering my love of biology and opening up the world of statistics you have truly set me up for an exciting and rewarding career – thank you! Your generosity with PRIMER/Permanova+ courses and software, is also deeply appreciated. The time we spent one on one using PRIMER together was a favourite part of my PhD! Also, thank you for encouraging me to present my research in Tahiti, America, Scotland, Hong Kong, and all around New Zealand. The communication and networking skills that I have learnt from these experiences have already begun to bear fruit!

David, I could not have done this thesis without you! Your patience with me was seemingly inexhaustible. It was a great experience sharing an office with you and getting to draw and discuss endless scenarios on the whiteboard with you. No problem was ever too big to conquer (and we had our fair share), and I will take that lesson with me as I move into my career. I will strive to emulate your work ethic, persistence, and attention to detail, and look forward to our future collaborations.

Libby, you have been such an amazing role model. Thank you for always being there for me both professionally and personally. As with David, no concern was ever too big or small for you. Thank you for always getting me involved with exciting projects and putting my name forward for things like the Kermadec trip (life changing), working with iwi, and always introducing me to the bigwigs at conferences!

Clive, I've known you for almost a decade now, how time fly's when you are having fun! My time with you and the fish team as a bright eyed 21 year old made me want to carry on with postgraduate research. I wouldn't be here without you! Thank you for turning me into a fish-mad Ichthyologist, I am *very* happy to be a part of the club. Conducting my lab work at Te Papa was one of the best experiences of my PhD, and I always looked forward to it. Thank you for all of your support and friendship over the years. I look forward to many more afternoon beers at the Tutukaka fishing club, measuring the marlins together!

Euan, you have been my mentor since day dot, and were the first person to see something in me as a youngster. I owe a lot to you. Thank you for always being there for me and giving me all of the wonderful opportunities that you have. I value your friendship dearly, and look forward to catching up for work and fun in Perth.

Thank you to the Te Papa fish team: Andrew, Carl, Jeremy and Salme. I know every time that I can down it meant more work for you guys, but you did it with a smile. I love hanging out with you all and being an occasional member of the fish team! Thank you for the technical support and friendship over the years, and for igniting my curiosity in fishes. A special thank you to Andrew Stewart for housing me during my trips to Wellington. It was great to hanging out, talk fish, politics and everything in between. Thank you for all of the lovely meals and crafties my friend!

Thank you to NZIAS for all of the support over the years, and for the financial support in my 4th year. Vesna, you so very helpful, prompt and caring! Mike, thanks for all of the IT support. Peter Schwerdtfeger, you brightened up my day on many occasions with our jovial encounters. You are a very funny man! Thank you for everything that you and NZIAS did for that one random deep-sea biologist in the department! Thank you Massey University for providing a great university to study at, and for the financial support in the form of a conference presentation grant, a doctoral completion bursary, and a Pūrehuroa Māori Postgraduate Award.

Thank you to Tāmaki Paenga Hira, The Auckland War Memorial Museum and the Sir Hugh Kawharu Foundation for the museum scholarship award. The museum scholarship not only supported me financially, but also encouraged me to learn to kōrero I te reo Māori and find out more about my whakapapa. I am forever grateful to Haare Williams who gave me a firm push in the right direction, and told me that Māori leadership starts with korero. I was very lucky to be able to use the extensive fish collection at the Auckland Museum, and in doing so, got to meet Tom Trnski and Severine Hannam. Thank you both for all of your help in accessing the collection. Tom, thank you for all of the good times in the lab, in the field, and underwater. Science is a hoot with you, and you have been one of my favourite mentors during my PhD. I won’t be forgetting my first rotenone experience in a hurry, what a blast!

Thank you to Blake NZ and the New Zealand Navy (specifically, the crew of HMNZS Canterbury) for the trip of a lifetime to the Kermadecs.

Thank you to Te Pūtea Whakatupu Trust for awarding me the Rona scholarship and for taking me to the Federation of Māori Authorities conference and Māori Fisheries Conference. You not only provided the funding, but also the aroha, guidance, and support to go with it, coming in the form of Karleen Everitt. Karleen, thank you for instilling a “go get em’” attitude, and for your constant belief and encouragement.

Kia ora to the Māori academic staff for all of the support throughout the years. It was great to catch up on a regular basis for kai and korero, and you always made sure that I had a full puku. I want to single out Messina Shaw, you have always been there for me, and I will miss seeing your smile around the place. Thank you for all of your tautoko and aroha.

To the Enderby trust, thank you for the scholarship and the opportunity to travel to New Zealand’s sub Antarctic Islands – a truly wild place. I will always remember my trip to the Southern Ocean, and will continue to tell it’s story.

I’d like to thank James Seager for creating the head morphometrics feature in Event Measure especially for me – it really helped my analysis!.

Cheers Dave Aguirre for the good company and laughs. We ventured near and far, armed with our toothpicks and our catfish. All in the name of science! You were always there to help with any curly issues I had, to take me critter collecting, and to share a coldie with.

Thanks to the Building 5 crew, and the marine group for the catchups, lunch breaks, and visits. Especially Wes Webb and Michelle Roper for always answering my endless PhD questions. Similarly, thanks to the Fish Ecology Lab at Curtin University in Perth for making my visits extra fun. It has been an awesome group to be part of for 7+ years!

To all of my friends and whanau. I couldn’t have completed this without you. Thanks to my girlfriends in Auckland/Massey, Andee, Michelle, Odette, Kristin and Irene for keeping me sane. Thank you to my family in Perth, my late Nana, my aunties Jo and Sue, and uncle Rooster for bringing me up and teaching me all that you did. I certainly wouldn’t have made it this far without you all, thank you for everything that you have done for me. To my Dad, it has been great getting to know you during my PhD, and to know your love. I am proud to have you as a father and hope to make more memories with you in the future. To my Tutukaka whanau, thank you to Shelley, Josh, Cass, Quinn, Dusty, Sam, Dan, Java, Sorcha, Peteie and Brenda, Wini, Dave, Tia, and Shaun for all of your love and support throughout this journey. Home is about people as much as it is about a place, and because of you all, Tutukaka will always be my home. Thanks for letting me stay this summer Shell, it was the best!

To Dane’s wonderful family, Sue, Ron, Alanna, Nick, Kit and Bianca, thank you for your generosity, for visiting us in NZ, and for giving us a place to stay and a car to borrow! It is really appreciated and has been a great help over the years. I really look forward to spending more time together back in Perth.

Finally, to my partner in crime, Dane. This thesis would be a pie in the sky without your constant love, support and reassurances. You were always there to encourage me when it all got too much, and to share all of the highs and lows. You are my best friend, and I couldn’t have done it without you. Thank you for taking a chance and moving across the ditch with me so that I could do this PhD.

Thanks for all of the fun trips and adventures that we had when I was supposed to be studying, they kept me sane and happy! I look forward to the next stage in our lives together, and for the fun times to keep on coming.

I'd like to dedicate this PhD thesis to my mum, Gail, and my Nana, Valerie. I'll always treasure the time we had together, and the lessons learnt from you both.

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1 General Introduction

1.1 Biodiversity

1.1.1 Patterns of Biodiversity at Global Scales

Understanding how the earth's biodiversity is distributed along large-scale spatial gradients, such as latitude, altitude, and depth, is a central goal of macroecology (Gaston 2000; Mora *et al.* 2003). Globally, the biological diversity of many taxa is often greatest in low latitudes, at shallow depths, and at low elevations (Hillebrand 2004a; Rahbek 2005). There are multiple theories about why species richness is higher in the tropics, many of them inter-related (e.g. Willig, Kaufman & Stevens 2003; Dowle, Morgan-Richards & Trewick 2013). One hypothesis is that a faster rate of species diversification exists in the tropics, due to faster molecular evolution at *higher temperatures* (Rohde 1992). This hypothesis has been recently challenged by Rabosky *et al.* (2018) who found a faster rate of species diversification for fishes in high latitude regions, and by Weir and Schluter (2011) and Rolland *et al.* (2016) who found no relationship for mammals or squamates with latitude/temperature. Another prominent hypothesis is that tropical areas are both *spatially larger* (in terms of habitable area) and more resource rich, providing more niche space for a greater number of species (the so called "energy richness-hypothesis", Currie *et al.* (2004)). Furthermore, the tropics are geologically and climatically *more stable* than temperate regions, enabling the survival of greater numbers of species (Mittelbach *et al.* 2007; Jetz & Fine 2012; Knope *et al.* 2020).

Marine taxa also show a latitudinal gradient in species richness, generally declining from the tropics to temperate regions (Hillebrand 2004b). Chaudhary, Saeedi and Costello (2016) found, however, that when marine animals from many taxa (i.e., fishes, benthic algae, gastropods, bivalves, sponges, foraminifera, stony corals, sea anemones) were pooled together, a bimodal distribution was observed, with a dip in richness occurring around the equator and peaks occurring at 30-50 degrees north and at 30 degrees south. Tittensor *et al.* (2010) also found that the species richness of oceanic taxa such as sharks, tuna, billfish, and squid tend to peak in mid-latitude bands. Recent work by Gregory *et al.* (2019), however, found an inverse pattern to Hillebrand (2004b), whereby the diversity of marine viruses peaked in the high-latitude Arctic region. Clearly, the pattern of species richness along latitudinal gradients varies according to the scale of observational data, the particular taxon examined, and the level of taxonomic grouping used.

Marine systems offer an opportunity to compare and contrast large-scale theories regarding these important drivers – such as temperature, spatial area, and stability – of diversity in natural systems. Despite a decrease in energy, deeper systems are geographically larger in size as well as having greater environmental stability than shallower systems (Grassle 1989; Costello & Chaudhary 2017; Danovaro *et al.* 2017). This contrasts with terrestrial biodiversity studies along altitude; while high-altitude systems also have decreased energy, they are smaller in area and more environmentally variable than low-altitude systems (Rahbek *et al.* 2019). Species richness is often described as being highest at low elevations (McCain 2009; Dehling *et al.* 2014), though when standardised for area, species richness may peak at mid-altitudes (Rahbek 1995; Rahbek 2005; Sanders & Rahbek 2012; Rahbek *et al.* 2019). Marine species richness decreases with increasing depth (Costello & Chaudhary 2017), but this pattern may be due to a bias in sampling effort, with very few studies at depths below the photic zone (>200 m depth). Biodiversity patterns in the deep sea are often difficult to measure, due to the logistic difficulties of sampling at depth, the large spatial extent of deep systems, and complexities associated with confirming taxonomic identifications (Hendriks, Duarte & Heip 2006; Worm *et al.* 2006; Rex & Etter 2010). Clearly, there is a need for a greater number of studies of biodiversity in marine systems, especially at deeper depths, to help us to disentangle the role of certain drivers of biodiversity more generally.

1.1.2 Characterising Biodiversity

Biodiversity has many aspects and can be measured from the gene to species level, and across whole communities and ecosystems (Magurran 2005; Sala & Knowlton 2006). Biodiversity measures commonly used across large global gradients broadly include those aimed at measuring taxonomic diversity (Snelgrove *et al.* 2016), functional diversity (Lamanna *et al.* 2014; Díaz *et al.* 2016), phylogenetic diversity (Tucker *et al.* 2017) or genetic diversity (Miraldo *et al.* 2016; Manel *et al.* 2020). Each of these facets of biodiversity have value and provide a unique perspective regarding the processes that generate and maintain biodiversity. Therefore, the choice of biodiversity features to quantify, and how they are measured, will be informed by the study objectives (Tolimieri *et al.* 2015).

Biodiversity is typically measured by first quantifying taxonomic species richness (i.e., the number of species in a given sampling unit) (Cardinale *et al.* 2012). Species richness is, however, dependent on the scale of the sampling unit; it is well known that the number of species increases with increases in the area sampled (Arrhenius 1921; Gleason 1922; Connor & McCoy 1979). Whittaker (1960; 1972) described a further partitioning of species richness into alpha (α), beta (β) and gamma (γ) components. Alpha diversity (richness) is the number of species at a local scale (an individual site or habitat), and gamma diversity is defined as richness at a broader regional scale. Beta diversity is the variation in composition between two or more sites within a given regional species pool, and hence provides a scaling between α and γ (Vellend 2001). It was originally defined as $\beta = \frac{\gamma}{\alpha}$ and can also be thought of as the turnover in species composition at a given spatial scale (Whittaker 1960; Whittaker 1972).

Although patterns of biodiversity are frequently measured using a species-centric approach (Bellwood, Goatley & Bellwood 2017), such measures on their own often lack biologically relevant information (McGill *et al.* 2006; Swenson *et al.* 2012). Information gleaned from species richness data gives equal weighting to every species regardless of their ecological role, despite species not contributing equally to ecosystem processes and services (Luck *et al.* 2009). Combining taxonomic and functional diversity in an ecological context provides a more integrative understanding of the potential mechanisms driving biodiversity and ecosystem services (Mouchet *et al.* 2010; Swenson 2011b; Swenson *et al.* 2012; Díaz *et al.* 2016; Bellwood *et al.* 2019). For instance, previous studies have documented a general decrease in species richness with increasing latitude, elevation, and depth (Gaston 2000; Hillebrand 2004a; Costello & Chaudhary 2017); however, functional diversity displays a variety of different patterns along gradients (Villéger *et al.* 2010; Mouillot *et al.* 2013b; Stuart-Smith *et al.* 2013). By comparing and contrasting patterns obtained using more than one aspect of biodiversity (e.g., taxonomic and functional), scientists can make stronger inferences regarding the potential underlying dynamics of ecological interactions that drive patterns of biodiversity observed from local to regional and global scales (Swenson 2011b). Trends in functional diversity will depend on the respective traits that are measured and the indices that are calculated from these.

1.2 Functional Diversity

1.2.1 Value of Functional Diversity in Understanding Biodiversity

Functional diversity is an aspect of biodiversity that describes the range of functions performed by organisms within assemblages, communities, or ecosystems, and generally focuses on biologically relevant traits (such as life-history characteristics) and roles (such as trophic level or biomass transfer) (Tilman 2001; Petchey & Gaston 2006). In recent years functional trait-based analyses have become a cornerstone in ecological studies of both terrestrial and marine systems (McGill *et al.* 2006; Violle *et al.* 2007; Webb *et al.* 2010; Mouillot *et al.* 2013b; Mindel *et al.* 2016a). Increasingly, scientists are accepting that a high species richness does not necessarily confer resilience to global climate changes and disturbances (Bellwood, Goatley & Bellwood 2017), and are focusing on understanding how the properties and functions of individual species within an ecosystem work together to promote resilience and maintain key ecological processes (Bremner 2008; Bellwood *et al.* 2019; McLean *et al.* 2019a). Functional diversity has also been used as a tool to understand how ecological processes influence patterns in the assembly of communities (Mason *et al.* 2008; Pavoine *et al.* 2011; Swenson *et al.* 2012; Mason *et al.* 2013; McLean *et al.* 2019b). In the marine realm, trait-based analyses have been used to measure: (1) the degree of functional redundancy present within a given community or ecosystem (Micheli & Halpern 2005; Johansson *et al.* 2013; Mouillot *et al.* 2014); (2) explain variation in the spatial positions of species' ranges (Sunday *et al.* 2015); (3) understand the impacts of fishing on deep-sea ecosystems (Mindel *et al.* 2016b); and (4) document the responses of ecosystems to other types of human-mediated disturbances (Villéger *et al.* 2010; Mouillot *et al.* 2014; McLean *et al.* 2019b).

1.2.2 Functional Traits

Functional diversity is estimated by measuring individual traits, or several traits in combination. A trait is a morphological, physiological or phenological feature of an organism that is measured at the individual level (Violle *et al.* 2007). More specifically, a *functional* trait is any biological characteristic that is measurable from an individual that is directly related to an ecological function, and influences the fitness of an organism (Violle *et al.* 2007; Mouillot *et al.* 2013b). This differs from a morphological trait, which is simply a phenological trait of unknown or unspecified relevance to function. There is much debate about the use of traits to represent a function (Gravel, Albouy & Thuiller 2016; Bellwood *et al.* 2019; Pigot *et al.* 2020). Often there is no measurable cause/effect or link to said function; rather, the trait acts as a proxy for a function (Bellwood *et al.* 2019). Nonetheless, in certain taxonomic groups, there are accepted norms in the functional traits used and clear understanding of their relevance (Villéger *et al.* 2010; Díaz *et al.* 2016). The analysis of species' functional traits can, therefore, be used to indicate biologically meaningful aspects of the ecology of the organisms studied (Wainwright 1994). In addition, the measurement of non-anatomical traits, such as behavioural traits, can also provide greater insight into new species functions and interactions in nature (Violle *et al.* 2007; Mouillot *et al.* 2013b).

Functional traits can broadly be categorised as either a *characteristic* (e.g., morphological, physiological or behavioural) of an organism that renders it capable of living and reproducing in a given biotic and/or physical environment, or as a specific *role* that an organism plays within the context of intra- or inter-specific interactions, such as its trophic level. This is analogous to the concept of a "response" or "effect" trait in plant literature (Violle *et al.* 2007). Measured traits often include a mixture of different types of variables. For example, many morphological variables are quantitative and continuous (such as the total length of a fish), whereas others are qualitative (such as feeding type: herbivore, planktivore, *etc*.) or binary (such as the presence/absence of a swim bladder). Thus, multivariate measures used to analyse trait data, which generally occur in the form of a species-by-trait matrix, must allow for mixed types of variables if both quantitative and qualitative traits are measured (Villéger, Mason & Mouillot 2008; Laliberté & Legendre 2010).

Freshwater and marine fishes are among the most well-described taxa in terms of traits. There are several different functions of fishes such as food acquisition, locomotion, defence and reproduction, that can be quantified by measuring specific traits (Schleuter *et al.* 2010; Villéger *et al.* 2010; Villeger *et al.* 2017). A study by Villéger *et al.* (2010) measured food acquisition and locomotion traits to examine changes in these functions of fishes in a coastal lagoon in response to habitat degradation. Species with specialised functional traits became less common as seagrass habitats were lost, indicating the homogenisation of food acquisition and locomotion traits following the sustained degradation of habitat (Villéger *et al.* 2010). In a global study of reef-fish diversity, Stuart-Smith *et al.* (2013) integrated behavioural traits (water-column position, gregariousness, and diel activity pattern), with habitat use, trophic niche, and abundance, to define new global abundance-weighted functional hotspots of diversity using these traits. Mindel *et al.* (2016b) described changes in body-size (a structural trait) with depth, highlighting the ontogenetic shift of individuals transitioning into deeper waters as they grow larger (i.e., Heincke's law; Heincke 1913), a trend shown to be exacerbated by selective fishing pressure of larger individuals (Frank *et al.* 2018).

Some traits are recorded in global databases, such as FishBase (Froese & Pauly 2019), and consist of both qualitative and quantitative measures. Alternatively, certain traits can be measured directly on freshly caught specimens in the field, *in situ* from stereo-video footage (explained in Chapter Three), or from museum specimens. Museum specimens are an important resource, enabling morphological measurements to be taken directly on preserved individuals. These can be used to help understand the biological responses of organisms to anthropogenic and natural disturbances (e.g., the comparison data from specimens collected decades, or even centuries ago, to present-day individuals)

(Meineke *et al.* 2019). Many of the morphological and functional traits that are measured for fishes have been designed to capture morphological variation in perciform-shaped fishes, and do not effectively measure the diversity of shapes of fishes from different orders (such as in the deep sea). This problem is discussed further in Chapter Two, with several new traits defined to capture the range of morphologies seen across multiple orders in the deep sea.

1.3 Measuring Functional Diversity

There are many different ways to measure functional diversity (Petchey & Gaston 2006; Villéger, Mason & Mouillot 2008; Schleuter *et al.* 2010), and each metric may capture a different aspect of functional diversity. We can consider that the traits of species (or individuals) are each a dimension (Maire *et al.* 2015) and that each species has a position along each dimension for each trait; hence can be represented as a single point in multidimensional trait space (Figure 1.1a). A set of species (i.e., an assemblage) therefore creates a cloud of points in multidimensional trait space (Figure 1.1b).

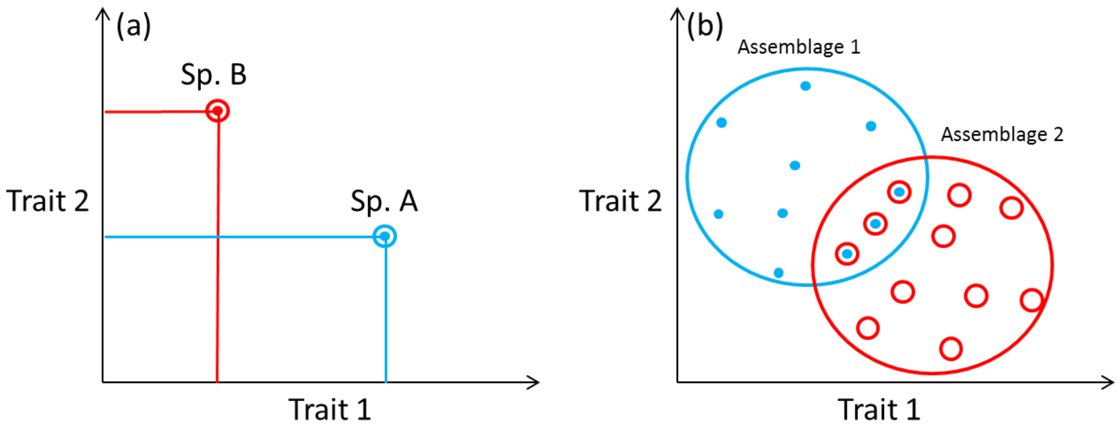


Figure 1.1 (a) Two species with different coordinates for trait 1 and trait 2, creating two points in two-dimensional functional trait space; (b) Assemblage 1 has 10 species (blue points), each with different values for Trait 1 and Trait 2, and Assemblage 2 has 11 species (red circles). Three species are shared.

There are several conceptual aspects of functional diversity that may be captured by different functional diversity measures. The most salient ones are functional alpha diversity (Fα), or local richness, and functional beta diversity (Fβ). Functional alpha diversity measures the total range of functional traits observed at a local sampling unit (Villéger *et al.* 2012). Functional beta diversity (Fβ) is the dissimilarity in functional structure between two or more communities (Villéger *et al.* 2012). Fβ measures how variable the average traits are across sampling units at a given site for a given spatial scale (Villéger *et al.* 2012). Changes in functional beta diversity can occur in many ways. Two assemblages may have no traits in common, hence have no overlap in trait space, resulting in complete turnover in trait space. Other assemblages may differ in functional alpha diversity, but one may be either partially or fully nested within another (Villéger, Grenouillet & Brosse 2013). These ideas mirror the notions of nestedness and turnover in taxonomic diversity (Baselga 2010; Baselga 2012; Villéger, Grenouillet & Brosse 2013). Functional differences among species can also be incorporated into the calculation of dissimilarities between pairs of sampling units, and measures of Fβ can be defined using this approach. For example, one may calculate the average distance, or the average nearest-neighbour distance through trait space between every pair of species occurring across two sampling units (Somerfield *et al.* 2008).

1.3.1 Use of Trait Data and Calculation of Functional Diversity in Community Analyses

Studies of functional diversity generally embark from at least two of the following data matrices: a species-by-trait matrix, a community data matrix (samples-by-species) containing abundance or presence-absence data, and an environmental data matrix (samples-by-environmental variables) (Villéger, Mason & Mouillot 2008). A species-by-trait matrix consists of either one measurement per species, or an average value across multiple individuals per species. To incorporate intraspecific trait variability into the calculation of functional metrics, an individual-by-trait matrix (i.e., multiple measures of a given trait for a species, and site-specific measures for a species) can be used in the place of a species-by-trait matrix. Environmental variables can consist of direct measurements such as sea surface temperature or particulate organic matter, as well as spatial information such as depth (m) or latitude (degrees). From functional trait data (species-by-traits), a matrix of dissimilarities between every pair of species can be calculated using either Gower's measure (Gower 1966), which allows for the inclusion of a mixture of different types of traits (e.g., continuous, ordinal or categorical) (Villéger, Mason & Mouillot 2008), or

Euclidean distance, which can be used for continuous traits (Laliberté & Legendre 2010).

The analysis of multivariate measures of functional alpha and beta diversity can be calculated using the aforementioned functional dissimilarity matrix across multiple trait variables. Multivariate measures can broadly be categorised into three aspects of functional diversity: richness, divergence (dispersion), and regularity (evenness). Functional richness measures the amount of functional space occupied by a set of species (or individuals) in multidimensional trait space, and can be calculated using a convex hull polygon (Villéger, Mason & Mouillot 2008) or *n*-dimensional hypervolume (Blonder *et al.* 2014). Functional dispersion metrics measure the mean distance in multivariate trait space of individual species to the centroid of all species (Laliberté & Legendre 2010). “Variation in taxonomic distinctness”, which measures the variation in path lengths connecting all species and captures the unevenness of a community across a given taxonomic tree (Clarke & Warwick 2001), can also be calculated in functional space (as suggested by Somerfield *et al.* 2008), and is independent of species richness and functional dispersion metrics. We shall refer to these, hereafter, as “functional regularity” measures, which essentially quantify the regularity of the distances among species in the functional space. Univariate analyses can also be done to model the relationships between individual traits and chosen gradients. Ultimately, the types of variables that have been measured, and the way that trait-space itself is defined, will determine which functional diversity measures can be calculated.

Building on the more conventional measures of functional diversity described in the literature (Mason *et al.* 2005; Villéger, Mason & Mouillot 2008;

Laliberté & Legendre 2010; Schleuter *et al.* 2010; Swenson 2014), recent work by Carmona *et al.* (2016) has developed a framework that integrates the probabilistic nature of functional traits (coming from the inclusion of intraspecific trait measurements) with existing concepts of niche-based multi-dimensional hypervolumes. The importance of understanding "functional rarity", the rarity of functions, or functional traits, has also been gaining much attention recently (Mouillot *et al.* 2013a; Leitao *et al.* 2016; Violle *et al.* 2017; Grenié *et al.* 2018). Although often overlooked, intraspecific trait variability has recently been highlighted as an important consideration in the overall estimation of functional diversity (Bolnick *et al.* 2011; Violle *et al.* 2012; Siefert *et al.* 2015; Des Roches *et al.* 2018). Disentangling individual-level variability *versus* species-level variation in functional trait space, including along environmental gradients, can provide novel insights into how communities are structured and maintained (Bolnick *et al.* 2011; Violle *et al.* 2012; Violle *et al.* 2014).

1.3.2 Interpreting patterns of functional diversity

When combined with taxonomic diversity, functional diversity can help to unravel community assembly rules across spatial and environmental gradients (Pavoine & Bonsall 2011; Swenson 2011a), and make generalisations about the way that ecosystems work. Certain processes leave a particular signature or pattern on an assemblage. For instance, it is well documented that when an assemblage undergoes environmental or habitat filtering, there is trait convergence upon key aspects of morphology that are favourable in the filtered habitat or environment, and generally, a reduction in the number of functional strategies (Swenson & Weiser 2014). In contrast, competition either between and/or within species can lead to trait divergence as a result of limiting similarity (MacArthur & Levins 1967). These and other processes are not mutually exclusive, however, and are likely to occur simultaneously (Violle *et al.* 2012; Swenson & Weiser 2014; Kraft *et al.* 2015). Combining trait-based and taxonomic-based analytical approaches may help to disentangle the influence of environmental *versus* biotic influences on the functional structure of communities and provide insight into mechanisms shaping biodiversity along large-scale environmental gradients.

One way to better understand the mechanisms shaping community assembly can be to also measure the functional diversity of individuals *within* a species (Violle *et al.* 2012; Carmona *et al.* 2016). In this context, Fα measures the niche (represented by the functional space) of multiple individuals of the same species within the overall functional trait space of the community. Previously, studies focusing on understanding intraspecific trait variability have done so in a univariate context, using a *single* trait (e.g., Violle *et al.* 2012). Currently, researchers lack the appropriate methods for partitioning the proportion of variance attributable to intra- versus interspecific trait variability at the community level using multiple trait variables (i.e., in a multivariate space; but see de Bello *et al.* (2011)). Variation in intraspecific traits can have important effects on population stability (Agashe 2009), species coexistence (Fridley & Grime 2010) and ecosystem processes (Crutsinger *et al.* 2006).

Species (or individuals) occupying similar positions in functional space may be more likely to perform similar functions and therefore be effectively functionally redundant (Mouillot *et al.* 2014). A community with a high level of functional redundancy offers greater insurance that any loss of a particular species, due to natural or anthropogenic disturbance, will not necessarily result in a loss of function (i.e*.,* the insurance hypothesis, Yachi and Loreau (1999)). However, high species and functional richness, such as on coral reefs, does not necessarily confer additional ecosystem functioning or functional redundancy. Work by Mouillot *et al.* (2014) found an uneven packing of many species into a few functions, and a large number of functions represented by a single species (i.e., functional over-redundancy). Investigating the link between the packing of species in functional space and the functional redundancy of an assemblage may reveal the susceptibility of key functions to species loss (Bellwood, Hoey & Choat 2003; Mouillot *et al.* 2013a; Mouillot *et al.* 2014; McLean *et al.* 2019a).

1.4 Global Patterns of Diversity for Marine Fishes

The world's oceans are estimated to contain around 16% of the named species catalogued on earth (Costello & Chaudhary 2017). Fishes are ubiquitous across the earth's oceans and are found down to depths of 8,200 m (Helfman *et al.* 2009; Yancey *et al.* 2014). They represent the largest group of vertebrate animals, with a recent estimate of marine fish species totalling ~ 17,500 (Eschmeyer 2014). Taxonomic experts estimate at least a further 5,000 or more undescribed fish species are held in museum collections and are new to science (Appeltans *et al.* 2012).

Globally, the species richness of fishes is greatest at low latitudes and in shallow reef habitats (Tittensor *et al.* 2010; Cowman & Bellwood 2013; Stuart-Smith *et al.* 2013). In a pattern similar to that observed for organisms in terrestrial systems, fish species richness generally declines from the tropics to more temperate regions (Mora *et al.* 2003; Tolimieri 2007; Guillemot *et al.* 2011; Stuart-Smith *et al.* 2013). The maximum species diversity of marine life, including fish diversity, is reported to radiate from the Indo-Australian Archipelago hotspot (Cowman & Bellwood 2013; Cowman *et al.* 2017). This decrease in the taxonomic alpha diversity of fishes has been recorded for both coral-reef and rocky-reef fishes (Connolly, Bellwood & Hughes 2003; Mora *et al.* 2003). Highly mobile pelagic tunas and billfishes, however, show a bimodal distribution in species richness, with peaks occurring at mid-latitudes and a drop in their α-diversity near the equator (Worm *et al.* 2005; Chaudhary, Saeedi & Costello 2016).

Although many studies have examined patterns of biodiversity of shallow-water fishes, relatively little is known about how fish biodiversity changes with increasing depth. The depth gradient, like altitude and latitude, is one of the steepest environmental gradients on earth; it strongly influences the spatial distributions of species, their functions and morphologies (Mindel *et al.* 2016a; Zintzen *et al.* 2017). Many studies have described a decrease in the α-diversity (species richness) of fishes with increasing depth (Moranta *et al.* 1998; Lorance, Souissi & Uiblein 2002; Tolimieri 2007). However, Mindel *et al.* (2016a) found that between depths of 300–2000 m off the coast of Scotland, species richness increased towards 2000 m. Tolimieri *et al.* (2015) found that species density between 55–1300 m depth was variable along the Californian coast, with peaks at shallow and intermediate depths along the southern and northern coasts respectively. A global assessment of deep-sea fish diversity found a unimodal pattern, where richness peaked at intermediate depths, and declined with increasing latitude (Snelgrove *et al.* 2016). Brown and Thatje (2014) found that the peak in species richness at intermediate depths may be caused by a combination of historic temperature-related colonisations into the deep sea, and the influence of hydrostatic pressure on the mutation of cells during the different stages of a fish's development that could increase the speciation process. The variation in these patterns in addition to the biological signal may also likely reflect the type of sampling gear used, differences in geographic regions, and type of biodiversity measure used in each study.

There have been few global studies on patterns of functional diversity for marine fishes. Generally, work is restricted to shallow systems in specific countries, seas, regions or oceans. For instance, Grenié *et al.* (2018) found that for low-latitude, equatorial regions, functional distinctness peaked around the Indo-Australian region, declining towards both the east and the west. Wiedmann *et al.* (2014) found functional distinctness was higher in the eastern part of the Barents Sea than the west. The global study by Stuart-Smith *et al.* (2013) found functional-group richness to follow species richness (highest in low-latitude regions), but after accounting for abundance and evenness, found discrete functional hotspots in temperate areas. Studies focused on the temporal change in functional diversity found that it can vary independently of species richness in response to changes in environmental variables, such as temperature (McLean *et al.* 2019b). In the context of the current cumulative impacts of global environmental change, quantifying the functional response of communities following habitat degradation (Villéger *et al.* 2010; Brandl *et al.* 2016) or marine protection (Coleman *et al.* 2015) can yield timely insights about the changing ecological roles of fishes. A study by Tebbett *et al.* (2020) found that the key function of macroalgal removal traverses both classical taxonomic and biogeographic barriers and is carried out by a trigger fish in the Caribbean, and a surgeon fish in the Great Barrier Reef. Similarly, across the same two biogeographic realms, Hemingson and Bellwood (2018) found that the functional composition of an assemblage was delineated according to habitat type (i.e., seagrass, mangrove, reef) rather than taxonomy. Studies on the functional diversity of fishes in shallow waters clearly have many applications, particularly around understanding the response of communities to natural and anthropogenic disturbances.

It is hypothesised that the physical changes associated with increasing depth (decreasing light availability and temperature, and increasing pressure) renders the deep sea an extreme environment for supporting life, leading to the environmental filtering of traits and a resultant reduction in both taxonomic and functional diversity (Keddy 1992; Mindel *et al.* 2016a). Mindel *et al.* (2016a) found that the functional richness of fishes peaked at 500–1000 m and that traits are unevenly distributed in functional trait space at both shallow (300 m) and deep (2000 m) areas. Work by Kumar *et al.* (2017) found that there was minimal niche overlap for the most abundant species at depths of 210–352 m, and that fine-scale niche partitioning *via* variation in locomotion and food acquisition traits aided species coexistence in this low-resource environment. Across a larger depth range (40–2200 m), functional diversity increased to 1400 m and, again, niche partitioning was achieved by abundant species occupying the periphery of functional space (Farré *et al.* 2016). Despite these findings, the deep sea is fundamentally understudied. Much work is required, especially in the deep sea, in order to adequately describe global patterns of marine biodiversity and to identify and characterise potential underlying broad-scale macroecological processes (Duffy & Chown 2017).

1.4.1 New Zealand Fishes

New Zealand's rich fauna of over 1262 fish species, with >20% endemism, spans warm sub-tropical, temperate, and cool sub-Antarctic areas of the Southwest Pacific Ocean. New Zealand marine waters include unique and wide-ranging environments in which to study functional fish diversity. Their latitudinal gradient spans over 30 degrees (29° to 52° S), and depths range from the intertidal to hadal depths of over 10,000 m in the Kermadec Trench (Gordon *et al.* 2010; Roberts, Stewart & Struthers 2015). The New Zealand Exclusive Economic Zone (EEZ), one of the largest in the world, covers an area of almost 4.2 million km^2 and is divided into five biogeographic regions: Kermadec, Northern, Central, Southern and Sub-Antarctic (Roberts, Stewart & Struthers 2015). Accurate identification and knowledge of the distributions of marine fishes within the New Zealand EEZ has been greatly strengthened recently by the most comprehensive authoritative guidebook for this region published to date: *The Fishes of New Zealand* by Roberts, Stewart and Struthers (2015).

Much of the information on the distribution of New Zealand fishes has been historically collected using trawl and SCUBA techniques (Francis 1996; McClatchie *et al.* 1997; Francis *et al.* 2002; Leathwick *et al.* 2006; Leathwick *et al.* 2008). There is an overall trend of reduction in species diversity with increasing latitude (Francis 1996). In an analysis of fisheries research trawl data, McClatchie *et al.* (1997) also found species richness for deeper communities (i.e., for fishes in the 80–898 m depth range) to decline with increasing latitude. There is, however, a notable hotspot of diversity along the Chatham Rise, which is a well-documented area of high productivity (McClatchie *et al.* 1997). Francis *et al.* (2002) found latitude to be the most important explanatory variable for inshore demersal fish assemblages based on trawl data, but depth was the most important explanatory variable for the continental shelf, upper and mid-slope assemblages. Depth was also the best predictor of variation in species richness for fish communities from trawls down to 1500 m, with richness peaking at intermediate depths of 900 m and 1000 m (Leathwick *et al.* 2006).

A joint Australia and New Zealand NORFANZ expedition in 2003 sampled using trawls, sledges, and dredges in deep-water habitats down to 2000 m on Norfolk Ridge and Lord Howe Rise, discovering many species new to science, and high levels of endemism at many of the seamounts sampled (Clark & Roberts 2008). Variation in the abundances of fishes was strongly affected by depth (67%), followed by latitude (21%) and longitude (12%). Recently, New Zealand marine fish communities have been sampled quantitatively along depth and latitudinal gradients using Stereo-Baited Remote Underwater Video systems (Stereo-BRUVs) (Zintzen *et al.* 2012; Zintzen *et al.* 2017). For three locations in northern New Zealand (the Three Kings Islands, Great Barrier Island and White Island), Zintzen *et al.* (2012) found the highest average species richness occurred at shallow depths (50 m). Richness then declined beyond 100 m before reaching a stable average value at depths between 700 m and 1200 m. Zintzen *et al.* (2017) reported a strong interaction between depth and latitude in their effects on fish community structure for 7 locations spanning 21 degrees of latitude in New Zealand, with fish communities from different latitudes becoming increasingly more similar to one another (in terms of the identities of species encountered) at greater depths. Both studies found a strong turnover in the identities of fishes with increasing depth.

Currently, there is a general lack of studies investigating patterns of functional fish diversity along large-scale gradients such as depth or latitude (but see Tolimieri *et al.* 2015; Mindel *et al.* 2016a). Recent work in the South-eastern Chatham Rise region of New Zealand found that with increasing depth (from 200–1300 m) the oral gape of 134 species of fishes and sharks increased with body size (mass), but had no relationship with trophic position, supporting the hypothesis of widespread generalist feeding behaviour with increasing depth (Ladds *et al.* 2020). Overall, however, there is a dearth of studies of functional diversity, covering a range of traits, at broad spatial scales. Additional study is required to characterise biodiversity patterns in taxonomic and functional diversity of New Zealand fish communities to understand their biogeographic context within the southwest Pacific Ocean and in the wider, global context.

1.5 Thesis aim and outline

The primary aim of this thesis was to quantify and characterise functional diversity of fishes along large-scale depth and latitude gradients to expand our understanding of the mechanisms that govern biodiversity in the understudied deep sea, and to disentangle the role of biotic versus abiotic drivers contributing to the assembly of deep-sea communities in the context of broader-scale macroecological processes. Towards this aim, I measured functional traits of New Zealand fishes from a range of depths *in situ*, using underwater stereo-video footage obtained from a structured, replicated ecological sampling design (Zintzen *et al.* 2012; Zintzen *et al.* 2017). The traits measured in this study focused on *locomotion*, and *food acquisition*. These *in situ* measurements were supplemented with additional trait data obtained from direct measurements of specimens held at the National Fish Collection (NFC), Museum of New Zealand Te Papa Tongarewa in Wellington and the Auckland War Memorial Museum. Additional supporting information for some traits was also gleaned from primary literature for New Zealand fishes (e.g., Roberts, Stewart & Struthers 2015).

This thesis contributes novel approaches and empirical data to the growing field of functional ecology and expands our understanding of large-scale patterns of functional diversity along environmental gradients for marine fishes. The thesis contains three empirical data chapters (Chapters Two, Three, and Four), and a general discussion chapter (Chapter Five). Chapters Two–Four have been prepared as peer-reviewed papers for publication; hence there is some repetition of methodological detail throughout the thesis, particularly for Chapters Three and Four. As these papers are co-authored, throughout I use “we” (first person plural) to acknowledge this (see “Declaration by Author” on page iv, and the DRC16 Statement of Contribution forms at the end of each chapter for details on authorship contributions). Chapter Two is published in the *Journal of Animal Ecology*, Chapter Three is under review for publication in the journal *Ecology and Evolution*, and Chapter Four has been prepared for submission to the journal of *Austral Ecology* as part of a special issue.

In **Chapter Two** I derive a range of ecomorphological traits from museum specimens and document patterns of change in each of these traits, on average, along depth and latitude gradients. I add three novel traits for fishes to the current literature that are particularly well-suited for morphological analysis of non-perciform-shaped fishes. This chapter demonstrates not only a number of novel fundamental patterns of large-scale changes in fish morphology that have never been described before, but also the importance of functional trait choice in the derivation of functional diversity measures. This chapter is published in the peer-reviewed *Journal of Animal Ecology* and has been adapted for presentation in this thesis.

Chapter Three describes a study that used measurements obtained from a combination of video footage derived from Stereo-BRUVs and museum specimens to calculate eight traits associated with food acquisition and locomotion. I measured seven complementary metrics of functional diversity to understand how the multidimensional trait space changes across depth and latitude at the local (alpha-diversity) level. I also included intraspecific trait variability in the analyses and provided a novel way to partition intra- *vs* inter-specific variability at the community level to yield new insights about the processes shaping communities along the unexplored depth gradient. This chapter is in review at the peer-reviewed journal *Ecology and Evolution* and has been adapted for presentation in this thesis.

Chapter Four describes a novel scientific description of functional turnover (beta diversity) for fishes along depth and latitude gradients, using a combination of multivariate and univariate measures. I used cluster analyses in trait spaces to identify functional bioregions around New Zealand and looked at the trait values within each bioregion and, hence, the typical fish morphologies that characterise them. This chapter is being prepared for submission in the special issue “*Methods and insights in the analysis of marine biodiversity data – a tribute to Bob Clarke*” in the journal *Austral Ecology.*

Chapter Five discusses the major findings across all chapters and draws conclusions based on the thesis as a whole. I also present future directions and potential research questions that have arisen as a result of this work.

Author contributions are indicated in each chapter.

2 Changes in key traits versus depth and latitude suggest energy-efficient locomotion, opportunistic feeding and light lead to adaptive morphologies of marine fishes.

2.1 Abstract

1. Understanding patterns and processes governing biodiversity along broad-scale environmental gradients, such as depth or latitude, requires an assessment of not just taxonomic richness, but also morphological and functional traits of organisms. Studies of traits can help to identify major selective forces acting on morphology. Currently, little is known regarding patterns of variation in the traits of fishes at broad spatial scales.

2. The aims of this study were: (i) to identify a suite of key traits in marine fishes that would allow assessment of morphological variability across broad-scale depth (50–1200 m) and latitudinal (29.15 – 50.91°S) gradients; and (ii) to characterise patterns in these traits across depth and latitude for 144 species of ray-finned fishes in New Zealand waters.

3. Here, we describe three new morphological traits: namely, fin-base-to-perimeter ratio, jaw-length-to-mouth-width ratio, and pectoral-fin-base-to-body-depth ratio. Four other morphological traits essential for locomotion and food acquisition that are commonly measured in fishes were also included in the study. Spatial ecological

distributions of individual fish species were characterised in response to a standardised replicated sampling design and morphological measurements were obtained for each species from preserved museum specimens.

4. With increasing depth, fishes, on average, became larger and more elongate, with higher fin-base-to-perimeter ratio and larger jaw-length-to-mouth-width ratio, all of which translates into a more eel-like anguilliform morphology. Variation in mean trait values along the depth gradient was stronger at lower latitudes for fin-base-to-perimeter ratio, elongation and total body length. Average eye size peaked at intermediate depths (500–700 m) and increased with increasing latitude at 700 m.

5. These findings suggest that, in increasingly extreme environments, fish morphology shifts towards a body shape that favours an energy-efficient undulatory swimming style and an increase in jaw-length *versus* mouth width for opportunistic feeding. Furthermore, increases in eye size with both depth and latitude indicate that changes in both the average ambient light conditions as well as seasonal variations in day-length can act to select ecomorphological adaptations in fishes.

Keywords: functional traits; jaw-length; eye size; anguilliform; deep-sea fishes; ecomorphology; environmental gradient.

2.2 Introduction

Body shape and morphological traits of organisms are not randomly distributed in space, but are a function of both abiotic and biotic conditions (Brown & Thatje 2014; Humphries *et al.* 2016). These conditions provide selective forces that can act on any traits related to the fitness of the organism. Ecomorphology is the intersection between species' morphology, ecology and behaviour, and was coined separately by Williams (1972) and Karr and James (1975). Ecomorphological traits are involved in key ecological functions and reflect biologically meaningful aspects of a species' ecology, such as how they utilize resources (Motta, Norton & Luczkovich 1995; Norton, Luczkovich & Motta 1995).

Changes in environmental conditions along broad-scale gradients such as altitude or latitude can provide important selective forces to structure ecomorphological traits (also known as adaptive or functional traits) of organisms. Temperature and trophic resources, for instance, are negatively correlated with altitude and latitude, and affect the metabolism and morphology of a wide diversity of organisms. For example, 'Bergmann's rule' describes how homeothermic individuals found in cooler climates at higher altitudes and latitudes have larger bodies to aid in heat conservation (McDowall 2008; Marquet 2009). Another striking latitudinal trend, observed in fishes, is called Jordan's rule, whereby the number of meristic counts of certain characters (*e.g.* fin rays or vertebrae*)* increases at high latitudes (Jordan 1922; Barlow 1961; McDowall 2008). Reduced water temperatures at higher latitudes result in a longer embryonic development time, which correlates with increases in the number of vertebrae (Barlow 1961), and is generally associated with body elongation (Ward & Mehta 2010). A species' morphology reflects a collection of trade-offs (Woods, Martin & Ghalambor 2015), and documenting the link between combinations of phenotypes and associated environmental conditions is essential to understand the potential roles of ecological functions present in communities (Lepš *et al.* 2011).

Bony fishes are widely dispersed across the entire marine realm and are the most speciose group of vertebrates on planet earth, with a tremendous diversity of body shape and size (Helfman *et al.* 2009; Eschmeyer, Fricke & Van der Laan 2018). Studies of fish morphology have identified several important ecomorphological traits; however, most studies have focussed on shallow-water ecosystems, often at small spatial scales. For example, Villéger *et al.* (2010) studied morphological structures related to food acquisition and locomotion, and found that changes in these traits reflected sustained degradation of estuarine habitats. In another shallow-water example, (Bejarano *et al.* 2017) found herbivorous coral reef fishes with a fusiform body shape were able to graze more effectively in areas of high wave exposure than herbivores possessing a laterally compressed body, which were more affected by unpredictable wave movements. Also on coral reefs, (Bridge *et al.* 2016) found that 'depth-generalist' fishes (inhabiting depths of ~30–50 m) tended to have more lunate-shaped caudal fins with a high aspect ratio, which may assist in "silent swimming" and facilitate prey capture in darker environments. Although these studies provide examples of ecomorphological traits important for 'perciform-shaped' fishes that dominate shallow ecosystems, the traits they examined do not capture the broader diversity of morphologies found across all marine fishes. A wider range of morphological traits for marine fishes needs to be described to enable a more thorough characterisation of trait variation across broad-scale spatial and environmental gradients.

Marine fishes are ubiquitous across the earth’s oceans (Helfman *et al.* 2009); they are distributed from shallow waters down to depths of 8,200 m (Yancey *et al.* 2014). The depth gradient is one of the steepest environmental gradients on earth; like altitude and latitude, depth strongly influences the spatial distribution of species, their functions and morphologies (Mindel *et al.* 2016a; Zintzen *et al.* 2017). Abiotic changes that occur with increasing depth are dramatic, including decreasing light, temperature, dissolved oxygen, food resources and increasing pressure (Priede 2017a). Marine organisms have developed a suite of behavioural, physiological and morphological traits specifically adapted to these biophysical constraints (Maurer 2009; Brown & Thatje 2014). Studies using multiple morphological traits to calculate multivariate measures of functional diversity in fishes (Farré *et al.* 2016; Mindel *et al.* 2016a; Kumar *et al.* 2017), suggest that both size and swimming capacity may influence species’ coexistence and resource partitioning along the depth gradient.

The most salient trend in an individual ecomorphological trait along the depth gradient is an increasingly elongate body shape (Neat & Campbell 2013; Farré *et al.* 2016). Generally, fishes become less fusiform-shaped and more elongate with increasing depth. This facilitates an anguilliform, sinusoidal, energy-efficient swimming method, which may increase their ability to travel long distances to acquire resources (Neat & Campbell 2013). However, our understanding of morphological changes along the depth gradient is limited by the traits we currently use to capture morphological variation in fishes. For example, currently traits designed to capture aspects of locomotion require measurement of the caudal peduncle, present in fishes having a perciform shape (*e.g.*Villéger *et al.* (2010)). However, fish lineages that occur at deeper depths, such as Anguilliformes, Gadiformes, Notocanthiformes, Ophidiformes, and Aulopiformes, lack a measurable caudal peduncle. Ideally we require traits that are quantitative, continuous, repeatable, and measurable (McGill *et al.* 2006; Violle *et al.* 2007) across the broad range of fish morphologies encountered along the depth gradient.

Our primary aim is to describe ecological patterns in the distribution of morphological traits of fishes along depth and latitude gradients, using New Zealand fishes as a case study. More specifically, we generalize the morphological framework used to assess morphological variability and functions of ray-finned marine fishes across large-scale depth (50–1,200 m) and latitudinal (29.15–50.91°S) gradients. We describe three new ecomorphological measures for fishes related to locomotion and food acquisition; specifically, fin-base-to-perimeter ratio, jaw-length-to-mouth-width ratio, and pectoral-fin-base-to-body-depth ratio. We describe ecological patterns in the distributions of these new traits, along with four previously described ecologically relevant aspects of body shape that are also expected to vary with depth and latitude, namely, eye size, body transversal shape (the ratio between body depth and body width) (Villéger *et al.* 2010), elongation (Claverie & Wainwright 2014), and total body length as an overall measure of body size (Smith & Brown 2002). We restricted our attention to traits that were measurable in the species we observed along the 50–1,200 m depth gradient.

We considered that patterns of variation in our newly described traits would provide meaningful insights into functional changes of benthic fishes along the depth gradient. For example, most fishes in mesopelagic and bathypelagic zones have an enlarged gape to accommodate a wider range of prey sizes in areas having limited resources (Ebeling & Cailliet 1974; Drazen & Sutton 2017). We therefore hypothesised that jaw-length-to-mouth-width ratio would increase with depth. Body elongation is also expected to increase with depth (Neat & Campbell 2013). Furthermore, with an elongate body, there is a greater area along the median line of dorsal and ventral surfaces for longer-based fins, which can help in undulatory and sustained swimming (Webb 1984). In light of this, we hypothesised that elongate fishes that swim using body and caudal-fin undulation, important at greater depths, will have a high fin-base-to-perimeter ratio. In contrast, we anticipated that the pectoral fin-base ratio, a proxy for manoeuverability, would be higher in areas of greater topographic complexity (Bejarano *et al.* 2017), which is generally typical of shallower environments. Eye size and body transversal shape have been shown previously to have positive (Warrant & Locket 2004; Ingram & Shurin 2009) and negative (Farré *et al.* 2016) trends, respectively, with increasing depth, and we expected to see similar trends in this study. Last, we hypothesized that total body length would increase with depth, as previously documented for both demersal and pelagic species (Smith & Brown 2002; Collins *et al.* 2005; Mindel *et al.* 2016b).

We tested these hypotheses by combining ecological information regarding the occurrences of individual species, obtained from underwater video footage taken in a large-scale stratified sampling design along depth and latitude gradients, with morphological measurements for each of these species, obtained from preserved museum specimens. By expanding the repertoire of ecologically meaningful traits, our study yields new insights into the morphological adaptations and functional biology of fishes in the deep sea.

2.3 Materials and Methods

Morphological traits were measured from museum specimens for each of 144 marine ray-finned fish species (Class Actinopterygii) that had been observed in 329 Stereo-BRUVs deployed in a stratified random sampling design, covering depths from 50 m to 1,200 m and locations spanning 21° of latitude in New Zealand waters. The stereo-BRUV imagery was collected from 2009 to 2012 during the austral summer months at each of seven locations (from north to south): Kermadec Islands (KER), Three Kings Islands (TKI), Great Barrier Island (GBI), White Island (WI), Kaikōura (KKA), Otago Peninsula (OTA) and the Auckland Islands (AUC). At each of these locations, the following depths were sampled by stereo-BRUV deployments along each of n = 6-7 transects: 50, 100, 300, 500, 700, 900 and 1,200 m, except for WI and AUC, which were not sampled at 1,200 m, due to poor weather conditions. For further technical details regarding stereo-BRUV methods and maps showing the full sampling design, see Zintzen *et al.* (2017) and (Zintzen *et al.* 2012). It is known that the use of bait in stereo-BRUV video deployments has an associated bias, causing an increase in the number of predators and scavengers observed, without affecting the numbers of herbivorous and omnivorous fishes (Harvey *et al.* 2007). For more information regarding the relative magnitude of this bias, see Hardinge *et al.* (2013) and Dorman, Harvey and Newman (2012). We extracted the species list for all fish seen in stereo-BRUV deployments across the full study design and took morphological measurements for each of these species from museum specimens. Morphological measurements were made on the left-hand side of one individual belonging to each of the 144 species from undamaged, preserved specimens with fins fixed in an erect position held at the Museum of New Zealand Te Papa Tongarewa, Wellington or the

Auckland War Memorial Museum. We assume in our ensuing analysis that each of the measured museum specimens represents an unbiased sample of the morphological characteristics for each species (see Appendix 2.4 for a comparison between the total length of museum specimens, and individuals measured *in situ* on stereo-BRUV footage). The list of species and associated registration numbers of individual specimens are provided in Appendix 2.1.

Twelve raw variables were measured on each fish specimen (Figure 2.1, Table 2.1): total body length (*TL),* body depth at pectoral fin, where the anterior point of insertion is the landmark for the measure (*PBd*), maximum body depth (*mBd),* perimeter omitting fins (*Pof*), perimeter intersecting fins (*Pif*), lower jaw length, measured from the anterior tip of the lower jaw to the corner of the mouth along the dentary section of the mandible (*Lj*), upper jaw length, measured as the distance from the tip of the jaw (premaxilla), to the posterior end of the maxilla (*Uj*), pectoral fin-base (*Pfb*), head depth (*Hd*), maximum eye diameter (*Ed*), maximum body width (*Bw*), and maximum mouth width across the mouth opening (*Mw*). Measurements were made point-to-point using Vernier callipers to the nearest 0.1 mm; however, where there was a curved perimeter or fin-base measurement, a length of cotton twine was used, and the twine’s length was measured to the nearest 1mm using a 2000 mm ruler.

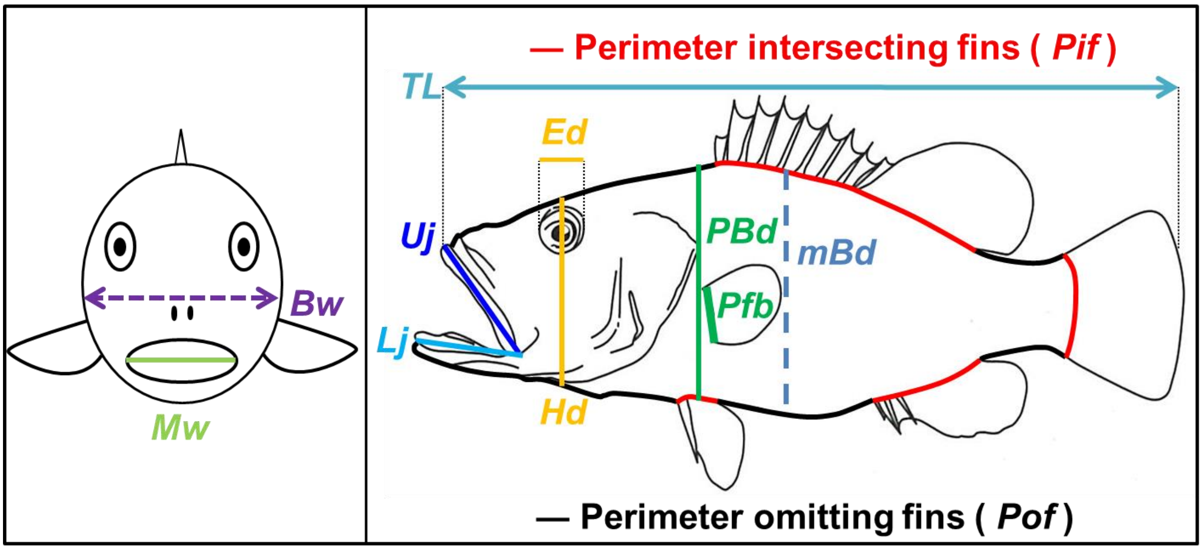


Figure 2.1. Schematic diagram of morphological measurements obtained from museum specimens: *Bw,* body width; *Mw,* mouth width; *TL,* total body length; *Ed,* eye diameter; *Uj,* upper jaw; *Lj,* lower jaw; *Hd,* head depth; *PBd,* body depth at pectoral fin, where the anterior point of insertion is the landmark for the measure; *Pfb,* pectoral-fin-base; *mBd,* maximum body depth; *Pif,* perimeter intersecting finsp; *Pof,* perimeter omitting fins. *Note *Pif* + *Pof* = total perimeter (*TP*), curved perimeter measurements are taken using a length of cotton twine.

Table 2.1. A summary of the ecomorphological traits of fishes studied here along with their abbreviations, derivation and original source. See Figure 2.1 for a schematic diagram of the raw variables measured from fishes.

Type	**Functional trait**	**Abbrev.**	**Equation**	**Source**
General	Total body length	TL	TL	Hubbs, Lagler, and Smith (2004)
Food acquisition	Jaw-length-to-mouth-width ratio	JM	$½ (Uj + Lj) / Mw$	This study
	Eye size	Es	Ed / Hd	Villéger et al. (2010)
Locomotion	Fin-base-to-perimeter ratio	FbP	$Pif / (Pif + Pof)$	This study
	Pectoral fin-base-to-body-depth ratio	$PfbBd$	Pfb / PBd	This study
	Body transversal shape	Bts	mBd / Bw	Villéger et al. (2010)
	Elongation	El	TL / mBd	Claverie and Wainwright (2014)

From these variables, seven traits of interest were derived and analysed in detail. Three of these were novel traits, described here for the first time and specifically designed to capture morphological changes in fish body plans expected to occur with increasing depth. These were: fin-base-to-perimeter ratio (*FbP*), jaw-length-to-mouth-width ratio (*JM*), and pectoral-fin-base-to-body-depth ratio (*PfbBd*). Four other individual traits, described in previous studies and also expected to change with depth and/or latitude, were also analysed individually here, namely: eye size (*Es*), elongation (*Elo*), body transversal shape (*Bts*), and total body length (*TL*).

Fin-base-to-perimeter ratio (*FbP = Pif* / (*Pif* + *Pof)*) is the total length along the bases of all fins that connect to the surface of the body along the body's perimeter (*i.e.*, dorsal, caudal, anal and pelvic fins), divided by the total perimeter of the body (*Pif* + *Pof*). In essence, this ratio quantifies how much of the body's outline (viewed laterally) is covered in fins. This measure generally increases in value for body plans that are more anguilliform (eel-like) in shape and that would use a greater degree of sigmoidal undulation for locomotion (Webb 1984).

Elongation (*Elo = TL / mBd*) is a metric of body shape and is measured as the ratio of total body length (from the snout to the posterior margin of the caudal fin) divided by the maximum body depth. This trait was described by (Gatz 1979), and was recently examined by (Claverie & Wainwright 2014), who noted the potential advantages of an elongate *versus* a deep-bodied shape for long-distance or sustained swimming. Steady swimming maintains a constant speed and direction, and is used for holding position in a current, seeking food, mates, or favourable abiotic conditions, predator avoidance and migration (Blake 1983; Plaut 2001).

Total body length (*TL*) can be used as a general proxy for overall body size (Mindel *et al.* 2016b). The overall size of a fish gives an indication of their trophic level or relative position in a food-web (Woodward *et al.* 2005). Owing to the wide range of orders (and morphologies) within this study we chose to use total length. We did not choose to use fork length because many species examined here do not have a forked tail. Standard length was not used here because these data are also the subject of a larger study involving video analysis where standard lengths are not measurable.

Jaw-length-to-mouth-width ratio ($JM = (\frac{1}{2}(Uj + Lj)) / Mw$) is the average length of the upper and lower jaws, divided by the mouth width. Previous studies (Villéger *et al.* 2010) have measured the shape of the oral gape using mouth depth (Md/Mw), but Md is often not feasible to measure from preserved specimens, due to the rigidity of structures (including the mouth) that occurs after fixing individuals in formalin. JM gives an indication of the size and shape of prey that can be ingested by a given fish species, yielding potential insights into their strategies used for food acquisition.

Eye size ($Es = Ed / Hd$) is the maximum eye diameter divided by the head depth, which is the length from the dorsal to the ventral edge of the head, as measured through the middle of the eye. This trait was previously described by (Villéger *et al.* 2010) and is of interest here given the dramatic change in light levels with increasing depth in marine ecosystems (Hammerschlag *et al.* 2017).

Pectoral-fin-base-to-body-depth ratio ($PfbBd = Pfb / PBd$) is the length of the base of the pectoral fin where it attaches to the body (described previously by Rouleau, Glémet and Magnan (2010)), divided by the total body depth at the point of insertion of the pectoral fin. $PfbBd$ measures indirectly the predominant type of swimming used by a fish: increasing values of *PfbBd* indicate greater manoeuvrability (*e.g.,* around reefs or other complex structures in shallower systems), or stability (*e.g.,* for benthic fishes that hold still in order to ambush their prey).

Body transversal shape (*Bts = mBd / Bw*) is the ratio between body depth and body width and is used to infer vertical position in the water column: generally, benthic fishes have vertically flattened or rounded bodies, and bentho-pelagic fishes are deeper-bodied (Sibbing & Nagelkerke 2000; Villeger *et al.* 2017).

For univariate analyses of traits, we considered all species that were present across the replicate stereo-BRUV units within each Depth x Location cell, and plotted means and standard errors across the study design for each trait of interest (see Figs 2.2-2.4 in results). For subsequent multivariate analyses of traits, we considered each stereo-BRUV unit in the above ecological sampling design as a replicate, and calculated the mean trait value across the list of species that were identified from that unit. We then calculated a mean trait value for each Depth x Location cell (n = 47), and these values were used to visualize holistic patterns of morphological changes in fishes across the overall study design (see Figs 2.5 & 2.6).

Permutational analysis of variance was used to partition variation using Type I (sequential) sums of squares for each of the above seven traits of interest according to the following three-factor experimental design: Location (fixed with 7 levels), Depth (fixed with 7 levels), and Transect (random, nested within Location and crossed with Depth). p-values for individual terms in the ANOVA model were obtained using 9,999 permutations under a reduced model (Freedman & Lane 1983; Anderson & ter Braak 2003). Pair-wise comparisons were done *a posteriori* to follow up significant terms in ANOVA models. Each of the pair-wise tests used 9999 permutations and an adjusted significance level of $P = .01$ was used to avoid increases in Type I error with multiple comparisons.

Trait variables are expected to display some degree of association with one another and with overall body length. Thus, we repeated the univariate PERMANOVA models and included Total length (*TL*) as a covariate to account directly for size-related differences in shape. We also examined correlations among variables using Pearson coefficients and performed multivariate analyses that allow for correlation structures among variables. All multivariate analyses were done on the basis of Euclidean distances for $p = 7$ normalised trait variables using PRIMER v7 (Clarke & Gorley 2015b) with the PERMANOVA+ add-on (Anderson, Gorley & Clarke 2008). To visualise simultaneous changes in multiple morphological traits along the depth gradient, metric multi-dimensional (mMDS) ordination was calculated on the Euclidean distances among depth centroids, and segmented bubbles for 5 salient traits of interest (namely: *FbP*, *JM*, *PecFB*, *Es* and *TL*) were superimposed.

An mMDS ordination was also constructed to examine patterns of differences in fish morphologies among depth-by-location centroids. We also explicitly measured latitudinal variation in fish morphology across all of these traits simultaneously by calculating the average distance-to-centroid among the location means separately within each depth stratum. A permutation test for homogeneity of multivariate dispersions (PERMDISP; (Anderson 2006)) was used to formally compare latitudinal variation in overall fish morphology among depth strata.

2.4 Results

The level of statistical significance of individual terms (*i.e.,* Depth, Location, and Depth x Location) in univariate analyses of individual variables did not change when total length (*TL*) was included as a covariate (*c.f.* Table 2.2, and Appendix 2.3), with the exception of the analysis of body transversal shape (*Bts*). In that case, the main effect of Depth was no longer significant; however, the Depth x Location interaction remained significant (see below for details). For simplicity in interpretation, we present the results of analyses done directly on derived traits; however the effects of Depth on body transversal shape should be interpreted with the understanding that these trends do covary with total length.

Fin-base-to-perimeter ratio (*FbP*)

Mean fin-base-to-perimeter ratio (*FbP*) increased with increasing depth, from 0.46 at 50 m (± 0.01 SE) to 0.67 at 1,200 m (± 0.01 SE) (Fig. 2.2a). The rate of increase varied with location (Table 2.2a; Depth × Location interaction term, $P = 0.0001$) and two distinct biogeographic regions (north and south) were identifiable for this trait (Fig. 2.2a, Appendix 2.2, a). Northern locations (KER, TKI, and GBI) showed a decrease in the average value of this trait from 50 m to 300 m, followed by a sharp increase from 500 m to 1200 m, whereas southern locations (KKA, OTA and AUC), showed a steady increase in mean *FbP* with increasing depth (Fig. 2.2a). The contrast between northern and southern locations, with southern locations having greater average *FbP*, was most distinct at 300 m and 500 m (Fig. 2.2a). However, at deeper depths (*i.e.,* at either 900 m or 1200 m depth), there were no significant differences in mean *FbP* among locations (Appendix 2.2, a.).

Elongation (*Elo*)

The mean elongation ratio (*Elo*) increased with increasing depth, from 4.62 at 50 m (± 0.25 SE) to 10.25 at 1200 m (± 0.31 SE) (Fig. 2.2b). The rate of increase varied among locations (Table 2.2b; Depth × Location interaction term, $P = 0.0001$) and there was a clear outlier at 900 m (TKI): this northern location had a very high mean (12.63) and SE (2.92) value for this variable. At southern locations (KKA and OTA), there was an increase in elongation to comparable mean values from 300 m to 900 m. In contrast, mean elongation remained relatively low at northern locations (KER, TKI, GBI and WI) from shallow depths right through to *ca*. 500 m in depth, with a steep increase observed from 500 m to 700 m (Fig. 2.2b).

Total body length (*TL*)

Mean total body length (*TL*) of fishes appeared roughly similar at depths spanning 50 m–500 m, and 700 m–1200 m, respectively (Fig. 2.2c, see also Appendix 2.2, c). Trends in mean total body length with increases in depth also depended on latitude (Table 2.2c; Depth × Location interaction term, $P = 0.0008$). Specifically, mean total body length did not vary significantly along the depth gradient at the two southern locations (OTA and KKA), but for all other locations, there was a clear increase in mean total body length after 500 m (Fig. 2.2c). In addition, latitudinal variation in mean total body length (*i.e.*, across all 7 locations) was smallest at the deepest depth (1,200 m).

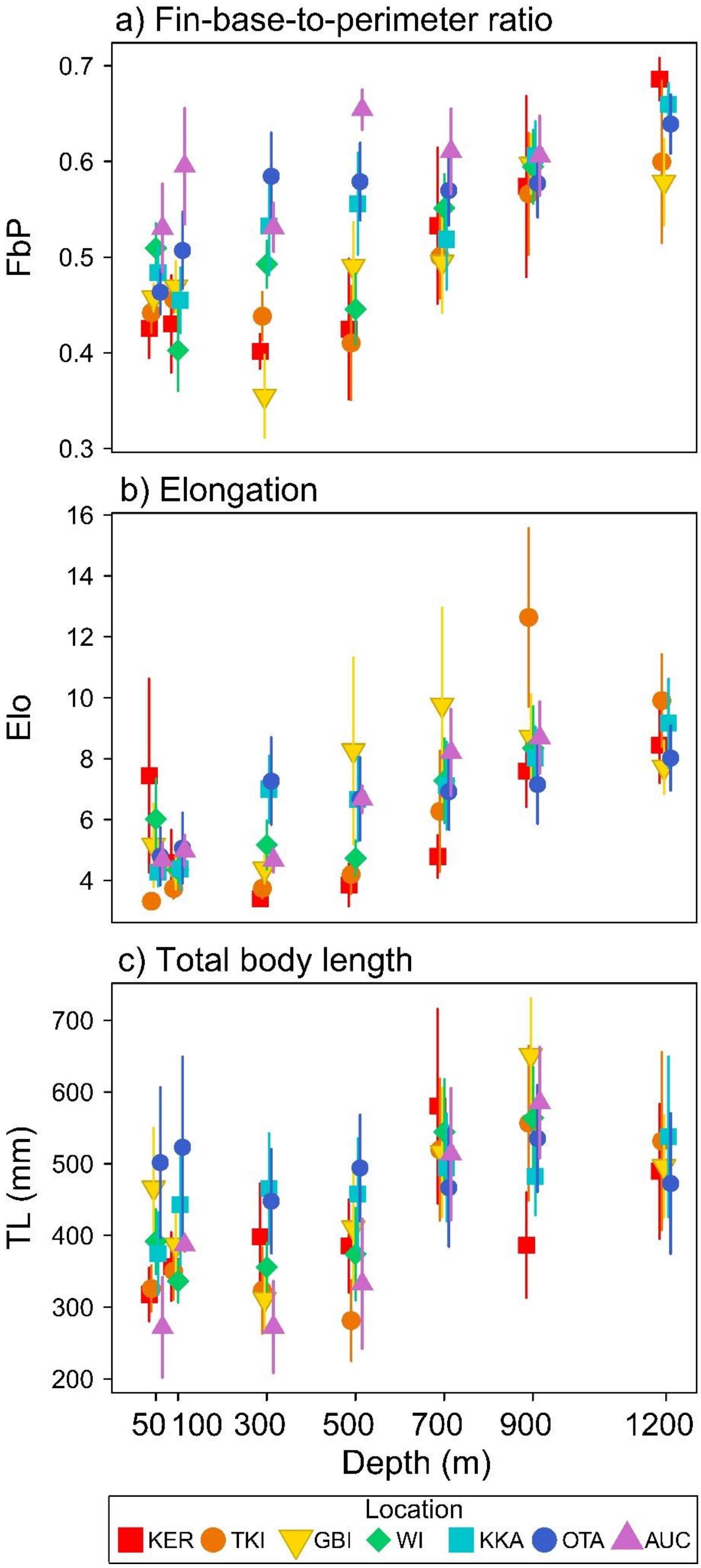

a) Fin-base-to-perimeter ratio
FbP
0.7
0.6
0.5
0.4
0.3
b) Elongation
Elo
16
14
12
10
8
6
4
c) Total body length
TL (mm)
700
600
500
400
300
200
50
100
300
500
700
900
1200
Depth (m)
Location
KER
TKI
GBI
WI
KKA
OTA
AUC

Figure 2.2. Mean (± 1 *SE*) values for 3 different morphological measurements of fishes (a. Fin-base-to-perimeter ratio, b. Elongation, c. Total body length) occurring at each of 7 depths (50 – 1,200 m) in each of 7 locations (colour-coded and ordered from north to south: KER = Kermadec Islands, TKI = Three Kings Islands, GBI = Great Barrier Island, WI = White Island, KKA = Kaikōura, OTA = Otago, and AUC = Auckland Islands). The number of species per Depth x Location cell (used to generate the standard errors) ranged from $n = 3$ to $n = 29$. Note: WI and AUC were not sampled at 1200 m.

Jaw-length-to-mouth-width ratio (*JM*)

Mean jaw-length-to-mouth-width ratio (*JM*) increased with increasing depth, from 1.17 at 50 m (± 0.02 SE) to 1.96 at 1200 m (± 0.12 SE) (Fig. 2.3a). The rate of increase in the mean value of *JM* with increasing depth was steepest from 700 m to 1200 m (Fig. 2.3a). Conversely, the range of mean values among shallower depth strata (*i.e.*, 50 m, 100 m, and 300 m) was much less pronounced (1.17 – 1.29) (Fig. 2.3a). Variation in *JM* within a given location (as measured by the standard error) was greatest at 1200 m (± 0.12), followed by 900 m (± 0.07), and 700 m (±0.05) (Fig. 2.3a). There were no significant differences in mean *JM* values among locations at 1200 m depth (Appendix 2.2, b; $P > 0.01$ for all pair-wise comparisons), and at shallower depths there was no clear north-south biogeographic pattern among locations. The Depth × Location interaction term was significant at the α-level of 0.05 (Table 2.2d; $P = 0.021$), with each location showing a different pattern with depth. For example, there is little variation in the mean jaw-length-to-mouth-width ratio across depths at KER, whereas at AUC mean values are similar at 50 – 300 m then steeply increase with increasing depth.

Eye size (*Es*)

Mean eye size (*Es*), as a ratio of head depth, was unimodal along the depth gradient, with a peak occurring at *ca*. 500 m (0.53 ± 0.01 SE) (Fig. 2.3b). Latitudinal differences in mean eye size were also apparent, although the sizes of these differences varied with depth (Table 2.2e; Depth × Location interaction term, *P* = 0.0001). In general, however, there was a pattern of increase in mean eye size with increases in latitude; with fishes at southern locations generally showing greater mean eye size than northern locations within a given depth stratum. A monotonic increase in eye size with increasing latitude was most apparent for the 700 m depth stratum (Fig. 2.3b).

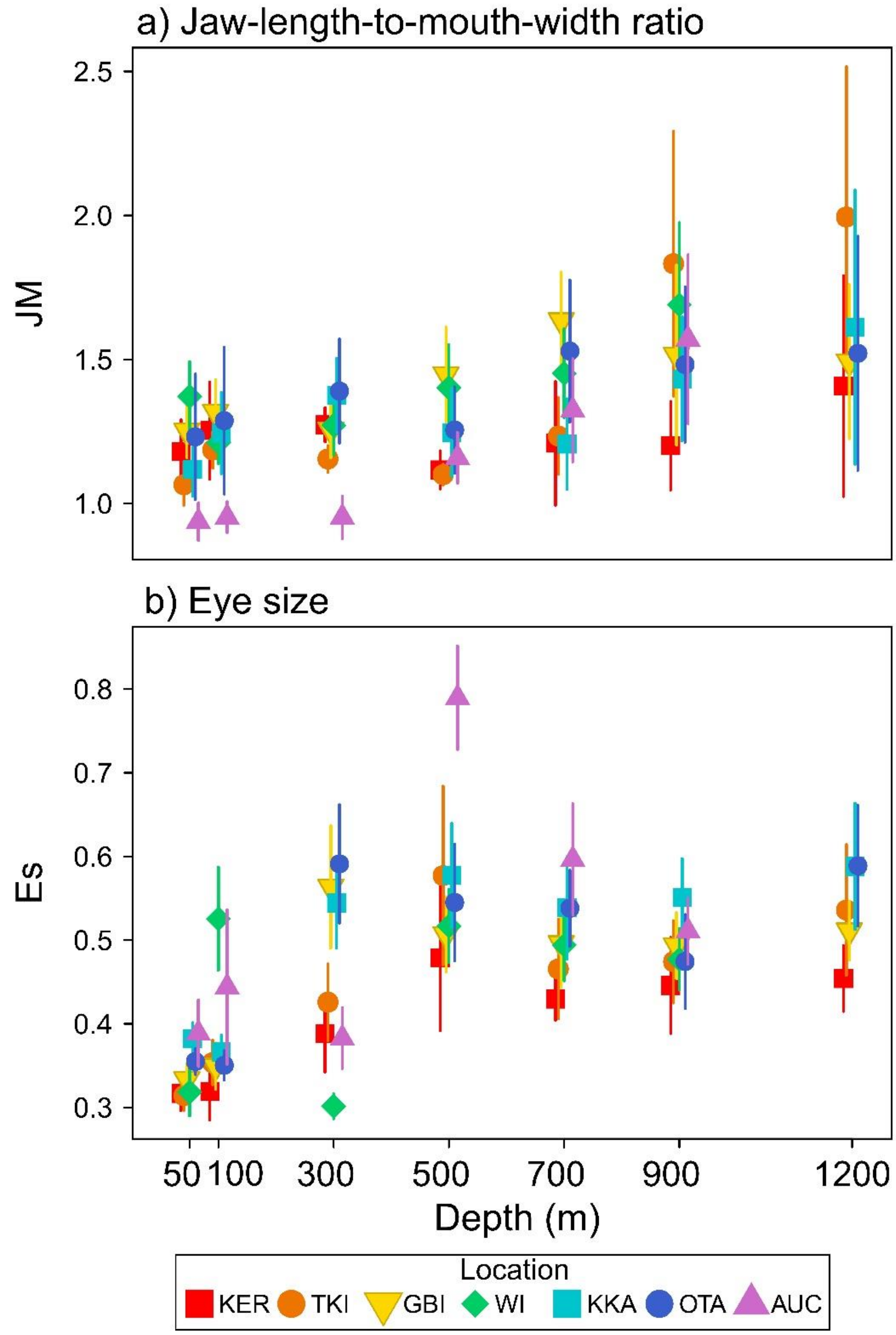


Figure 2.3. Mean (± 1 *SE*) values for 2 different morphological measurements of fishes (a. Jaw-length-to-mouth-width ratio, b. Eye size) occurring at each of 7 depths (50 m – 1200 m) in each of 7 locations (colour-coded and ordered from north to south: KER = Kermadec Islands, TKI = Three Kings Islands, GBI = Great Barrier Island, WI = White Island, KKA = Kaikōura, OTA = Otago, and AUC = Auckland Islands). The number of species per Depth x Location cell (used to generate the standard errors) ranged from *n* = 3 to *n* = 29. Note: WI and AUC were not sampled at 1200 m.

Pectoral-fin-base-to-body-depth ratio (*PfbBd*)

Mean pectoral fin-base (*PfbBd*) values varied significantly among depth strata, but the observed pattern of change in the means of this trait with increasing depth depended on the location (Table 2.2f; Depth × Location interaction term, *P* = 0.0001). For some locations (KKA, KER), average *PfbBd* decreased with increasing depth, with the greatest decrease occurring between 100 m and 500 m. For other locations (TKI, GBI), there was an increase in the average value of this trait from 100 m to 300 m, followed by a decrease and plateau at deeper depths. In contrast, OTA showed quite variable average values for this trait across all depth strata, with no clear trend. Although generally the variation in mean *PfbBd* values across locations within each depth stratum was small, there were notable exceptions: at 50–100 m AUC had significantly higher average values for this trait; TKI had a higher average at 500 m, and KER had a higher average at 900 m, compared to other locations (Fig. 2.4a).

Body transversal shape (*Bts*)

Trends in mean body transversal shape with depth depended on latitude (Table 2.2g; Depth × Location interaction term, *P* = 0.0001). Specifically, fishes at southern latitudes had consistently low mean *Bts* values (but see KKA, Fig. 2.4b), while fishes at northern locations showed higher mean *Bts* values at shallow depths that decreased significantly with increasing depth. At shallow and intermediate depths (50 m–500 m) the mean *Bts* was highly variable among locations, but location-level variation in this trait decreased at deeper depths, particularly at 1200 m (Fig. 2.4b).

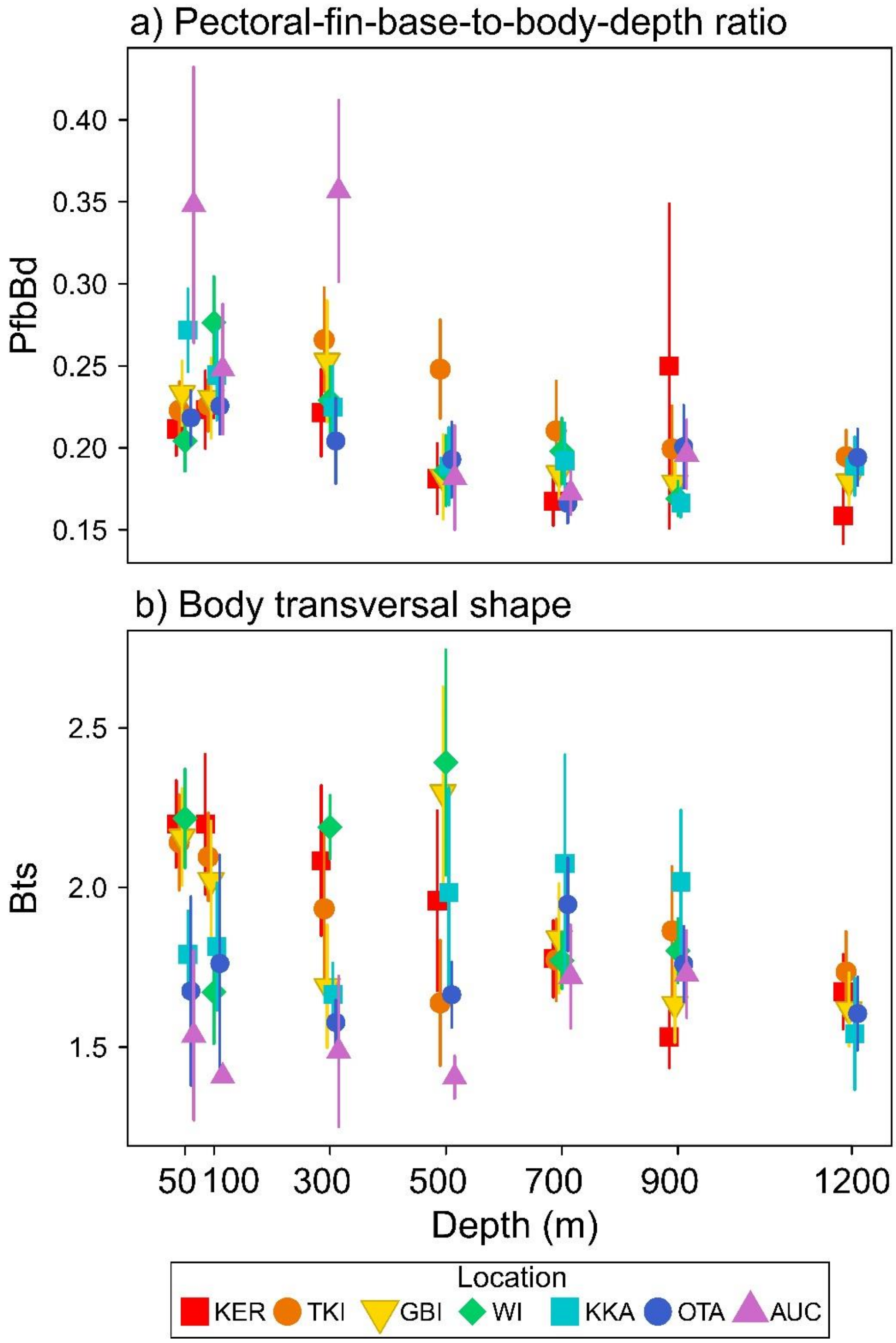


Figure 2.4. Mean (± 1 SE) values for 2 different morphological measurements of fishes (a. Pectoral fin-base, b. Body transversal shape) occurring at each of 7 depths (50 m – 1200 m) in each of 7 locations (colour-coded and ordered from north to south: KER = Kermadec Islands, TKI = Three Kings Islands, GBI = Great Barrier Island, WI = White Island, KKA = Kaikōura, OTA = Otago, and AUC = Auckland Islands). The number of species per Depth x Location cell (used to generate the standard errors) ranged from *n* = 3 to *n* = 29. Note: WI and AUC were not sampled at 1200 m.

Multivariate results

Joint changes in morphological characteristics of fishes along the depth gradient were evident in the plot of multivariate centroids (Fig. 2.5a). *FbP, JM,* and *TL* all increased with depth, *Es* was consistently larger between 300 m and 1200 m, and *PecFB* was larger in shallow and intermediate depths compared to deeper depths (Fig. 2.5a). These trends were not driven entirely by increases in the overall sizes of fishes with depth. Indeed, *JM, FbP* and *Elo* were only weakly positively correlated with *TL*, while *Bts, Es* and *PfbBd* were weakly negatively correlated with *TL* (Fig. 2.5b). *Bts* was negatively correlated with all other traits examined here except *JM*, while *Elo* was positively correlated with *FbP* and *JM* (Fig. 2.5b).

There was also a strong trend of gradual change in fish morphology with increasing depth shown in the mMDS ordination of depth-by-location centroids (*i.e.*, from left to right along MDS axis 1, Fig. 2.6a) across all locations. Furthermore, there were significant differences in the variability of morphologies at different depths (PERMDISP, $F_{6,\ 40}$ = 4.0378, P = 0.0227). Latitudinal variation in fish morphology was greater at shallower depths (*viz*. the larger spread of centroids across different locations along MDS axis 2 at depths of 50–100 m), with northern locations also being more tightly clustered than southern locations (Fig. 2.6a). Latitudinal variability in morphology was highest at 500 m (Fig. 2.6b), and morphologies at northern locations more closely resembled those at shallow depths, while morphologies at southern locations were more similar to those observed in deeper strata (Fig. 2.6a). At deeper depths, (*i.e*., 700 m–1200 m), variation in morphology among locations was greatly reduced (centroids were more tightly clustered in the plot, see Fig. 2.6a).

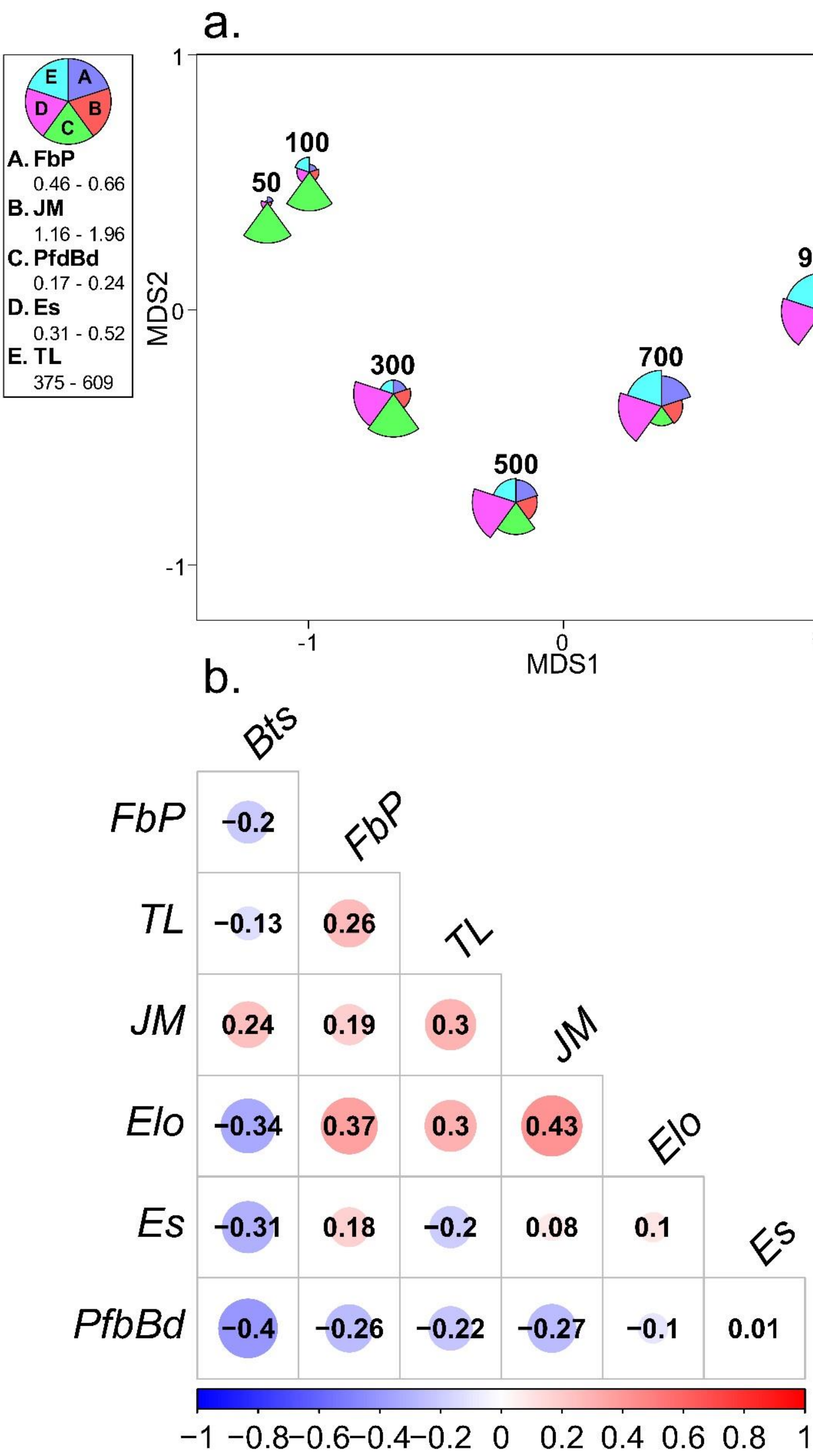

a.
E A D B C
A. FbP
0.46 - 0.66
B. JM
1.16 - 1.96
C. PfdBd
0.17 - 0.24
D. Es
0.31 - 0.52
E. TL
375 - 609
2D Stress: 0.03
50
100
300
500
700
900
1200
MDS2
1
0
-1
MDS1
-1
0
1
b.
Bts
FbP
TL
JM
Elo
Es
PfbBd
−0.2
−0.13
0.26
0.24
0.19
0.3
−0.34
0.37
0.3
0.43
−0.31
0.18
−0.2
0.08
0.1
−0.4
−0.26
−0.22
−0.27
−0.1
0.01
−1
−0.8
−0.6
−0.4
−0.2
0
0.2
0.4
0.6
0.8
1

Fig. 2.5 (a) Metric multi-dimensional scaling (mMDS) ordination on the basis of Euclidean distances among depth centroids (labelled 50-1,200) for p = 7 normalised morphological traits of fishes. Segmented bubbles are overlaid for each of the following traits: fin-base-to-perimeter ratio (FbP), jaw-length-to-mouth-width ratio (JM), pectoral-fin-base-to-body-depth ratio (PecFB), eye size (Es), total length (TL). The relative size of the bubble section for each variable reflects the relative average value for that variable within its range (shown in the legend). b. Heat map showing Pearson correlations among morphological trait variables.

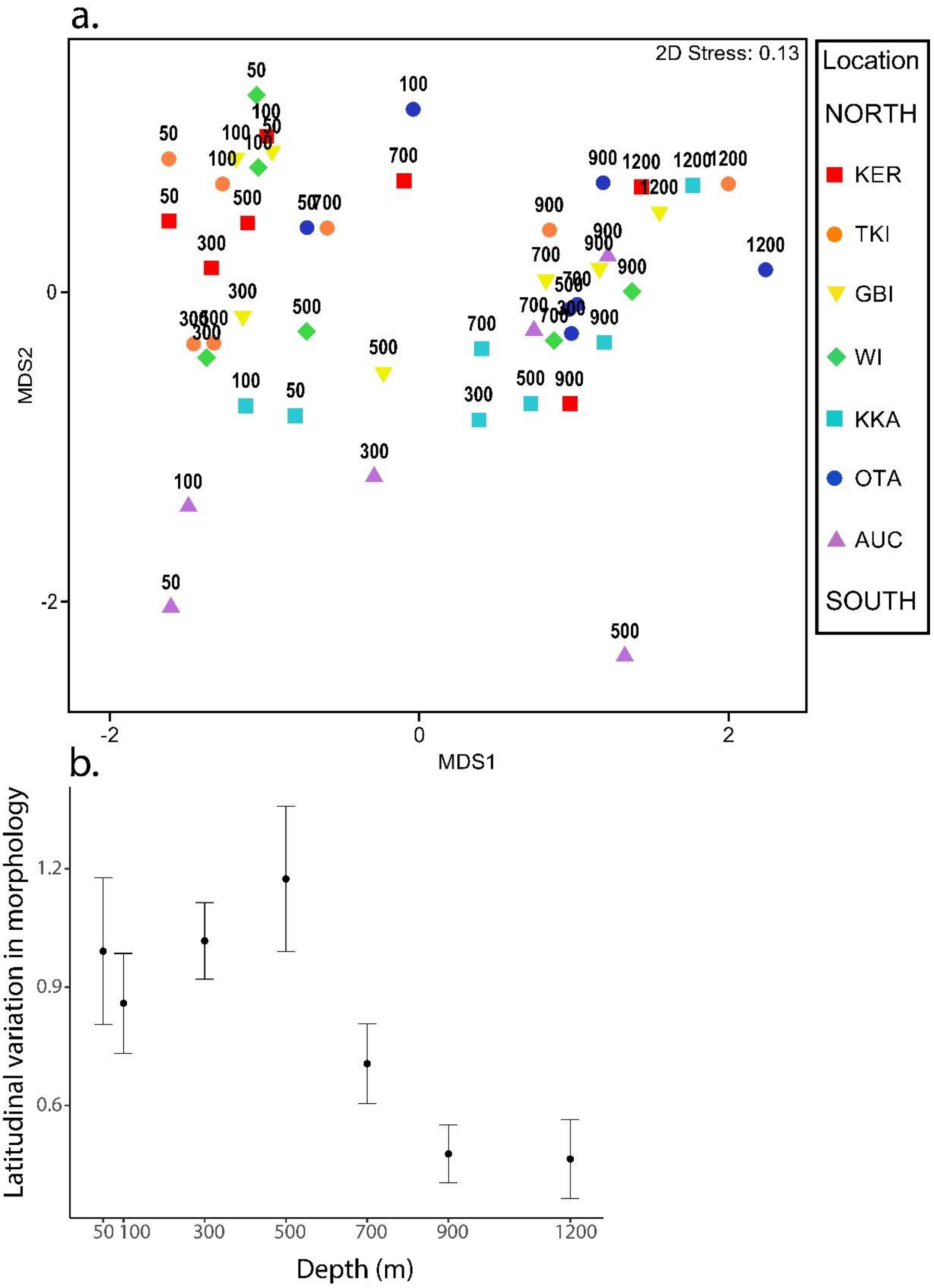


Figure 2.6. a. Metric multi-dimensional scaling (mMDS) ordination on the basis of Euclidean distances among depth-by-location centroids for *p* = 7 normalised morphological traits. Each cell has a symbol to indicate the location (colour-coded and ordered from north to south: KER = Kermadec Islands, TKI = Three Kings Islands, GBI = Great Barrier Island, WI = White Island, KKA = Kaikōura, OTA = Otago, and AUC = Auckland Islands) and a label to indicate the depth. (Note: no measurements were taken at 1200 m for WI or AUC). b. Latitudinal variation in morphology, calculated as the average Euclidean

distance-to-centroid (± 1 SE) on the basis of $p = 7$ normalised morphological traits, at each of seven depths.

Table 2.2. Analysis of variance (ANOVA) for each of seven individual morphological variables (a through g) in response to the 3-factor stratified random sampling design, with *p*-values obtained using 9,999 permutations of residuals under a reduced model. Note that 12 of the original 341 deployments were omitted prior to analysis due to no bony fish (Actinopterygii) being present. MS: Mean square.

		a) Fin-base-to-perimeter ratio			b) Elongation			c) Total body length			d) Jaw-length-to-mouth-width ratio		
	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Depth	6	15.18	106.53	0.0001	11.24	86.48	0.0001	6.89	43.11	0.0001	7.40	64.73	0.0001
Location	6	3.23	17.11	0.0001	0.91	8.35	0.0001	2.70	10.71	0.0001	1.09	8.06	0.0001
Transect (Loc)	50	0.16	1.15	0.2624	0.1	0.72	0.8658	0.21	1.38	0.077	0.11	1.02	0.3975
Depth x Loc	33	0.59	4.19	0.0001	0.59	4.47	0.0001	0.34	2.21	0.0008	0.19	1.67	0.021
Residual	233	0.14			0.13			0.15			0.11		

		e) Eye size			f) Pectoral fin-base-to-body-depth ratio			g) Body transversal shape		
	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Depth	6	14.84	104.26	0.0001	5.38	23.79	0.0001	0.59	3.28	0.0027
Location	6	3.37	24.02	0.0001	4.49	6.39	0.0001	4.09	17.57	0.0001
Transect (Loc)	50	0.12	0.84	0.7570	0.61	2.88	0.006	0.20	1.12	0.281
Depth x Loc	33	0.57	4.0	0.0001	0.69	3.33	0.0001	0.65	3.63	0.0001
Residual	233	0.14			0.21			0.17		

2.5 Discussion

We have provided a description of three new ecomorphological traits (fin-base-to-perimeter ratio, jaw-length-to-mouth-width ratio, and pectoral fin-base-to-body-depth ratio) extending the diversity of morphological measurements that can characterise ray-finned fishes along broad-scale environmental gradients, such as depth and latitude. These traits and a number of others (eye size, elongation, body transversal shape, and total body length) varied significantly and interactively along depth and latitudinal gradients for New Zealand fishes. More specifically, total body length, elongation, fin-base-to-perimeter ratio and jaw-length-to-mouth-width ratio all generally increased, on average, with increasing depth. Eye size showed a unimodal pattern with depth and also increased with latitude. Pectoral fin-base generally declined with depth, although it varied somewhat idiosyncratically across latitude, while body transversal shape decreased strongly with latitude, but only at shallower depths.

Locomotion is a key ecological function contributing to the survival of fishes, facilitating food acquisition and predator avoidance (Webb 1986; Sfakiotakis, Lane & Davies 1999). Locomotion is energetically taxing and can be made more difficult by undersea currents and variation in water viscosity, all of which increase energy requirements in the already resource-limited environment that occurs at deeper depths (Langerhans 2008). Our hypothesis of an increase in fin-base-to-perimeter ratio, elongation and total body length with increasing depth was supported by the data and reflected an apparent shift towards traits that enable energy-efficient locomotion (Neat & Campbell 2013). At deeper depths, we found fishes had a greater mean total body length, and a more ‘anguilliform’, elongate body shape, with a longer average fin-base.

All of these morphological traits are linked to an undulatory swimming method (Webb 1984; Neat & Campbell 2013). Fishes that swim using undulation generate a wave that propagates down the body or fins. This is considered to be a more energy-efficient swimming method than swimming by oscillating paired fins (Webb 1984). The trend of an increasingly anguilliform body shape with increasing depth suggests that fishes living in the deep sea may require greater energy efficiency for locomotion (Lauder 2015), and that minimising the cost of transport is a major driving force of body shape selection for many species (Tokić & Yue 2012). This trend was seen across multiple orders, (*i.e.,* Gadiformes, Notacanthiformes, and Ophidiiformes), and has been noted elsewhere as a point of convergence in morphologies of benthopelagic fishes (Gage & Tyler 1991). A recent study of some of the earliest vertebrate fishes suggested that fishes with a gracile, slender body plan had more success migrating from shallow coastal seas to deeper-water environments than robustly-shaped fishes (Sallan *et al.* 2018). Fin-base-to-perimeter ratio, elongation and total body length also have greater average values at southern (KKA, OTA) compared to northern locations at 300 m–500 m (Fig. 2.2 a-c), suggesting that latitude-related environmental gradients (such as temperature) also play an important role in driving energy-efficient adaptations.

Our results also showed a clear trend of increasing mean total body length with depth. Fish with larger bodies can cover greater distances with more speed and endurance than smaller-bodied fish, which is crucial in an environment characterised by spatially sporadic benthic “food-falls” that may require extended bouts of locomotion to reach (Collins *et al.* 2005; Priede 2017a). For fishes, the increase in body size with depth is known as Heincke’s law. This law has also been observed to occur across individuals within a given species and has been attributed to an ontogenetic shift in habitat with growth (Heincke 1913) or the selective removal of larger, older fishes from shallower depth strata by fishing (Frank *et al.* 2018). Another possibility is that Heincke's law is the marine equivalent to the Bergmann rule described for terrestrial animals. Specifically, in terrestrial organisms, a larger body size preserves heat, minimises energy loss and increases fasting endurance in cooler climates (Ashton 2002); this phenomenon may be mirrored by similar advantages for fishes occurring at greater depths, where temperatures are lower on average than in shallow-water systems.

Another energy-related link between morphology and physical changes in the deep sea can be explained by the "visual interactions hypothesis" (Childress 1995), whereby declining light levels lead to fewer visual interactions and a reduction of the interaction distance between predators and their prey. This has been hypothesised to lead to a relaxation in the selection of rapid locomotory capabilities, and an associated drop in metabolism for visual species with increasing depth (Childress 1995; Drazen & Seibel 2007). Under this hypothesis, we would also expect to see a trend toward energy-efficient methods of locomotion in the deep sea and would expect to find relevant associated concomitant changes in the visual sensory organs of fishes.

Food acquisition in the deep sea is improved by enhanced sensory abilities, such as an enlarged eye which captures more light and helps to find prey in dark or dimly lit environments (Warrant & Locket 2004). Across the depth range of this study, eye size had a unimodal peak at 500–700 m. At those same depths, we also observed a smooth trend of increasing eye size with increasing latitude (Fig. 2.3b). This is a novel result for fishes, described here for the first time. We consider that increases in eye size with latitude may be a consequence of seasonal changes in day-length and associated light levels becoming a limiting factor of eye size (a trend described in humans, see Pearce and Dunbar (2012)). Available light drives eye-size evolution, and, like terrestrial animals, the eyes of fishes play an important role in not only food acquisition, but also in avoiding predators and finding mates for reproduction (Warrant & Locket 2004).

Jaw-length-to-mouth-width ratio increased with depth, in accordance with our hypothesis. Jaw length is linked to gape size, speed and the force of bites (Wainwright & Richard 1995), and is likely to be important for food acquisition in a resource-limited environment. Generalist feeding behaviour in the deep bathypelagic is considered an effective strategy for surviving in a low-resource environment, where many fishes have enormous oral gapes (e.g. gulper eels; Priede 2017a). However, deep-sea demersal fishes are comprised of several different trophic guilds that include scavenging and non-scavenging species, and there is likely to be greater specialisation, partitioning of resources and a wider variety of niches than previously thought (Drazen & Sutton 2017; Kumar *et al.* 2017). We consider that an increased jaw-length, as tends to occur in fishes inhabiting deeper environments, will allow consumption of a broader range of potential food items, regardless of their type. For example, Conley and Hopkins (2004) showed that larval myctophids with large gapes consumed a range of small to large prey items, and that a large mouth did not necessitate the consumption of large-sized prey. We therefore propose that a large jaw-length-to-mouth-width ratio facilitates opportunistic feeding behaviour which may be a particularly useful food-acquisition strategy in deep-sea ecosystems.

Multivariate analyses revealed a clear turnover in fish morphologies from shallow to deep environments (Fig. 2.6a). Latitudinal variation in fish morphology within depth strata (Fig. 2.6b) is likely influenced by greater heterogeneity in habitat and temperature at shallower *versus* deeper depths (Zintzen *et al.* 2011; Zintzen *et al.* 2017). Patterns found for individual traits, how they covary with one another, and their contribution towards overall changes in morphology along the depth gradient are important to consider. We found that several newly described traits showed contrasting patterns (Fig. 2.5a). Although there was a modest positive correlation between *FbP* and *Elo* (+ 0.37), and these two traits were also (to a lesser extent) positively correlated with *TL* (+ 0.26 and + 0.30, respectively), they do measure different aspects of locomotion and food-acquisition strategies, and are not so correlated as to be considered redundant (Fig. 2.5b).

The generality of these ecomorphological patterns for marine fishes needs to be investigated across other areas of the globe, particularly tropical areas and at depths beyond 1200 m. Nevertheless, we would expect these overall patterns to hold widely. This study has identified how several key individual traits of fishes vary interactively with depth and latitude. Our results collectively reveal a convergence in morphology of deep-sea fishes toward a body shape that decreases the energetic cost of locomotion and increases the opportunity for energy intake (food acquisition). A natural next step will be to investigate the extent to which these traits may be phylogenetically conserved. For example, increasing variation in taxonomic distinctness with increasing depth already suggests the existence of clusters of specialists in the deep sea (Zintzen *et al.* 2011). Furthermore, new tools that can incorporate phylogenetic relationships among species into analyses of ecological gradients hold great promise for teasing out phylogenetical signals linked to traits (e.g. Pillar & Duarte 2010; de Bello *et al.* 2017). Our study has identified variation in several key traits of fishes along broad-scale depth and latitude gradients, facilitating the development of a more comprehensive understanding of fish ecology and the environmental drivers of morphological adaptations in the deep sea.

2.6 Acknowledgements

We thank the three anonymous reviewers whose comments greatly improved the paper. This work was supported by the Royal Society of New Zealand, Marsden Grant 15-MAU-132. E. M. V. Myers was also supported by a Sir Hugh Kawharu Scholarship, and a Te Pūtea Whakatupu Trust Rona Scholarship. M. J. Anderson was also supported by a James Cook Fellowship from the Royal Society of New Zealand (Grant JCF-15-MAU-006). L. Liggins was supported by a Rutherford Foundation Postdoctoral Fellowship (Grant RFT-15-MAU-003-PD). C. D. Roberts was supported by the NZ National Institute of Water and Atmospheric Research Ltd (NIWA) Core Funded Coasts & Oceans Programme 2: Biological Resources. We thank Te Papa's Acquisition Program for assisting the development of an extensive fish tissue collection over the last 15 years, which enabled this research, and particularly Andrew Stewart, Carl Struthers, Jeremy Barker and Salme Kortet for access to the fish collection. We also thank Tom Trnski and Severine Hannam at Tāmaki Paenga Hira Auckland War Memorial Museum for access to the fish collection.

2.7 Authors' Contributions

E.M.V.M., M.J.A., D.E., L.L. and C.D.R. conceived and designed the study. E.M.V.M. developed new traits and measured all of the traits from museum specimens. E.M.V.M, D.E. and M.J.A. analysed the data and produced the figures. E.M.V.M. drafted the initial manuscript and all authors contributed towards the interpretations of results, the initial drafting and the revisions of the final manuscript.

2.8 Supporting information

This chapter has been adapted from the following published paper:

Myers, E.M., Anderson, M.J., Eme, D., Liggins, L. & Roberts, C.D. (2019) Changes in key traits versus depth and latitude suggest energy-efficient locomotion, opportunistic feeding and light lead to adaptive morphologies of marine fishes. *Journal of Animal Ecology,* **89(2),** 309-322.

https://doi.org/10.1111/1365-2656.13131

2.9 Appendices

Appendix 2.1. Museum voucher specimens of 144 New Zealand actinopterygian fish species examined. See Roberts, Stewart and Struthers (2015) for details of classification, nomenclature, distribution, and biology of each species. Specimens listed in phylogenetic order, followed by unique collection registration number. Prefix: AK and MA – Tāmaki Paenga Hira Auckland War Memorial Museum, The Domain, Parnell, Auckland; P – National Fish Collection, Museum of New Zealand Te Papa Tongarewa, 169 Tory Street, Wellington.

Order	**FAMILY**	**Genus Species**	**Reg. no**
Notacanthiformes	HALOSAURIDAE	*Halosaurus pectoralis*	MA4287
	NOTACANTHIDAE	*Notacanthus sexspinis*	P.042185
Anguilliformes	CONGRIDAE	*Gorgasia japonica*	P.035166
		Bassanago bulbiceps	P.044020
		Conger verreauxi	AK135203
	MURAENIDAE	*Gymnothorax berndti*	P.034433
		Gymnothorax nubilus	AK655313
		Gymnothorax porphyreus	AK655399
		Gymnothorax prasinus	P.044073
		Gymnothorax prionodon	P.004867
	OPHICHTHIDAE	*Ophisurus serpens*	MA046347
		Scolecenchelys castlei	P.044497
	SYNAPHOBRANCHIDAE	*Diastobranchus capensis*	P.044025
		Simenchelys parasitica	P.044094
		Synaphobranchus affinis	P.044083
Argentiniformes	ALEPOCEPHALIDAE	*Alepocephalus australis*	P.046858
Stomiiformes	CHAULIODONTIDAE	*Chauliodus sloani*	P.042448
Aulopiformes	IPNOPIDAE	*Bathypterois longifilis*	P.042010
		Scopelosaurus hamiltoni	P.046766
	PARAULOPIDAE	*Paraulopus nigripinnis*	P.042473
		Paraulopus okamurai	P.054938
Polymixiiformes	POLYMIXIIDAE	*Polymixia* cf. *busakhini*	P.056079
Ophidiiformes	OPHIDIIDAE	*Brotulotaenia nigra*	P.045943
		Genypterus blacodes	P.044057

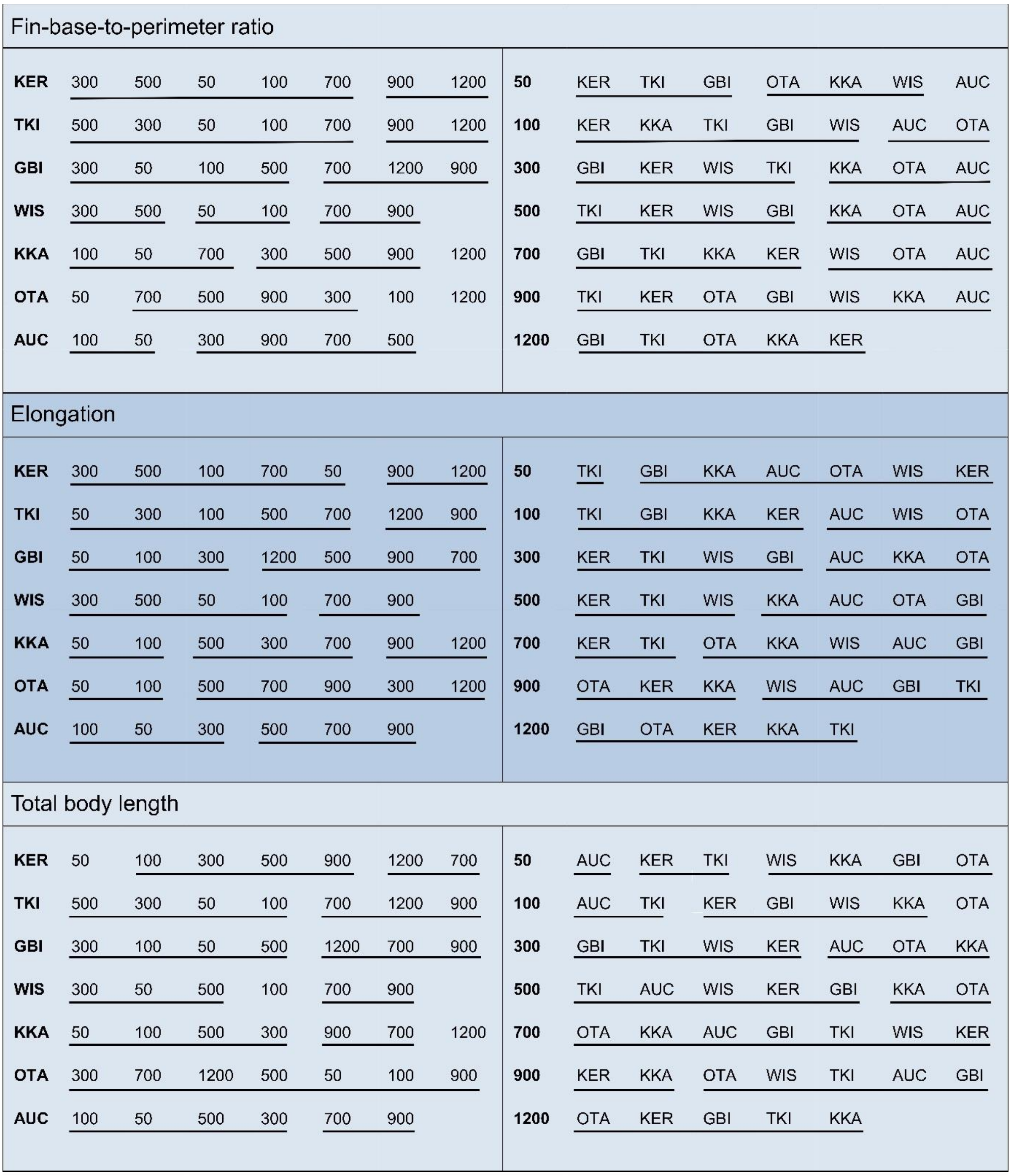
Gadiformes	BATHYGADIDAE	*Bathygadus cottoides*	P.054706
		Gadomus aoteanus	P.023310
	MACROURIDAE	*Coelorinchus acanthiger*	P.038935
		Coelorinchus aspercephalus	P.005256
		Coelorinchus biclinozonalis	P.034780
		Coelorinchus bollonsi	P.023348
		Coelorinchus fasciatus	P.023370
		Coelorinchus innotabilis	P.023565
		Coelorinchus kermadecus	P.038988
		Coelorinchus mycterismus	P.039350
		Coelorinchus mystax	P.039439
		Coelorinchus oliverianus	P.023538
		Coryphaenoides murrayi	P.046951
		Coryphaenoides rudis	P.039706
		Coryphaenoides serrulatus	P.037130
		Coryphaenoides subserrulatus	P.021692
		Lepidorhynchus denticulatus	P.025859
		Lucigadus nigromaculatus	P.039606
		Macrourus carinatus	P.026961
		Malacocephalus laevis	P.034757
		Nezumia new sp.	P.034712
	TRACHYRINCIDAE	*Trachyrincus aphyodes*	P.049413
		Trachyrincus longirostris	P.030155
	MERLUCCIIDAE	*Lyconus pinnatus*	P.053343
		Macruronus novaezelandiae	P.052479
	MORIDAE	*Antimora rostrata*	P.047831
		Laemonema robustum	P.044032
		Lepidion microcephalus	P.047098
		Lepidion schmidti	P.042216
		Mora moro	P.042435
		Notophycis marginata	P.023561
		Pseudophycis bachus	P.049678
		Pseudophycis barbata	P.052745
		Tripterophycis gilchristi	P.044506
	MURAENOLEPIDIDAE	*Muraenolepis orangiensis*	P.032946
Beryciformes	BERYCIDAE	*Beryx decadactylus*	P.033364
		Beryx splendens	P.054054
		Centroberyx affinis	P.050476
	TRACHICHTHYIDAE	*Hoplostethus atlanticus*	P.030202
		Hoplostethus mediterraneus	P.046055
Zeiformes	CYTTIDAE	*Cyttus novaezealandiae*	P.052391
	MACRORAMPHOSIDAE	*Centriscops humerosus*	P.039438
	OREOSOMATIDAE	*Allocyttus niger*	P.053972
		Neocyttus rhomboidalis	P.052588

		Oreosoma atlanticum	P.032973
	ZEIDAE	*Zeus faber*	P.044254
	ZENIONTIDAE	*Capromimus abbreviatus*	P.042055
		Zenion sp.	P.052317
Scorpaeniformes	PSYCHROLUTIDAE	*Psychrolutes microporos*	P.037011
	SCORPAENIDAE	*Scorpaena cardinalis*	P.037092
		Scorpaena papillosa	P.048324
	SEBASTIDAE	*Helicolenus barathri*	P.047352
		Helicolenus percoides	P.047376
	TRIGLIDAE	*Chelidonichthys kumu*	P.046491
		Pterygotrigla andertoni	P.046349
Perciformes	ARRIPIDAE	*Arripis xylabion*	P.051988
	CALLANTHIIDAE	*Callanthias australis*	P.039226
	CARANGIDAE	*Pseudocaranx georgianus*	P.045523
		Seriola lalandi	P.044121
		Seriola rivoliana	P.045522
	CENTROLOPHIDAE	*Hyperoglyphe antarctica*	P.054908
		Seriolella brama	P.003996
	CEPOLIDAE	*Cepola haastii*	P.053890
	CHAETODONTIDAE	*Amphichaetodon howensis*	P.050218
	CHEILODACTYLIDAE	*Cheilodactylus francisi*	P.041671
		Cheilodactylus spectabilis	P.048640
		Nemadactylus douglasii	P.046502
		Nemadactylus macropterus	P.037127
		Nemadactylus new sp.	P.046489
	ECHENEIDAE	*Echeneis naucrates*	P.037943
	GEMPYLIDAE	*Rexea solandri*	P.039338
		Ruvettus pretiosus	P.024449
		Thyrsites atun	P.046811
	GIRELLIDAE	*Girella cyanea*	P.050060
	LABRIDAE	*Bodianus flavipinnis*	P.054009
		Bodianus unimaculatus	P.052742
		Coris picta	P.004809
		Coris sandeyeri	P.049928
		Notolabrus cinctus	P.047827
		Notolabrus fucicola	P.053862
		Notolabrus inscriptus	P.050183
		Pseudolabrus luculentus	P.049891
		Pseudolabrus miles	P.046497
		Suezichthys arquatus	P.050188
		Suezichthys aylingi	P.053897
	LATRIDAE	*Latridopsis ciliaris*	P.032933
		Latridopsis forsteri	P.032932
		Latris lineata	P.053323
	LUTJANIDAE	*Etelis coruscans*	P.034455
	MULLIDAE	*Parupeneus spilurus*	P.050266

		Upeneichthys porosus	P.057407
	NOTOTHENIIDAE	*Notothenia angustata*	P.053299
		Notothenia microlepidota	P.047327
	PINGUIPEDIDAE	*Parapercis binivirgata*	P.045603
		Parapercis colias	P.046566
		Parapercis gilliesii	P.052402
	POLYPRIONIDAE	*Polyprion americanus*	P.056097
		Polyprion oxygeneios	P.053547
	POMACENTRIDAE	*Chromis abyssicola*	P.046274
		Chromis dispila	P.050125
	SERRANIDAE	*Aulacocephalus temminckii*	P.050123
		Caesioperca lepidoptera	P.048552
		Caprodon longimanus	P.052743
		Epinephelus daemelii	P.046364
		Hypoplectrodes spB	P.052735
		Lepidoperca inornata	P.052506
		Plectranthias bilaticlavia	P.038143
		Plectranthias maculicauda	P.053099
	SPARIDAE	*Chrysophrys auratus*	P.048499
	TRICHIURIDAE	*Lepidopus caudatus*	P.039460
	TRIPTERYGIIDAE	*Forsterygion flavonigrum*	P.053907
		Forsterygion maryannae	P.028344
		Matanui profundum	P.052462
	ZOARCIDAE	*Melanostigma gelatinosum*	P.046973
Tetraodontiformes	DIODONTIDAE	*Allomycterus pilatus*	P.039274
	MONACANTHIDAE	*Meuschenia scaber*	P.054644
		Thamnaconus analis	P.050301
	TETRAODONTIDAE	*Canthigaster callisterna*	P.040694
		Lagocephalus cheesemanii	P.057045
		Torquigener altipinnis	P.052229

Appendix 2.2. Summary of pair-wise comparisons of mean values for each of several individual ecomorphological traits measured from fishes (a) fin-base-to-perimeter ratio, elongation, total body length, b) jaw-length-to-mouth-width ratio and eye size, c) pectoral fin-to-body-depth ratio and body transversal shape), as indicated to follow the significant Depth x Location interactions uncovered by the full-model ANOVA partitioning (see Table 2.2). Note that for each trait, two separate sets of comparisons were done: the left-hand panel summarizes comparisons of mean values for traits among depth strata, done separately for each location (north to south: KER through AUC); and the right-hand panel summarizes comparisons of mean values among locations, done separately for each depth stratum (50 m, 100 m, 300 m, 500 m, 700 m, 900 m, 1200 m). Location and depth are given in the order of their increasing mean value for the trait, and underlying bars indicate groups whose means were not statistically significantly different ($P > 0.01$). Note: WI and AUC were not sampled at 1200 m.

a)



Fin-base-to-perimeter ratio

KER	300	500	50	100	700	900	1200
TKI	500	300	50	100	700	900	1200
GBI	300	50	100	500	700	1200	900
WIS	300	500	50	100	700	900	
KKA	100	50	700	300	500	900	1200
OTA	50	700	500	900	300	100	1200
AUC	100	50	300	900	700	500	

50	KER	TKI	GBI	OTA	KKA	WIS	AUC
100	KER	KKA	TKI	GBI	WIS	AUC	OTA
300	GBI	KER	WIS	TKI	KKA	OTA	AUC
500	TKI	KER	WIS	GBI	KKA	OTA	AUC
700	GBI	TKI	KKA	KER	WIS	OTA	AUC
900	TKI	KER	OTA	GBI	WIS	KKA	AUC
1200	GBI	TKI	OTA	KKA	KER		

Elongation

KER	300	500	100	700	50	900	1200
TKI	50	300	100	500	700	1200	900
GBI	50	100	300	1200	500	900	700
WIS	300	500	50	100	700	900	
KKA	50	100	500	300	700	900	1200
OTA	50	100	500	700	900	300	1200
AUC	100	50	300	500	700	900	

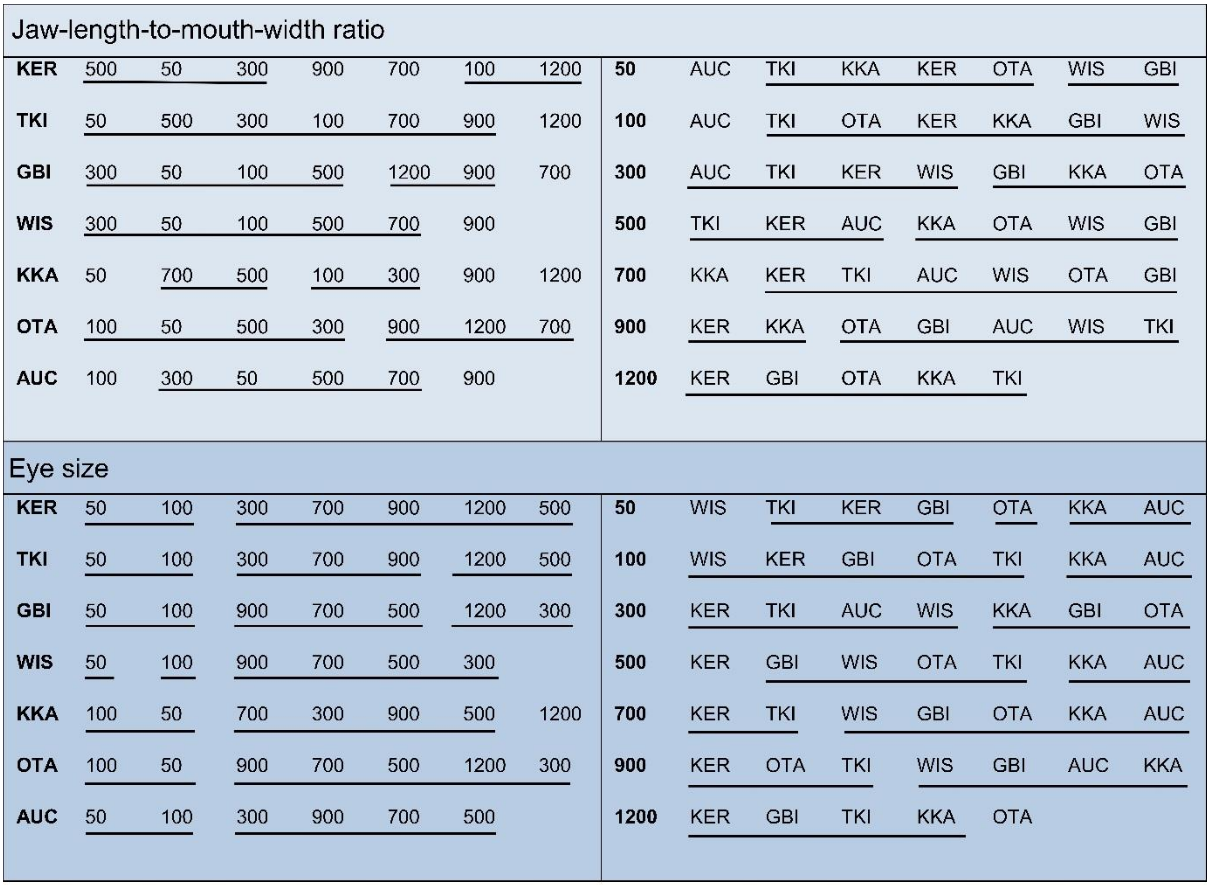
50	TKI	GBI	KKA	AUC	OTA	WIS	KER
100	TKI	GBI	KKA	KER	AUC	WIS	OTA
300	KER	TKI	WIS	GBI	AUC	KKA	OTA
500	KER	TKI	WIS	KKA	AUC	OTA	GBI
700	KER	TKI	OTA	KKA	WIS	AUC	GBI
900	OTA	KER	KKA	WIS	AUC	GBI	TKI
1200	GBI	OTA	KER	KKA	TKI		

Total body length

KER	50	100	300	500	900	1200	700
TKI	500	300	50	100	700	1200	900
GBI	300	100	50	500	1200	700	900
WIS	300	50	500	100	700	900	
KKA	50	100	500	300	900	700	1200
OTA	300	700	1200	500	50	100	900
AUC	100	50	500	300	700	900	

50	AUC	KER	TKI	WIS	KKA	GBI	OTA
100	AUC	TKI	KER	GBI	WIS	KKA	OTA
300	GBI	TKI	WIS	KER	AUC	OTA	KKA
500	TKI	AUC	WIS	KER	GBI	KKA	OTA
700	OTA	KKA	AUC	GBI	TKI	WIS	KER
900	KER	KKA	OTA	WIS	TKI	AUC	GBI
1200	OTA	KER	GBI	TKI	KKA		

b)



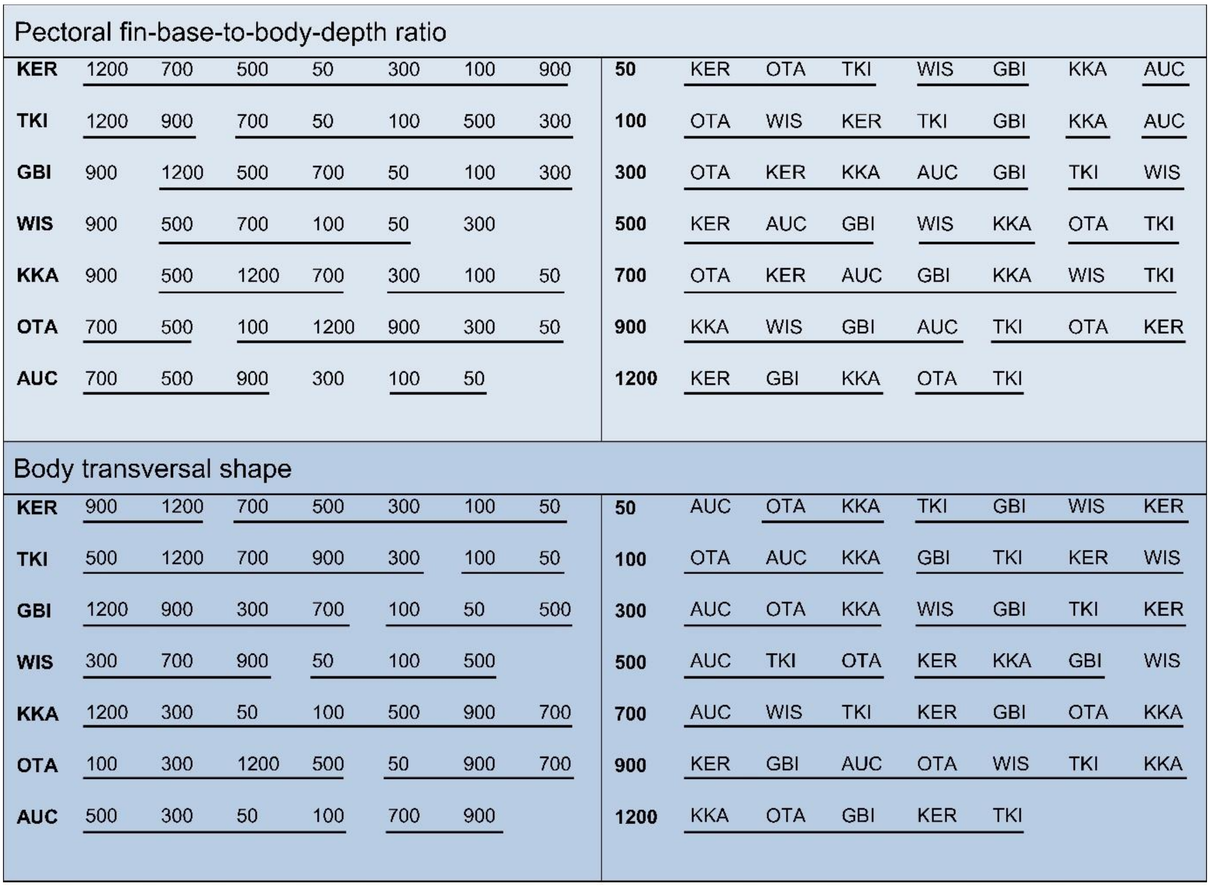
Jaw-length-to-mouth-width ratio

KER	500	50	300	900	700	100	1200	**50**	AUC	TKI	KKA	KER	OTA	WIS	GBI
TKI	50	500	300	100	700	900	1200	**100**	AUC	TKI	OTA	KER	KKA	GBI	WIS
GBI	300	50	100	500	1200	900	700	**300**	AUC	TKI	KER	WIS	GBI	KKA	OTA
WIS	300	50	100	500	700	900		**500**	TKI	KER	AUC	KKA	OTA	WIS	GBI
KKA	50	700	500	100	300	900	1200	**700**	KKA	KER	TKI	AUC	WIS	OTA	GBI
OTA	100	50	500	300	900	1200	700	**900**	KER	KKA	OTA	GBI	AUC	WIS	TKI
AUC	100	300	50	500	700	900		**1200**	KER	GBI	OTA	KKA	TKI		

Eye size

KER	50	100	300	700	900	1200	500	**50**	WIS	TKI	KER	GBI	OTA	KKA	AUC
TKI	50	100	300	700	900	1200	500	**100**	WIS	KER	GBI	OTA	TKI	KKA	AUC
GBI	50	100	900	700	500	1200	300	**300**	KER	TKI	AUC	WIS	KKA	GBI	OTA
WIS	50	100	900	700	500	300		**500**	KER	GBI	WIS	OTA	TKI	KKA	AUC
KKA	100	50	700	300	900	500	1200	**700**	KER	TKI	WIS	GBI	OTA	KKA	AUC
OTA	100	50	900	700	500	1200	300	**900**	KER	OTA	TKI	WIS	GBI	AUC	KKA
AUC	50	100	300	900	700	500		**1200**	KER	GBI	TKI	KKA	OTA		

c)



Pectoral fin-base-to-body-depth ratio

KER	1200	700	500	50	300	100	900	**50**	KER	OTA	TKI	WIS	GBI	KKA	AUC
TKI	1200	900	700	50	100	500	300	**100**	OTA	WIS	KER	TKI	GBI	KKA	AUC
GBI	900	1200	500	700	50	100	300	**300**	OTA	KER	KKA	AUC	GBI	TKI	WIS
WIS	900	500	700	100	50	300		**500**	KER	AUC	GBI	WIS	KKA	OTA	TKI
KKA	900	500	1200	700	300	100	50	**700**	OTA	KER	AUC	GBI	KKA	WIS	TKI
OTA	700	500	100	1200	900	300	50	**900**	KKA	WIS	GBI	AUC	TKI	OTA	KER
AUC	700	500	900	300	100	50		**1200**	KER	GBI	KKA	OTA	TKI		

Body transversal shape

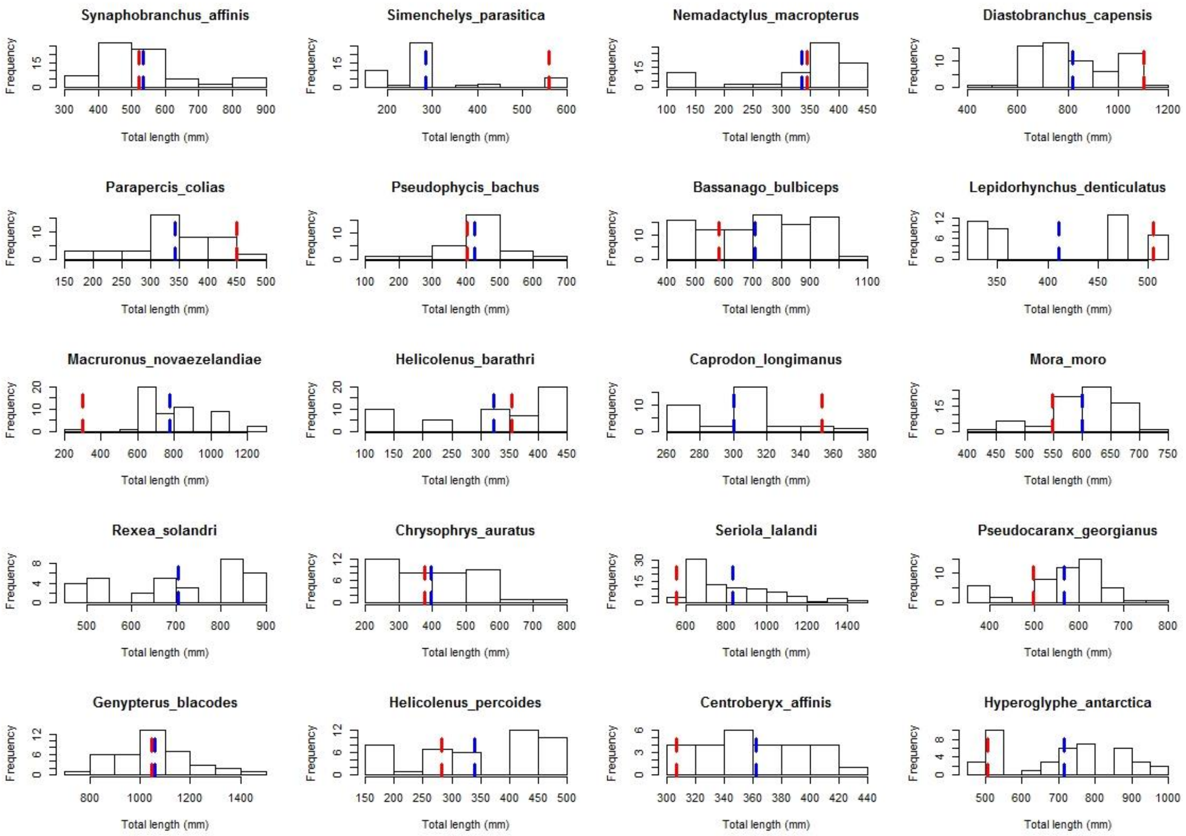
KER	900	1200	700	500	300	100	50	**50**	AUC	OTA	KKA	TKI	GBI	WIS	KER
TKI	500	1200	700	900	300	100	50	**100**	OTA	AUC	KKA	GBI	TKI	KER	WIS
GBI	1200	900	300	700	100	50	500	**300**	AUC	OTA	KKA	WIS	GBI	TKI	KER
WIS	300	700	900	50	100	500		**500**	AUC	TKI	OTA	KER	KKA	GBI	WIS
KKA	1200	300	50	100	500	900	700	**700**	AUC	WIS	TKI	KER	GBI	OTA	KKA
OTA	100	300	1200	500	50	900	700	**900**	KER	GBI	AUC	OTA	WIS	TKI	KKA
AUC	500	300	50	100	700	900		**1200**	KKA	OTA	GBI	KER	TKI		

Appendix 2.3. Analysis of variance (ANCOVA) for each of six individual morphological variables (a through f) with total length (TL) as a covariate in response to the 3-factor stratified random sampling design, with *p*-values obtained using 9999 permutations of residuals under a reduced model. Note that 12 of the original 341 deployments were omitted prior to analysis due to no bony fish (*Actinopterygii*) being present. MS: Mean square.

		a) Fin-base-to-perimeter ratio			b) Elongation			c) Jaw-length-to-mouth-width ratio		
	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Total length	1	52.88	366.86	**0.0001**	49.83	461.32	**0.0001**	37.19	408.02	**0.0001**
Depth	6	7.14	50.49	**0.0001**	4.45	37.49	**0.0001**	3.01	31.7	**0.0001**
Location	6	2.75	16.3	**0.0001**	0.35	3.91	**0.0044**	0.28	3.22	**0.0095**
Transect (Loc)	50	0.14	1.06	0.37	0.08	0.71	0.89	0.08	0.83	0.7387
Depth x Loc	33	0.56	3.97	**0.0001**	0.51	4.27	**0.0001**	0.19	1.98	**0.0043**
Residual	233	0.14			0.12			0.09		

		d) Eye size			e) Pectoral fin-base-to-body-depth ratio			f) Body transversal shape		
	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Total length	1	2.71	22.99	**0.0001**	24.71	73.97	**0.0001**	3.05	15.82	**0.0002**
Depth	6	14.79	119.94	**0.0001**	2.39	10.45	**0.0001**	0.21	1.17	0.3247
Location	6	3.97	32.98	**0.0001**	3.77	5.90	**0.0001**	4.07	16.28	**0.0001**
Transect (Loc)	50	0.10	0.85	0.7416	0.57	2.69	**0.0109**	0.22	1.24	0.1529
Depth x Loc	33	0.54	4.41	**0.0001**	0.68	3.25	**0.0001**	0.61	3.46	**0.0001**
Residual	232	0.12			0.21			0.18		

Appendix 2.4. Distributions of sizes of fishes (total length) for the top 20 most abundant species obtained from the stereo-video footage, and also show the value for the museum specimen (in red) along with the mean from these *in situ* observations (in blue). Overall, these graphics provide no evidence that there is any consistent bias, either positive or negative; in the lengths of museum specimens compared to the average lengths of individuals of the same species measured directly in the field (note however that for the species *Rexea solandri*, the value for the museum specimen is out of range at 354 mm).



2.10 DRC16 Statement of Contribution

3 Unexpected high functional diversity in deep-sea fish communities, and inverse trends for inter-specific versus intra-specific trait variation with increasing latitude

3.1 Abstract

1. An important focus of biodiversity studies in community ecology is to uncover how key functional traits of organisms vary along broad-scale environmental or spatial gradients, such as latitude, elevation or depth. Variation in both inter- and intra-specific traits affect community dynamics, yet we know little regarding the relative importance of external environmental filters *vs* internal biotic interactions that shape the functional space of communities along gradients.

2. We examined changes in several key aspects of functional alpha-diversity for marine fishes along depth and latitude gradients by quantifying intra- and inter-specific richness, dispersion and regularity in functional trait space.

3. We derived eight functional traits related to food acquisition and locomotion, and calculated seven complementary indices of functional diversity for 144 species of marine ray-finned fishes along large-scale depth (50 m–1200 m) and latitudinal gradients (29°–51° S) in New Zealand waters. Traits were derived from morphological measurements taken directly from video footage obtained using Stereo-BRUVs and museum specimens. We partitioned functional variation into intra- and inter-specific components for the first time using a PERMANOVA

approach. We also implemented two tree-based diversity metrics in a functional distance-based context for the first time: namely, the variance in pairwise functional distance, and the variance in nearest-neighbour distance.

4. Functional alpha-diversity increased with increasing depth, and decreased with increasing latitude. More specifically, the overall functional hypervolume occupied by species, the dispersion and mean nearest-neighbour distances among species in trait-space, and intra-specific trait variability all increased with depth. In contrast, functional hypervolume, dispersion and regularity indices all decreased with increasing latitude; however, intra-specific trait variation increased with latitude, suggesting that intra-specific trait variability becomes increasingly important at higher latitudes.

5. These results suggest that competition within and among species are key processes shaping functional multi-dimensional space for fishes in the deep sea. Increasing morphological dissimilarity with increasing depth may facilitate fine-scale niche-partitioning to promote coexistence, whereas abiotic filtering may be the dominant process structuring communities with increasing latitude.

Keywords: biodiversity, biotic interactions, deep-sea fishes, depth gradient, environmental filtering, functional trait, morphology, niche-partitioning.

3.2 Introduction

Studying biodiversity across large-scale environmental gradients plays a key role in aiding scientists to understand potential mechanisms shaping species' distributions. Analyses of taxonomic diversity (*e.g.* species richness) are useful, but a more integrative understanding and insights regarding potential mechanisms driving biodiversity and ecosystem services can be obtained through analyses of phylogenetic and functional diversity (Swenson 2011b; Díaz *et al.* 2016). Previous studies have documented a general decrease in species richness with increasing latitude, elevation, and depth (Gaston 2000; Hillebrand 2004a; Costello & Chaudhary 2017). However, functional diversity displays a variety of different patterns along gradients (Villéger *et al.* 2010; Mouillot *et al.* 2013a; Stuart-Smith *et al.* 2013; Blonder *et al.* 2014). Furthermore, trends in functional diversity will depend on the particular traits that are measured and the indices that are calculated from these.

Functional diversity is inherently multivariate, where each trait is a variable, and species (or individuals) occupy a particular position in multivariate trait space. There are many ways to measure functional diversity (Villéger, Mason & Mouillot 2008; Laliberté & Legendre 2010; Mouchet *et al.* 2010), and each metric may capture a different aspect of functional diversity. For example, one might measure the functional hypervolume covered by a set of species ('space'), or the packing (*i.e*. the proximity of neighbouring species) within this volume (Blonder *et al.* 2014; Swenson & Weiser 2014). Patterns in these different aspects of functional diversity along environmental gradients vary, depending on the focal taxa and traits included, as well as the resolution and spatial scale of the study. For example, both functional space and species richness were found to decline with increasing latitude for plants in the New World (Blonder *et al.* 2014). In contrast, high species richness for birds at low elevations was not coupled with high functional richness, but rather a greater density (packing) of species in functional space (Pigot, Trisos & Tobias 2016). Simultaneous analysis of multiple functional diversity measures, along with species richness, therefore yields more comprehensive biodiversity information regarding community assembly.

External processes operating *outside* of the functional trait space of a community, such as abiotic filtering, and internal processes operating *within* the community, such as density-dependent interactions (*e.g.* competition) work in tandem to shape functional space (Violle *et al.* 2012; Swenson & Weiser 2014; Kraft *et al.* 2015). External filtering is assumed to reduce the number or type of functional strategies, reducing the volume of occupied functional space, whereas internal community processes are generally expected to affect the packing (or density) of species or individuals (Swenson & Weiser 2014). For example, increasing competition for resources is expected to decrease the packing of functionally similar taxa in a functional space (Swenson & Weiser 2014).

External or internal drivers can also affect intra-specific variation in functional trait space. Variation in traits among individuals within a species may be particularly important in species-poor regions, for taxa with narrow geographic ranges, or that live in stressful environmental conditions (Hoffmann & Merilä 1999; Siefert *et al.* 2015). Disentangling individual-level variability *versus* species-level variation in functional trait space, including along environmental gradients, can provide novel insights into how communities are structured and maintained (Bolnick *et al.* 2011; Violle *et al.* 2012; Violle *et al.* 2014).

The depth gradient is one of the steepest environmental gradients on earth, yet is one of the least studied in terms of functional diversity. Changes with increasing oceanic depth are dramatic, including decreasing light, temperature, dissolved oxygen, food and increasing pressure (Priede 2017b). These changes strongly influence the spatial distribution of species, their functions and morphologies (Mindel *et al.* 2016a; Zintzen *et al.* 2017; Myers *et al.* 2019). One of the most striking patterns is a decline in species richness with increasing depth. Assuming that a transition from shallow to deep waters, from low to high altitudes, or from sub-tropical to sub-antarctic latitudes represents a progression from a benign environment to an abiotically harsher, more extreme environment, we generated three contrasting conceptual models regarding expected functional changes in communities along these gradients. Each model yields specific predictions (hypotheses) regarding expected changes in functional diversity indices, indicative of the strength of influence of abiotic (external) *vs* biotic (internal) potential drivers (Fig. 3.1):

a). Abiotic filtering will increase with increasing depth, altitude, or latitude, occurring more strongly in harsh environments (Swenson 2011b). This will lead to a decrease in functional hypervolume, but species packing should remain constant (Fig. 3.1a).

b). Biotic interactions, such as competition for limited resources, will intensify with increasing depth, altitude, or latitude. These interactions will decrease the packing of species (or individuals) in functional space, but the overall volume of the functional space will remain unchanged (Fig. 3.1b).

c). Both abiotic and biotic filtering will jointly affect functional diversity, decreasing both the volume and the packing of species (or individuals) in deeper, higher altitude, or higher latitude regions (Fig. 3.1c).

Here, we tested these predictions by quantifying patterns of change in functional diversity for 144 species of marine ray-finned fishes along large-scale depth (50 m–1200 m), and latitudinal gradients (29°–51° S) in New Zealand waters. We obtained morphological measurements of individual fishes *in situ* using Stereo-BRUVs, allowing quantification of both inter-specific and intra-specific trait variation. We focused on 8 functional traits related to food acquisition and locomotion and calculated 7 complementary functional diversity indices to examine their relationships with depth and latitude using univariate and multivariate approaches. By examining trends for a suite of different functional diversity metrics *vs* depth and latitude, we are able to characterise, more specifically, the *type* of change occurring in the functional space, thus we can begin to differentiate among competing underlying models that might explain functional variation along these large-scale gradients.

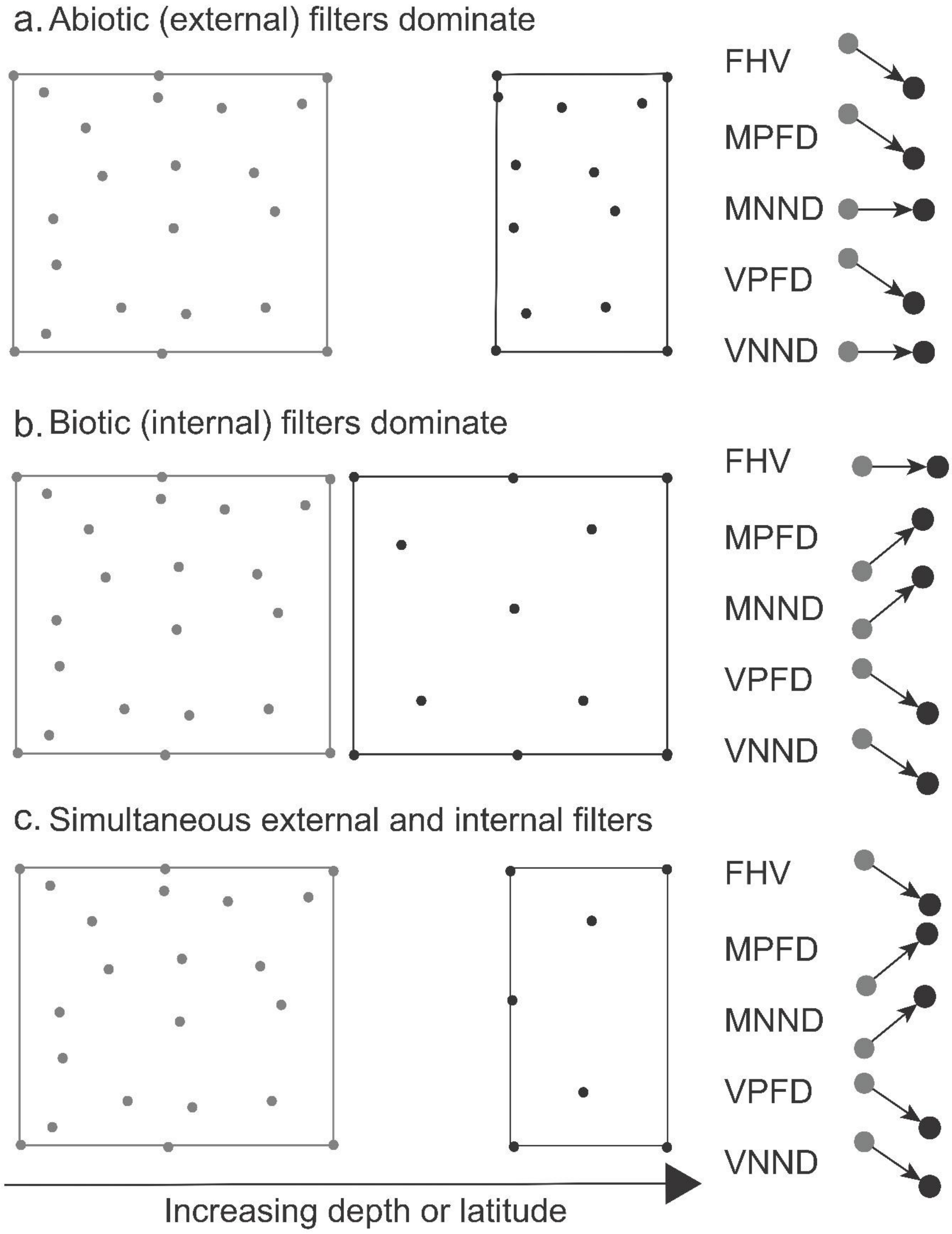


Figure 3.1. Schematic diagram of three conceptual models of changes in functional space (and functional diversity metrics) when moving from a relatively benign (grey), to a more extreme environment (black). Points represent species (or individuals), and the squares represent the bounds of functional space. a) Abiotic filters cause a decrease in functional volume, but species packing remains unchanged. b) Biotic filters, such as increased competition for limited resources, does not affect volume, but decreases the packing of species (or individuals) in

functional space. c) Harsh abiotic conditions, decreased resources, and increased competition combine to yield a decrease in volume and also in the packing of species. FHV = functional hypervolume, MPFD = mean pairwise functional distance, MNND = mean nearest-neighbour distance, VPFD = variance in pairwise functional distance, VNND = variance in nearest-neighbour distance.

3.3 Materials and Methods

Fish community data

We observed 144 species of marine ray-finned fishes (Class Actinopterygii) on Stereo-BRUV footage. Stereo-BRUVs were deployed in a stratified random sampling design, with *n* = 5–7 replicate units at each of seven targetted depths: 50m, 100m, 300m, 500m, 700m, 900m and 1200m, within each of seven locations spanning 21° of latitude in New Zealand waters. In total, the footage from 329 deployments (3 hours each) across 47 depth-by-location cells was analysed. For further details regarding the sampling design and stereo-BRUV methodology, see Zintzen *et al.* (2012) and Zintzen *et al.* (2017).

Measurements from fish and derivation of traits

Stereo-BRUVs are typically used to estimate relative abundance and biomass of fishes (Cappo *et al.* 2003), but can also be used to make fine-scale point-to-point measurements of distances between specified morphological features (e.g. Harvey *et al.* 2003). To ensure the accuracy and precision of measurements, stereo-BRUVs were calibrated before and after deployment (Boutros, Shortis & Harvey 2015). Measurements were made using EventMeasure software (www.seagis.com.au) with the following rules: individuals must be within 7 m of stereo-BRUVs, have a maximum root-mean-square error of 20mm (a quality measure indicating accuracy), and a maximum precision-to-length ratio of 10% (Harvey & Shortis 1998).

We identified 15 morphological measurements on the basic body plan for fishes to calculate functional traits pertaining to locomotion and food acquisition (Supplement 1, Fig. S3.1; and Villéger *et al.* 2010). For each stereo-BRUVs deployment we aimed to measure at least one full ‘set’ of 15 measurements for at least one individual of each species present. Care was taken to prevent measuring the same individual twice. To get the most accurate measurements, individuals were preferentially chosen according to: i) proximity to the camera, ii) unobscured view, iii) body position being side-on/perpendicular to the camera, and iv) unconstrained configuration of morphological features.

From the raw morphological measurements, we derived eight functional traits (Table 3.1). Locomotion was captured by traits documenting eye position, pectoral fin position, caudal peduncle throttling, and elongation, while food acquisition traits included eye size, oral gape position, and jaw length/head length. Body size (considered to be a universal trait, Bellwood *et al.* (2019)) was measured as total length.

Table 3.1. Definitions of eight functional traits derived from raw morphological length measurements of individual fishes (see Figure S3.1 for an illustration). *CFd* = caudal fin depth, *CPd* = caudal peduncle depth, *Ed* = maximum eye diameter, *Eh* = eye height, *Hd* = head depth, *Hl* = head length, *Lj* = lower jaw length, *mBd* = maximum body depth, *Mo* = mouth open, *PFb* = body depth at pectoral fin base, *PFi* = pectoral fin insertion, *TL* = total body length, *Uj* = upper jaw length. Traits adapted from Villéger *et al.* (2010) are identified by an asterisk.

	Functional Trait	**Calculation**	**Ecological relevance**
Universal trait	Total body length	*TL*	Proxy for overall body size; indication of trophic level or relative food-web position
Food acquisition	Eye size*	*Ed / Hd*	Prey detection
	Oral gape position*	*Mo / Hd*	Feeding method in the water column
	Jaw length	$\frac{1}{2}$ *(Uj + Lj) / Hl*	Proxy for size of oral gape; indication of the size of potential prey
Locomotion	Elongation	*TL / mBd*	Indication of overall body shape; greater elongation indicates steady swimming ability (Claverie & Wainwright 2014)
	Eye position*	*Eh / Hd*	Indication of vertical position in the water column
	Caudal peduncle throttling*	*CFd / CPd*	Indication of the efficiency of caudal propulsion; reduction of drag
	Pectoral fin position*	*PFi / PFb*	Indication of manoeuvrability using pectoral fins

Inferring missing data using a hierarchical approach

Complete morphological measurement data were not available for all of the species observed on the stereo-BRUVs footage. To fill in missing trait information, we followed a two-step procedure. First, to guarantee an estimate of every trait for every species seen on the stereo-BRUVs footage, we obtained raw morphological measurements directly from well-preserved museum specimens from the National Fish Collection at the Museum of New Zealand Te Papa Tongarewa, Wellington (see Myers *et al.* 2019 for details, including species list and voucher registrations). Next, for individuals missing 3 or fewer measurements (out of 15), and for which there were 5 or more occurrences of that species with complete trait information across the dataset, we imputed missing values. This was done using a random-forest machine-learning model built from all conspecific individuals across the full study design that had the full set of 15 morphological measurements. The random-forest approach handles complex non-linear relationships, is computationally fast, and estimates imputation error (Stekhoven & Bühlmann 2012; Penone *et al.* 2014). We used the "missForest" R package (Stekhoven & Bühlmann 2012) and set the *maxiter* argument to 20 iterations and the *ntree* to 300 decision trees. We performed 20 runs and used the averaged output as our imputed result.

Choice of individuals to use to represent individual species' traits

We analysed data on the basis of the species present (observed in video footage) within each of the 47 depth-by-location cells. There were 144 species recorded, and 509 species-by-cell occurences. Our original dataset was comprised of a complete set of 15 raw morphological measurements for a total of 722 individuals (140 of these required some random-forest imputation). To generate a single table of unique species in each cell (509 rows) by 8 traits (columns), we randomly drew 1 individual from the list of all complete individuals for each species observed *in situ* in the stereo-BRUVs footage obtained within each depth-by-location cell. To maintain any spatial structures in trait variability as well as possible, we drew an individual for each species within each cell from conspecific individuals that were (in order of preference): a) in the same depth-by-location cell, b) at the same depth, or c) from anywhere across the study design or from the museum dataset. We replicated this procedure 100 times, to generate 100 species-by-trait (509 × 8) tables. All species-level functional metrics (*i.e.*, FHV, MPFD, MNND, VPFD and VNND; see section 2.5 below) were calculated for each replicate table, and we calculated the mean across all 100 tables for every metric for subsequent analyses. For metrics focusing on intra-specific trait variability (*i.e.,* MPFD.I and Prop.I; see section 2.6 below) we used the full original base dataset (*i.e.,* 722 individuals x 8 traits).

Functional metrics

All functional metrics were calculated using 8 normalised continuous traits. We calculated the following species-level metrics for each depth-by-latitude cell, for each of the 100 species-by-trait (509 x 8) data matrices after calculating Euclidean distances: (i) mean pairwise functional distance (MPFD; (Clarke & Warwick 1998; Somerfield *et al.* 2008; Swenson 2014), (ii) mean nearest-neighbour distance (MNND; Swenson & Weiser 2014), (iii) variance in pairwise functional distance (VPFD; adapted from Clarke and Warwick (2001) and Somerfield *et al.* (2008)), and (iv) variance in nearest-neighbour distance (VNND; Swenson (2014).

MPFD is the functional analogue to average taxonomic distinctness (Clarke & Warwick 1998), and mean phylogenetic pairwise distance (Swenson 2014). It is highly correlated with functional dispersion (Laliberté & Legendre 2010), and Rao's quadratic entropy (Botta-Dukát 2005), but is independent of species richness and only weakly influenced by outliers. MNND has been used previously in both phylogenetic (Webb *et al.* 2002), and functional contexts (Swenson & Weiser 2014; Pigot, Trisos & Tobias 2016). It measures the average minimum distance in the functional strategies of co-occurring species, and has previously been used to estimate functional originality (Mouillot *et al.* 2013b; Leitao *et al.* 2016).

VPFD quantifies the regularity of the distances among species in the functional space. This measure was originally proposed by Clarke and Warwick (2001) in a taxonomic setting. Here, we calculate it in functional space (as suggested by Somerfield *et al.* 2008), and it is independent of species richness and MPFD. Similarly, VNND also quantifies regularity, but focuses on functional similarity between nearest neighbours. It was proposed by Swenson (2014) in a phylogenetic context, but we calculated it here in functional space.

We also performed principal component analysis (PCA) on the normalised traits in order to calculate functional hypervolume (FHV; Blonder *et al.* 2014; Blonder *et al.* 2018). FHV was calculated using the first 4 principal component axes (which accounted for 70.2–74.4 % of the total variation in the 8D functional trait space across the 100 species-by-trait tables). We did not retain all 8 dimensions due to difficulties associated with calculating FHV when few species were present. FHV has been used as a proxy to estimate niche space, including high-dimensional, irregular spaces (Blonder *et al.* 2014; Cooke, Eigenbrod & Bates 2019). The Gaussian kernel density estimation method was chosen to form a "loose wrap" around the data (Blonder *et al.* 2018). We used a quantile threshold of 0.05, retaining 95% of the total probability density, and estimated the bandwidth vector using the Silverman method (Blonder *et al.* 2018).

Quantifying intra-specific trait variability

Next, we calculated individual-level trait variation, and determined its contribution towards total functional trait variation (among species and among individuals), within each cell. From the original base dataset (722 individuals) we first calculated mean pairwise functional distance (MPFD.I) directly, considering only the intra-specific distances. In addition, partitioning was done by performing a PERMANOVA on the Euclidean distances among all complete individuals separately within each cell. Different species were treated as different levels of the factor “Species”, and individuals within each species were treated as replicates in a one-factor design. The expectations of mean squares were used to calculate functional multivariate analogues to the classical unbiased ANOVA estimators’ univariate variance components. More specifically,

$\hat{\sigma}_I^2 = MS_{Res}$ and $\hat{\sigma}_S^2 = \frac{(MS_{Species} - MS_{Res})}{n_0}$

where $\hat{\sigma}_I^2$ is the estimated individual-level trait variance, $\hat{\sigma}_S^2$ is the estimated species-level trait variance, MS_{Res} is the residual mean square, $MS_{Species}$ is the “Species” factor’s mean square from the PERMANOVA partitioning, and n_0 is a divisor that allows for unequal numbers of individuals (n_i) per species $(i = 1, \cdots, S)$ within each cell, calculated as follows (Sokal and Rohlf (1981), p. 214):

$$n_0 = \frac{1}{(a-1)}\left\{\sum^{a} n_i - \left(\sum^{a} n_i^2 \middle/ \sum^{a} n_i\right)\right\}$$

The proportion of total trait variation (within each cell) attributable to individual-level variation (*i.e.*, Prop.I) is then calculated as

Prop.I = $\frac{\hat{\sigma}_I^2}{\hat{\sigma}_S^2 + \hat{\sigma}_I^2}$

This is the first time, to our knowledge, that individual and species-level functional variation have been partitioned and calculated in this way for full-dimensional multivariate trait space. Importantly, the estimators $\hat{\sigma}_I^2$ and $\hat{\sigma}_S^2$ are independent of species richness. Also, while small or unbalanced sample sizes (n_i, the number of individuals per species) will necessarily affect the precision of the estimates (*i.e.*, small numbers of individuals or species will yield more variable estimates), they will not, however, affect the accuracy of these measures, which are unbiased. There was very high correlation in the values of $\hat{\sigma}_I^2$ and MPFD.I (*r* = 0.93), and in the values of $\hat{\sigma}_S^2$ and MPFD (*r* = 0.89) (Figure S3.3), so we present results only for MPFD, MPFD.I and Prop.I in what follows. Finally, note that Prop.I and MPFD.I could only be calculated when there were two or more individuals representing the same species within a depth-by-location cell.

Statistical analysis

Univariate models

For modelling, we considered depth and latitude as continuous predictor variables, and included quadratic and cubic terms to allow for non-linearities in response variables along these gradients. We normalised depth and latitude to ensure polynomial terms remained orthogonal. We analysed all metrics described above as response variables; VPFD and VNND were transformed to $y' = \log_{10}(y)$ prior to analysis to improve normality. We used linear mixed-effects models, first treating depth as a fixed factor and latitude as a random factor, then treating latitude as fixed and depth as random (see Supplement 2, Tables S3.1 – S3.2 for further details).

Multivariate analyses

To visualise changes in multiple functional metrics along depth and latitude gradients simultaneously, we did a metric multi-dimensional (mMDS) ordination on (*i*) depth centroids and (*ii*) latitude centroids (see Figure S3.4 for metric multi-dimensional (mMDS) ordination of all 47 depth-by-location cells). We super-imposed bubbles corresponding to species richness and vectors to show partial correlations of functional metrics with mMDS axes. Three-dimensional shade plots were obtained to visualise potential interactions between depth and latitude for each of FHV, MPFD, MNND, MPFD.I, and Prop.I (Figure S3.2). All multivariate analyses were done on the basis of Euclidean distances for p = 7 functional metric variables using PRIMER v7 (Clarke & Gorley 2015a) with the PERMANOVA+ add-on (Anderson, Gorley & Clarke 2008).

3.4 Results

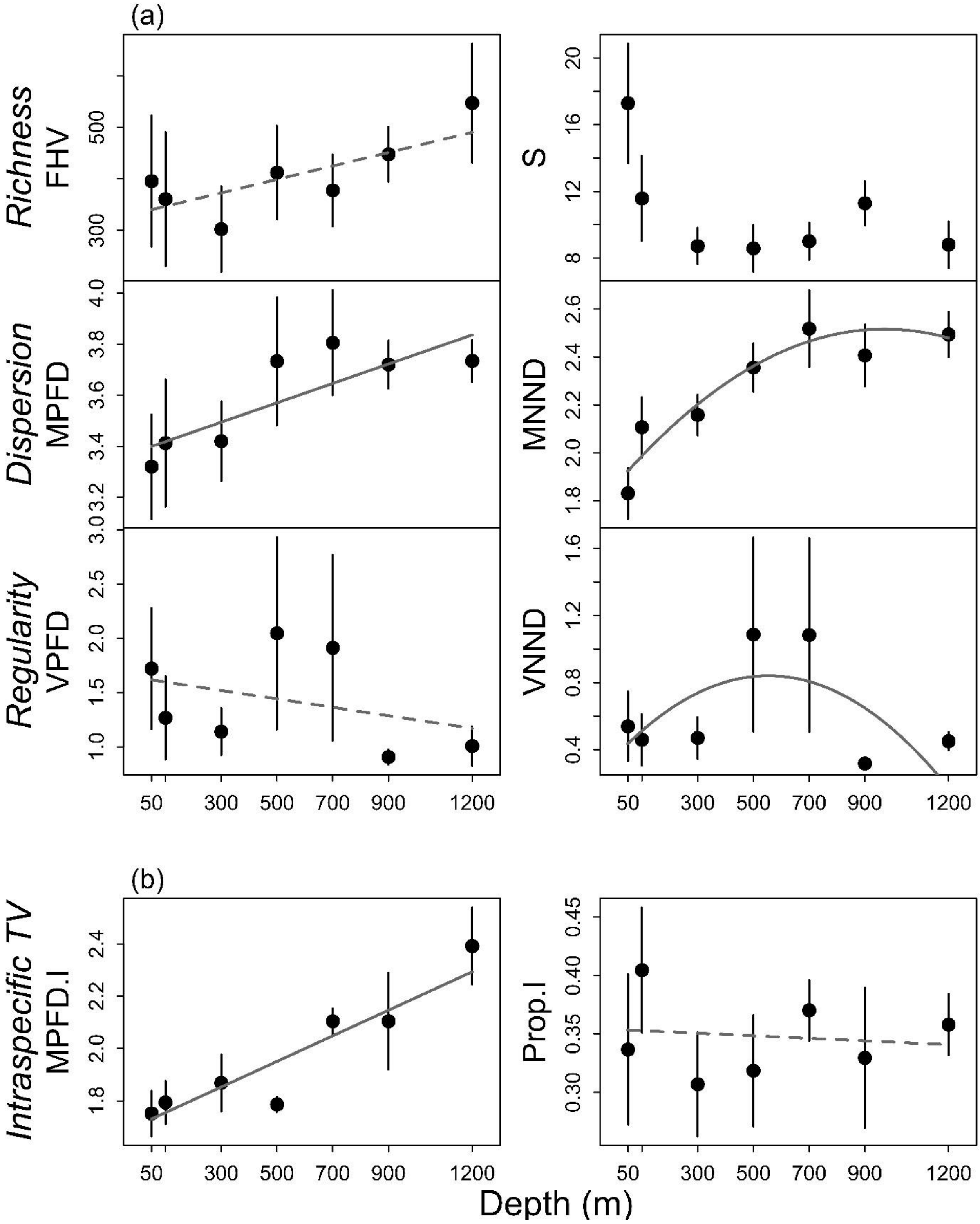


Figure 3.2. Relationships between functional diversity metrics (mean ±1SE across 7 locations) and depth: (a) species-level metrics (S = Species Richness) and (b) intra-specific trait variability metrics. Lines correspond to fitted values for the best model when depth is considered a fixed factor, and latitude a random factor (see Table S3.1 in Supplementary Material). Solid lines show statistically

significant trends (*P* < 0.05); dashed lines show trends that did not reach statistical significance at the 0.05-level. VNND was represented with a solid line due to the near-significant trend (*P* = 0.07; Table S3.1).

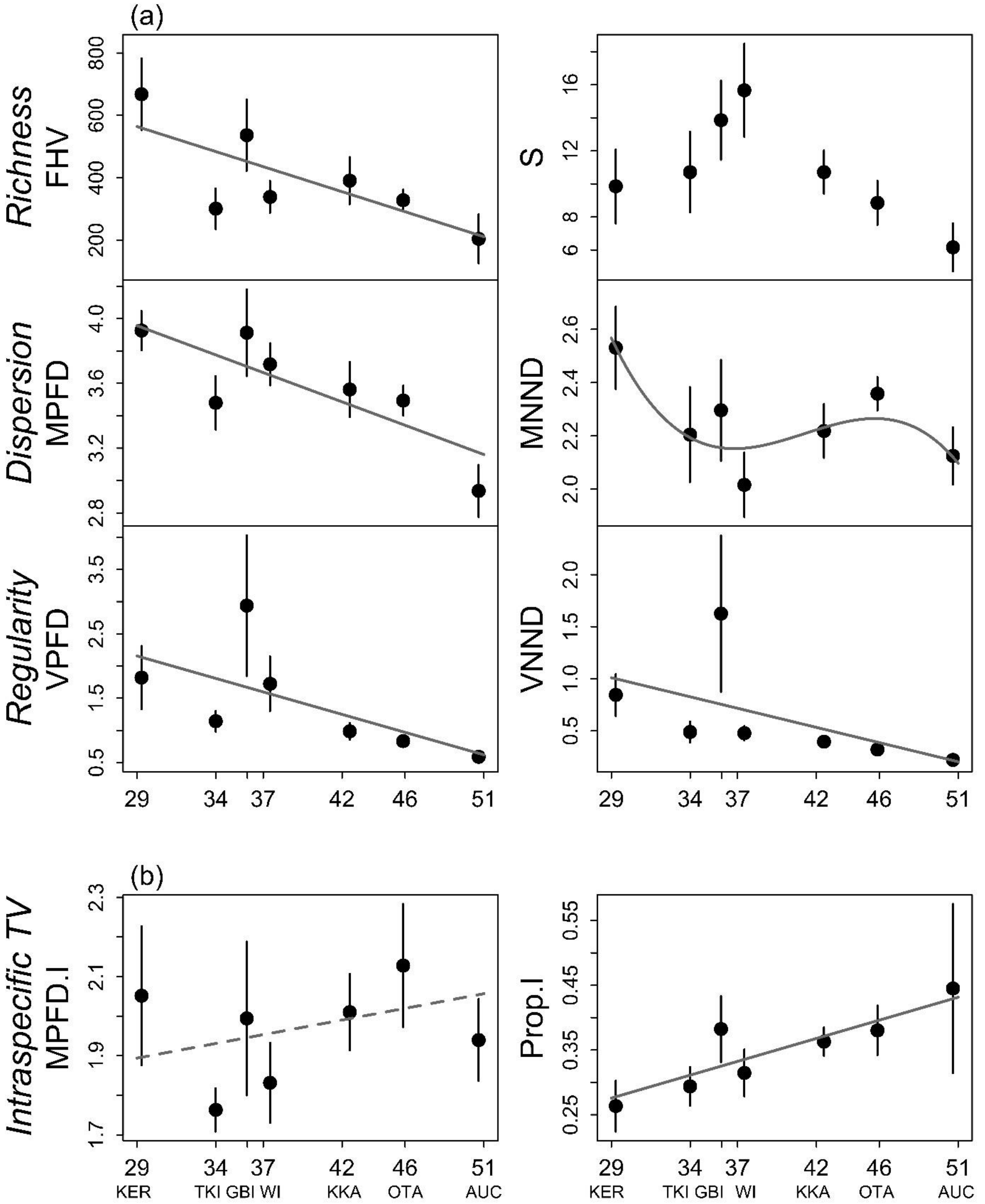


Figure 3.3. Relationships between functional diversity metrics (means ± 1SE across 7 depth strata) and latitude in degrees south (KER = Kermadec Islands, TKI = Three Kings Islands, GBI = Great Barrier Island, WI = White Island, KKA = Kaikōura, OTA = Otago, and AUC = Auckland Islands): (a) species-level metrics, (S = Species Richness) and (b) intra-specific metrics (see text for details). Lines show fitted values for the best model for each metric when latitude is considered a fixed factor, and depth a random factor (see Table S3.2 in Supplementary Material). Solid lines show statistically

significant trends (*P* < 0.05); dashed lines show trends that did not reach statistical significance at the 0.05-level. Note: Prop.I was represented with a solid line due to the near-significant trend (*P* = 0.07).

Contrary to all of the predictions derived from our conceptual models, functional hypervolume (FHV) generally increased with increasing depth (Fig. 3.2a), though the relationship was not statistically significant (*P* > 0.05). Functional dispersion metrics increased significantly with increasing depth, consistent with predictions arising from our second and third models (Fig. 3.1b), with MPFD showing a clear break between shallow (50 m–300 m) and deep (500 m–1200 m) areas (Table S3.1, *P* = 0.02), whereas MNND increased steeply from shallow to intermediate depths, followed by a plateau between 700 m and 1200 m (Table S3.1, *P* < 0.01 and *P* < 0.05 for the linear and quadratic terms, respectively). Regularity indices (VPFD and VNND, Fig. 3.2a) neither increased nor decreased with increasing depth, but instead were characterised by high latitudinal variability at intermediate depths (500 m–700 m) and low variability at deeper depths (900 m–1200 m). Intra-specific trait variability (MPFD.I) increased significantly with increasing depth (Table S3.1, *P* < 0.01), whereas Prop.I showed no clear trend with depth, averaging around 30 – 40% of total trait variation across all depths (Table S3.1, Fig. 3.2b). In general agreement with our first model (Fig. 3.1a, abiotic filtering dominates) all inter-specific metrics (except MNND) decreased monotonically with increasing latitude (Fig. 3.3a). Regularity indices (VPFD and VNND) were highly variable at GBI compared to other locations. Although intra-specific trait variation (MPFD.I) did not increase significantly with latitude, the proportion of functional trait variation attributable to intra-specific differences (Prop.I) did increase significantly with increasing latitude, and was most variable at the southernmost latitude (AUC) (Table S3.2, Fig. 3.3b). Latitudinal variation (as a random effect) exceeded variation attributable to the (fixed) effects of depth for FHV, MPFD, VPFD, VNND and Prop.I, whereas depth effects exceeded latitudinal variation for

MNND and MPFD.I (*cf.* Marginal R^2 and Conditional R^2 values, Table S3.1, see also Table S3.2).

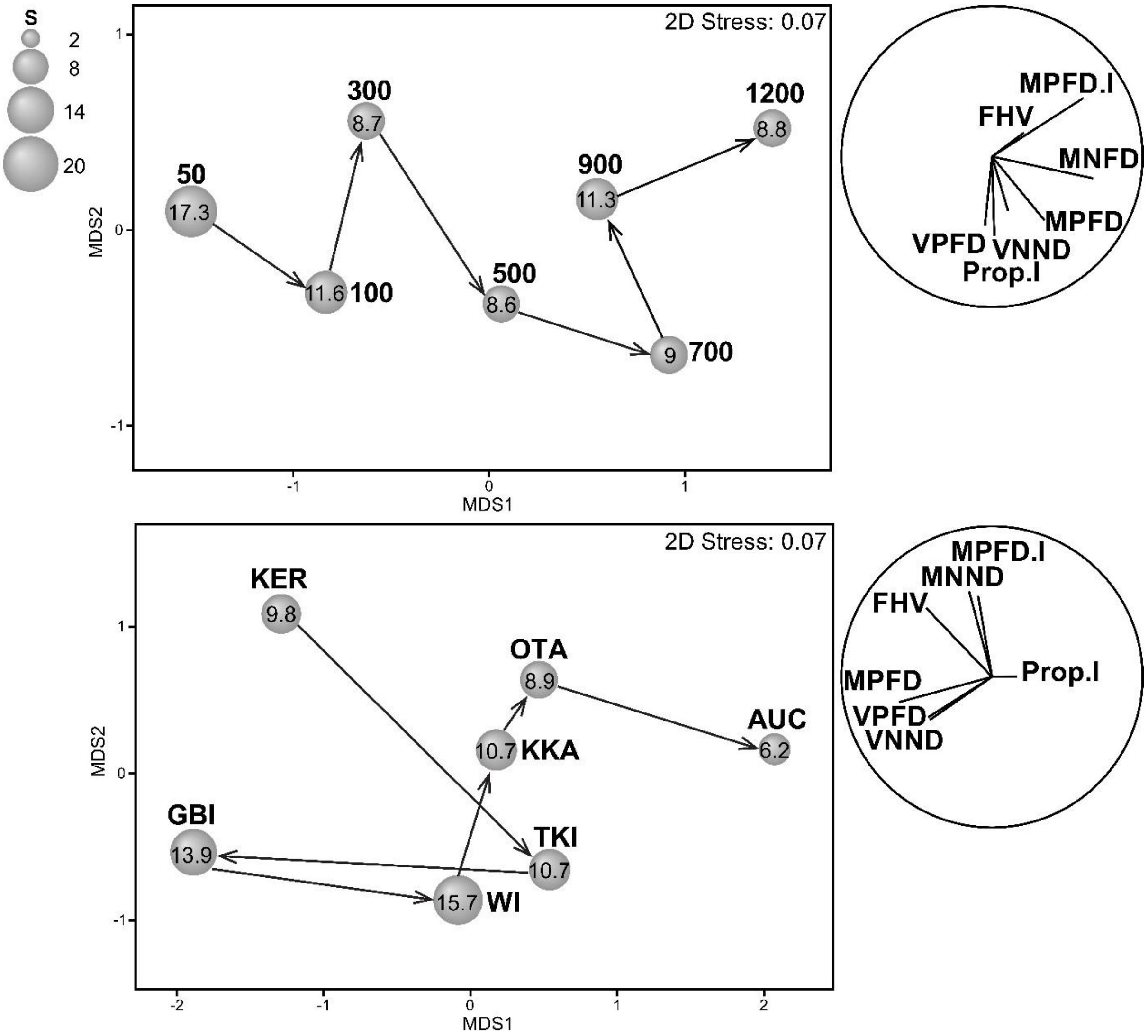


Figure 3.4. Metric multi-dimensional scaling (mMDS) ordination of normalised functional diversity metrics on the basis of Euclidean distances among a) depth centroids (50 m to 1200 m) and b) location centroids. Bubble sizes are proportional to mean species richness (also provided as a value inside each bubble). Vectors (right) show multiple partial correlations for each of p = 7 functional metrics with the mMDS axes.

There were clear gradual changes in the functional diversity of fishes along the depth gradient from shallow to deep environments (*i.e.,* from left to right along MDS axis 1 in Fig. 3.4a). This was primarily characterised by increases in MNND and MPFD.I at deeper depths (Fig. 3.4a). There was also separation of northern and southern latitudes along MDS axis 1, and there was clear evidence of a location effect at GBI (Fig. 3.4b). Northern locations were generally characterised by higher richness (FHV), dispersion (MPFD, MNND) and regularity (VPFD, VNND) values, while southern locations tended to have higher intra-specific variation (MPFD.I, Prop.I). Great Barrier Island, however, was clearly distinguishable from all other locations, having very high regularity values (VPFD, VNND) (Fig. 3.4b, Fig. S3.4).

3.5 Discussion

This study examined several functional diversity metrics simultaneously, and also partitioned variation in functional space into intra- and inter-specific components, enabling novel inferences regarding the relative contributions of external *vs* internal filters shaping fish communities along depth and latitude gradients. Functional alpha-diversity increased with increasing depth, and decreased with increasing latitude for New Zealand's ray-finned marine fishes. More specifically, with increasing depth there were increases in: (i) the overall functional hypervolume occupied by species, (ii) the dispersion and nearest-neighbour distances among species within the trait space, and (iii) intra-specific trait variation (MPFD.I). Regularity indices were characterised by high latitudinal variability at intermediate depths (500 m–700 m) and low variability at deeper depths (900 m–1200 m).

These results suggest that species occurring at deeper depths have diverged from one another to occupy distant morphological niches, with low levels of clustering, leading to a decrease in the *packing* of functional space with increasing depth. These results are consistent with our second conceptual model (Fig. 3.1b) whereby biotic interactions, such as competition for limited resources, are the dominant processes shaping functional space. However, none of our conceptual models would predict an increase in functional volume (FHV) with depth (Fig. 3.1). In addition, we found that functional hypervolume, functional dispersion and functional regularity indices decreased with increasing latitude. These results are consistent with our first conceptual model (Fig. 3.1a), in which environmental filtering is the dominant process. Interestingly, although species-level metrics decreased with increasing latitude, individual-level metrics increased (Fig. 3.3), suggesting that there was a gradual change in the source of functional diversity, with intra-specific trait variability becoming increasingly important at higher latitudes.

The two gradients of depth and latitude showed contrasting patterns with respect to functional hypervolume (Figs. 3.2-3.3), which generally increased with increasing depth, but decreased with increasing latitude. Increases in functional diversity with depth was a wholly unexpected result, and is inconsistent with the idea that functions will be filtered more strongly in harsh environments (Swenson 2011b). Instead, abiotic conditions such as limited trophic resources and habitat availability, decreasing temperature, and increasing pressure may represent key selection pressures on individuals living in the deep sea (Ramirez-Llodra *et al.* 2010). Species living in extreme conditions may be subject to greater disruptive selection and/or character displacement, potentially contributing to distinct morphologies, trait combinations, or functional strategies (Weiher & Keddy 1995) that enable a greater variety of unique biotic adaptations for resource acquisition (Leitao *et al.* 2016). This may allow greater partitioning of limited resources, consistent with the limiting similarity hypothesis (MacArthur & Levins 1967). Morphological dissimilarities among deep-sea species reflects low niche overlap, which can promote coexistence in a low-resource environment (Kumar *et al.* 2017). Decreasing functional hypervolume with increasing latitude, however, follows a more classical stress-gradient hypothesis, whereby traits are filtered more strongly in harsh than in benign environments (Weiher & Keddy 1995; Swenson 2011b). This pattern has been documented for plants *versus* latitude (Blonder *et al.* 2014), for birds *versus* altitude (Pigot, Trisos & Tobias 2016), and for macroinvertebrate assemblages *versus* depth (Ashford *et al.* 2018).

The packing, or density, of species within functional space decreased with increasing depth, as the mean distance between species and mean nearest-neighbour distances both increased (Fig. 3.2a). Previous work has shown that variance in pairwise taxonomic distances (Zintzen *et al.* 2011) among fish species increases with depth in New Zealand waters. In contrast, we found that variance in functional distances among species was minimal at 900 m and 1200 m, suggesting species are evenly distributed in functional space (albeit comparatively widely), with nearest-neighbours in functional space being far apart, despite the fact that taxonomically, nearest-neighbours are tightly clustered. Thus, it appears that species occurring at deeper depths diverge from one another functionally to occupy distant morphological niches. Morphological dissimilarities may help relax competition among species for limited resources (*i.e.,* a stabilizing niche difference, *sensu* HilleRisLambers *et al.* (2012)) aiding in niche-partitioning, and preventing the exclusion of inferior competitors (Swenson & Weiser 2014).

In trait-based ecology, studies advocating measurement of intra-specific trait variability are becoming increasingly common (Violle *et al.* 2012; Siefert *et al.* 2015; Des Roches *et al.* 2018). This is the first time, to our knowledge, that multivariate variation across multiple functional traits has been partitioned into intra- and inter-specific components using a hierarchical PERMANOVA approach (but see Albert *et al.* 2010; Jordani *et al.* 2019 for univariate examples using linear mixed models). We found an increase in intra-specific trait variability (MPFD.I, Fig. 3.2b) with depth but, interestingly, the proportion of variance attributed to individual-level variability was constant along the depth gradient. However, the proportion of total functional trait variation attributable to individual-level variability increased with increasing latitude (Prop.I, Fig. 3.3b), supporting the idea that intra-specific trait variation becomes important in species-poor communities with narrow environmental breadth (Siefert *et al.* 2015). For example, the high-latitude sub-Antarctic Auckland Islands (AUC) had the highest value for Prop.I, and was characterised by low species diversity, and a narrow temperature range from shallow to deeper environments (9.3°C–5.5°C). We suggest that increasing levels of intra-specific trait variation (ITV) *versus* depth (increasing MPFD.I) and latitude (increasing Prop.I) may promote the coexistence of functionally similar species by reducing inter-specific competition *via* shifting resource use or resource-acquisition traits, and favouring species that occur in lower densities (*i.e.*, a stabilizing niche difference) (Turcotte & Levine 2016; Violle *et al.* 2017; Bittebiere, Saiz & Mony 2019). Furthermore, high levels of intra-specific phenotypic variability may contribute to the higher rates of speciation in fishes in the deep-sea and at high latitudes (Rabosky *et al.* 2018), boosting the evolutionary potential of populations (Jump, Marchant & Peñuelas 2009); intra-specific variation begets speciation, which, in turn, begets inter-specific variation (Darwin & Costa 2009; Pfennig & Pfennig 2010). These results emphasise the importance of considering ITV in trait-based studies, particularly regarding its potential role in relaxing competition for limited resources.

Our study has provided novel insights into how functional diversity changes along environmental gradients at the local (alpha) scale. We consider that future work should examine turnover and nestedness components of functional beta diversity to yield further potential insights into how ecological processes may structure communities. We also consider that functional traits from under-sampled taxa *and* environments need additional study (Borgy *et al.* 2017). In addition, multivariate analyses of mophological traits should be extended to include behavioural traits, life-history strategies, trophic positions and/or physiological traits, for a more holistic measure of biologically relevant trait space (Violle *et al.* 2007; Bellwood *et al.* 2019).

3.6 Conclusions

These results suggest that inter-specific and intra-specific competition act as key processes shaping the functional diversity of fishes in the deep sea. Increasing morphological dissimilarity with increasing depth may help to facilitate fine-scale niche-partitioning and promote coexistence, whereas external abiotic filtering may be the dominant factor structuring communities with increasing latitude. In an era characterised by rapid and unprecedented change to deep-sea environments, with increasing anthropogenic pressures from fishing, deep-sea mining, and global climate change (Watson & Morato 2013; Levin & Le Bris 2015; Levin *et al.* 2016), understanding how functional diversity changes along gradients may help to predict potential responses of ecological communities to disturbances. In summary, this study quantified trait variation in marine fishes across broad-scale depth and latitudinal gradients, shedding new light on the potential roles of abiotic filtering, biotic interactions and fine-scale niche-partitioning, to further our understanding of the mechanisms underlying large-scale biogeographic gradients of biodiversity.

3.7 Acknowledgements

We thank James Seager from SeaGIS for developing the head morphometrics feature of EventMeasure specifically for this project. This work was supported by the Royal Society of New Zealand, Marsden Grant 15-MAU-132. E. M. V. Myers was supported by a Sir Hugh Kawharu Scholarship, and a Te Pūtea Whakatupu Trust Rona Scholarship. M. J. Anderson was supported by a James Cook Fellowship from the Royal Society of New Zealand (Grant JCF-15-MAU-006). L. Liggins was supported by a Rutherford Foundation Postdoctoral Fellowship (Grant RFT-15-MAU-003-PD). C. D.

Roberts was supported by the NZ National Institute of Water and Atmospheric Research Ltd (NIWA) Core Funded Coasts & Oceans Programme 2: Biological Resources. We thank Te Papa's Acquisition Program for assisting the development of an extensive fish collection over the last 15 years, which enabled this research, and particularly Andrew Stewart, Carl Struthers, Jeremy Barker and Salme Kortet for collection access. We also thank Tom Trnski and Severine Hannam at Tāmaki Paenga Hira Auckland War Memorial Museum for access to their fish collection.

3.8 Authors' Contributions

E.M.V.M., M.J.A., D.E., L.L., E.S.H and C.D.R. conceived and designed the study. E.M.V.M. measured all of the traits from the stereo-BRUV footage and museum specimens. E.M.V.M, D.E. and M.J.A. analysed the data and produced the figures. M.J.A. conceived and devised the methodology for the PERMANOVA partitioning. E.M.V.M. drafted the initial manuscript and all authors contributed towards the interpretations of results, the initial drafting and the revisions of the final manuscript.

3.9 Supplementary Materials

Supplement 1: A description of raw morphological measurements taken from individual fishes identified in video footage (stereo-BRUVs) or from museum specimens (Fig. S3.1).

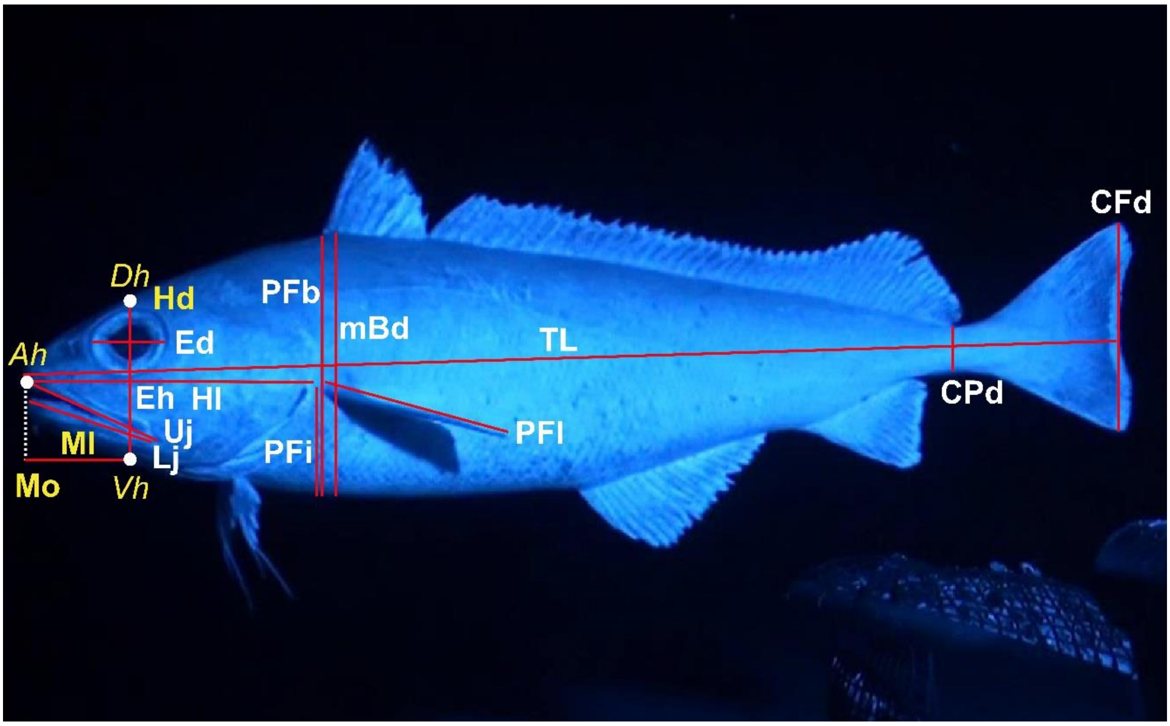


Figure S3.1. Raw morphological measurements obtained directly from stereo-BRUV footage; *CFd* = caudal fin depth, *CPd* = caudal peduncle depth, *Ed* = maximum eye diameter, *Eh* = eye height (length between the centre of the eye, and the white point denoted *Vh* (ventral head), *Hd* = head depth, *Hl* = head length, *Lj* = lower jaw length, *mBd* = maximum body depth, *Ml* = mouth length, *Mo* = mouth open (distance from the top of the mouth to the bottom of the head along the head depth axis), *PFb* = body depth at pectoral fin base, *PFi* = pectoral fin insertion, *PFl* = pectoral fin length, *TL* = total body length, *Uj* = upper jaw length. Note: *Mo, Hd,* and *Ml* (in yellow) are derived from a sequence of three measured 3D points within a single frame (*Dh* = dorsal head, *Ah* = anterior head, *Vh* = ventral head), and are obtained internally within EventMeasure software (www.seagis.com.au), using the "Head Morphometrics" feature of EventMeasure version 4.4.

Supplement 2: Statistical analyses

Univariate models

Our primary aim was to model patterns of change in functional diversity metrics along the depth (or latitude) gradient and examine variations in these patterns with latitude (or depth). We therefore used linear mixed-effects models treating depth (or latitude) as a fixed factor and latitude (or depth) as a random factor. First, the best random-effects structure was chosen under a REML optimization (Zuur *et al.* 2009), using a small-sample corrected Akaike information criterion (AICc), from the following potential models: 1) a correlated random intercept and slope model, 2) an uncorrelated random intercept and slope model, and 3) a random intercept model. For this first step, we set the fixed model structure to include (normalised) linear, quadratic and cubic terms. Next, we set the random structure in place and performed the model selection considering the linear, quadratic and cubic terms as potential predictors, once again choosing a best model using AICc and under ML optimisation. Finally, we estimated a marginal R^2 (variance explained by the fixed effect only) and a conditional R^2 (attributable to fixed and random effects) (see Nakagawa & Schielzeth 2013; Nakagawa, Johnson & Schielzeth 2017). In addition, semipartial marginal R^2 values were estimated for the different terms of the fixed effect (Jaeger *et al.* 2017). We used the nlme (Pinheiro *et al.* 2015), MuMIn (Barton 2009) and r2glmm (Jaeger 2017) R packages to perform the mixed modeling, the model selection and to estimate R^2 values (marginal, conditional and semipartial).

Table S3.1. Parameter estimates, proportion of explained variance, and statistical significance of individual terms for the best models (using AICc) for each of 7 functional diversity metrics *vs* depth, using a linear mixed-effects model with latitude as a random effect. The best random structure for latitude (considering a random intercept model (RI), an uncorrelated random intercept and slope model (URIS), or correlated random intercept and slope model (CRIS)) and the best fixed effect (considering linear, quadratic and cubic terms for depth) were selected using AICc. VPFD and VNND were transformed to $y' = \log_{10}(y)$. The estimated standard deviation for the random slope in the CRIS model for FHV was 125.25 and the estimated correlation between the random intercept and slope was *r* = -0.75.

	Metric	**Best Random Structure**	**sd (β_0)**	**Marginal R^2 (Fixed)**	**Conditional R^2 (Fixed + Random)**	**Parameter**	**Semi-partial R^2**	**Value**	**Std.Error**	**df**	***F***	***P***
Richness	**FHV**	CRIS	139.28	0.03	0.56	Intercept	-	400.0	58.30	39	6.86	**<0.01**
						Depth		49.66	53.87	39	0.92	0.36
Dispersion	**MPFD**	RI	0.28	0.07	0.36	Intercept	-	3.57	0.12	39	29.30	**<0.01**
						Depth	-	0.14	0.06	39	2.34	**0.02**
	MNND	RI	0.1	0.33	0.41	Intercept	-	2.35	0.07	38	31.40	**<0.01**
						Depth	0.331	0.23	0.04	38	5.09	**<0.01**
						Depth^2	0.086	-0.1	0.04	38	-2.21	**0.03**
Regularity	**VPFD**	RI	0.16	<0.001	0.32	Intercept	-	0.04	0.7	39	0.6	0.54
						Depth	-	-0.02	0.03	39	-0.73	0.47
	VNND	RI	0.18	0.05	0.35	Intercept	-	-0.28	0.08	38	-3.18	**<0.01**
						Depth	0.013	0.03	0.04	38	0.93	0.36
						Depth^2	0.047	-0.07	0.04	38	-1.81	0.07
Intra-specific Trait Variability	**MPFD.I**	URIS	0.12	0.32	0.45	Intercept	-	1.95	0.03	35	50.81	**<0.01**
						Depth	-	0.19	0.06	35	3.12	**<0.01**
	Prop.I	URIS	0.08	0.01	0.40	Intercept	-	0.34	0.01	34	21.52	**<0.01**
						Depth	-	-0.01	0.03	34	-0.40	0.68

Table S3.2. Parameter estimates, proportion of explained variance, and statistical significance of individual terms for the best models (using AICc) for each of 7 functional diversity metrics *vs* latitude, using a linear mixed-effects model with depth as a random effect. The best random structure for depth (considering a random intercept model (RI), an uncorrelated random intercept and slope model (URIS), or correlated random intercept and slope model (CRIS)) and the best fixed effect (considering linear, quadratic and cubic terms for depth) were selected using AICc. VPFD and VNND were transformed to $y' = \log_{10}(y)$.

	Metric	**Best Random Structure**	**sd (β_0)**	**Marginal R^2 (Fixed)**	**Conditional R^2 (Fixed + Random)**	**Parameter**	**Semi-partial R^2**	**Value**	**Std.Error**	**df**	***F***	***P***
Richness	**FHV**	URIS	55.38	0.19	0.23	Intercept	-	400.34	31.93	39	12.54	**<0.01**
						Latitude	-	-109.58	38.55	39	-2.84	**<0.01**
Dispersion	**MPFD**	RI	0.10	0.23	0.27	Intercept	-	3.58	0.07	39	47.95	**<0.01**
						Latitude	-	-0.25	0.06	39	-3.81	**<0.01**
	MNND	RI	0.21	0.10	0.42	Intercept	-	2.19	0.10	37	21.44	**<0.01**
						Latitude	0.017	0.11	0.10	37	1.1	0.28
						Latitude^2	0.055	0.09	0.04	37	2.02	**0.05**
						Latitude^3	0.055	-0.10	0.05	37	-2.04	**0.05**
Regularity	**VPFD**	RI	<0.01	0.25	0.25	Intercept	-	0.04	0.03	39	1.28	0.2
						Latitude	-	-0.14	0.03	39	-3.94	**<0.01**
	VNND	RI	0.07	0.26	0.32	Intercept	-	-0.35	0.04	39	-7.38	**<0.01**
						Latitude	-	-0.16	0.03	39	-4.26	**<0.01**
Intra-specific Trait Variability	**MPFD.I**	RI	0.2	0.01	0.35	Intercept	-	1.96	0.08	35	22.26	**<0.01**
						Latitude	-	0.04	0.04	35	1.06	0.3
	Prop.I	URIS	0.03	0.11	0.21	Intercept	-	0.34	0.01	34	20.75	**<0.01**
						Latitude	-	0.04	0.02	34	1.83	0.07

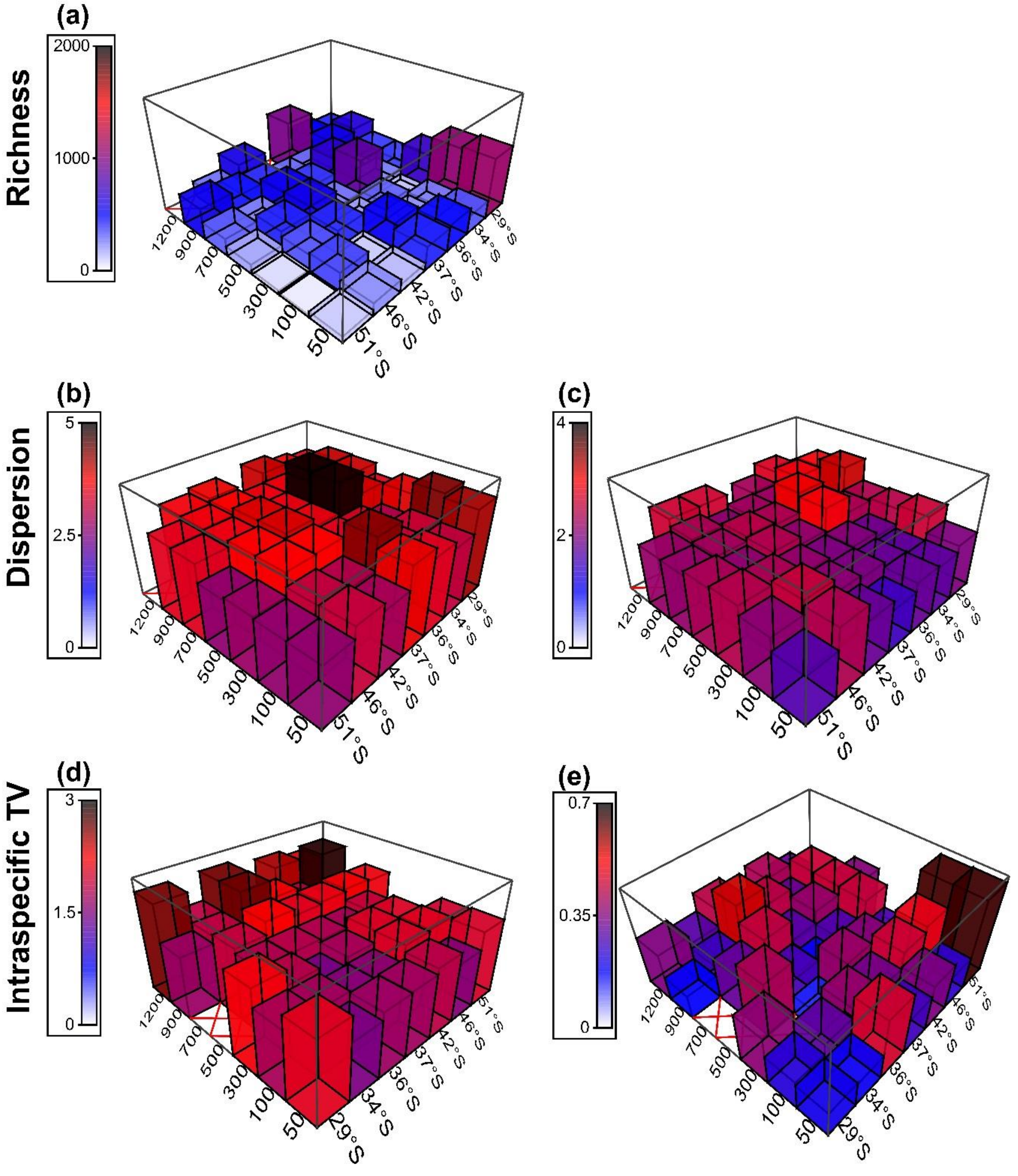


Figure S3.2. Three-dimensional shade plots showing the potential interactions between depth and latitude for interspecific metrics (a) FHV = functional hypervolume, (b) MPFD = mean pairwise functional distance, (c) MNND = mean nearest neighbour distance, and metrics documenting intraspecific trait variability (d) MPFD.I = intraspecific mean pairwise functional distance, and (e) Prop.I = proportion of variance explained by individual (intraspecific) variation.

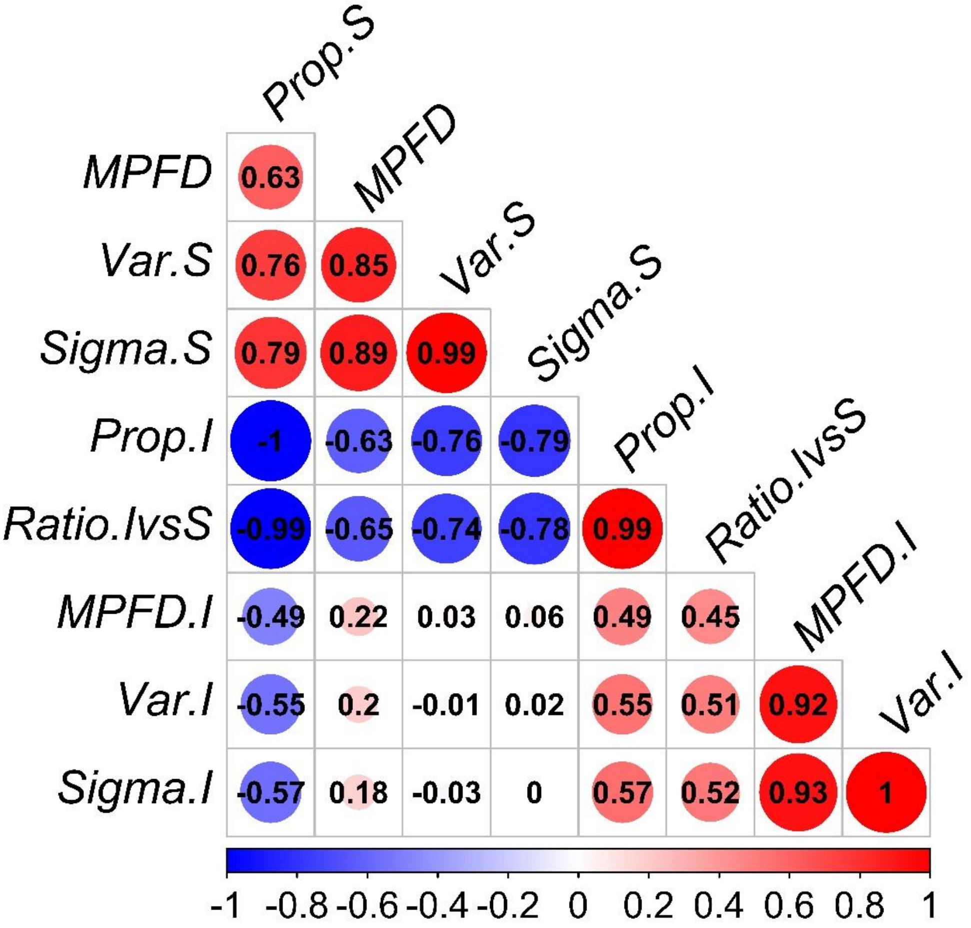


Figure S3.3. Heat map showing Pearson correlations among measures related to the partitioning of variance using a PERMANOVA approach whereby Var.S = variation in traits among different species, Sigma.S = square root of Var.S, Prop.I = proportion of total trait variation attributable to variation among individuals (var.I / (var.S + var.I)), Ratio.IvS = Ratio of individual versus species-level variation (Sigma.I / Sigma.S), MPFD.I = mean pairwise distance between all pairs of individuals belonging to the same species, Var.I = variation in traits among the individuals within a species, Sigma.I = square root of Var.I, and the functional metric, MPFD = mean pairwise functional distance.

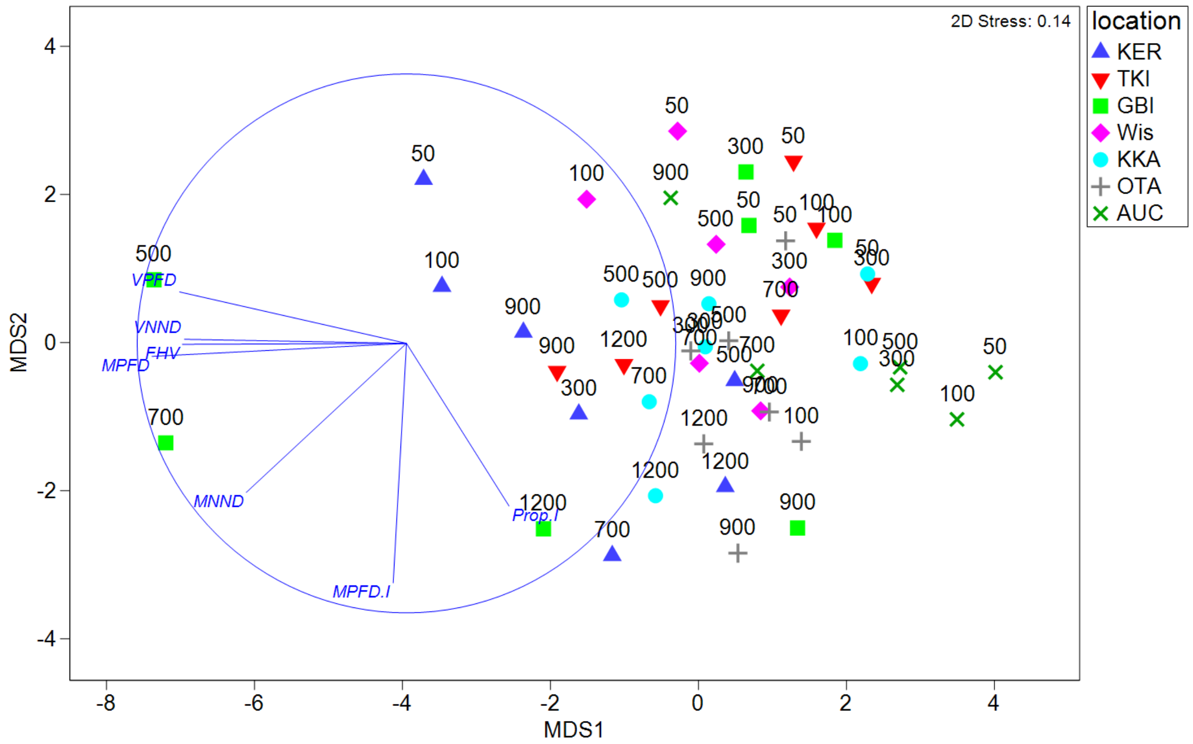


Figure S3.4. Metric multi-dimensional scaling (mMDS) ordination on the basis of Euclidean distances among depth-by-location centroids for *p* = 7 functional diversity metrics: functional hypervolume (FHV), mean pairwise functional distance (MPFD), variance of mean pairwise functional distance (VPFD), mean nearest neighbour distance (MNND), variance of mean nearest neighbour distance (VNND), mean pairwise distance, considering only intra-specific distances (MPFD.I), proportion of total trait variation attributable to variation among individuals (Prop.I). Labels represent depth (50 m – 1200 m) and symbols represent location (ordered here from north to south): KER = Kermadec Islands, TKI = Three Kings Islands, GBI = Great Barrier Island, WIs = White Island, KKA = Kaikōura, OTA = Otago, and AUC = Auckland Islands.

3.10 DRC16 Statement of Contribution

4 Functional beta diversity of New Zealand fishes: characterising morphological turnover along depth and latitude gradients, with derivation of functional bioregions

4.1 Abstract

Changes in the functional structures of communities are rarely examined along multiple large-scale environmental gradients. Here, we describe patterns in functional beta diversity for New Zealand marine fishes vs depth and latitude, including broad-scale delineation of functional bioregions. We derived eight functional traits related to food acquisition and locomotion and calculated complementary indices of functional beta diversity for 144 species of marine ray-finned fishes occurring along large-scale depth (50–1200 m) and latitudinal gradients (29°–51° S) in the New Zealand EEZ. We focused on multivariate functional space defined by a suite of morphological traits calculated directly from in situ footage obtained using Stereo-BRUVs and museum specimens. We found that functional changes were primarily structured by depth followed by latitude, and that latitudinal functional turnover decreased with increasing depth. Functional turnover among cells increased with increasing depth distance, but this relationship plateaued for greater depth distances (>750 m). Functional turnover did not change significantly with increasing latitudinal distance at 700–1200 m depths. Shallow functional bioregions (50–100 m) were distinct at different latitudes, whereas deeper bioregions extended across broad latitudinal ranges. Fishes in shallow depths had a body shape more conducive to efficient propulsion, suitable for catching prey and eluding predators. Fishes in deeper depths were more elongated, enabling energy-efficient locomotion in low-resource environments, and had large eyes, enhancing vision in darker environments. Environmental filtering may be a primary driver of broad-scale patterns of functional beta diversity in the deep sea. Greater environmental homogeneity may lead to greater functional homogeneity across latitudinal gradients at deeper depths (700–1200 m). These results suggest that communities living at depth follow a 'functional village hypothesis', whereby the same functions are present among communities over large spatial scales. Mechanistic drivers may only be investigated, however, after quantifying salient patterns of broad-scale changes in functional beta diversity. We provide baseline information regarding turnover of key functions in New Zealand fishes, to formulate hypotheses for processes shaping communities, and to inform better ecosystem-based management.

Keywords: functional homogeneity, spatial turnover, trait, deep-sea fishes, beta diversity.

4.2 Introduction

A primary goal of ecology is to understand the distribution of species and their interactions, often in relation to an environmental gradient. Beta diversity measures the variation in species composition among locations or sites, and provides a link between regional gamma (γ) and local alpha (α) diversity (Whittaker 1960; Whittaker 1972). It has been used to address key questions in ecology such as what makes communities more similar or different, or understanding how the magnitude of those differences vary along spatial or temporal gradients (Vellend 2001; Anderson *et al.* 2011). One type of beta diversity, 'turnover', measures the change in species composition along a predefined gradient which can be geographical (e.g. distance), or environmental (e.g. moisture, salinity or depth) (Nekola & White 1999; Anderson *et al.* 2011). Turnover has been used to define the scale over which species and communities change in response to variations in environmental conditions along large spatial gradients (Kraft *et al.* 2011). Understanding turnover in communities can help to define the breaks between biogeographic regions, and denote the spatial areas over which communities and their constituent species are similar (Ficetola, Mazel & Thuiller 2017).

Global patterns in beta diversity across taxa tend to change predictably according to environmental variability, whereby areas of high turnover often coincide with environmental transition zones, and areas of low turnover occur in environmentally homogeneous regions (Anderson, Tolimieri & Millar 2013). Trends in terrestrial systems such as the decline in beta diversity with increasing latitude (e.g., for woody plants, Kraft *et al.* 2011) are also mirrored in marine systems, but tend to more modest due to greater homogeneity of the conditions in the marine environment (Soininen, Lennon & Hillebrand 2007). Beta diversity declines along another important spatial gradient, depth, from shallow coastal waters to the deep ocean for Asteroidea (Price, Keeling & O'callaghan 1999), bivalves (McClain, Stegen & Hurlbert 2012) and fishes (Zintzen *et al.* 2011; Zintzen *et al.* 2017). Of pressing concern for marine ecosystems is the fast-paced compositional change – a trend occurring faster in marine than terrestrial habitats (Blowes *et al.* 2019) – which is leading to the rapid reorganisation and biotic homogenisation of assemblages globally (Magurran *et al.* 2015; Blowes *et al.* 2019; Eriksson & Hillebrand 2019). Biotic homogenisation (reductions in beta diversity) can occur in a variety of forms, and the patterns scientists observe will depend on the type of beta diversity being measured: e.g., taxonomic, phylogenetic, or functional.

Functional diversity has been widely studied within localised regions (Swenson & Weiser 2014; Pigot, Trisos & Tobias 2016; McLean *et al.* 2019b), but ecologists have limited understanding regarding functional turnover along large-scale spatial gradients, particularly in the ocean (Stuart-Smith *et al.* 2013; Mindel *et al.* 2016a). Functional beta diversity is related to variation in environmental conditions, and measures the morphological or functional dissimilarity between two or more assemblages (Swenson, Anglada-Cordero & Barone 2011; Swenson *et al.* 2012; Siefert *et al.* 2013; Penone *et al.* 2016). Environmental conditions can change dramatically along large-scale spatial gradients such as depth or latitude, and extreme conditions may filter out organisms lacking the required functional strategies for survival (e.g., under environmental filtering; Kraft *et al.* 2011). On the other hand, dispersal limitation may lead to an increase in the functional dissimilarity of communities with increasing environmental distance (Penone *et al.* 2016). The pattern and strength of the relationship between dissimilarities in communities and geographic/environmental distances has been investigated across a range of ecological systems and taxonomic groups (e.g., birds, trees, fishes) with a view to understanding potential mechanisms underlying community assembly (e.g., Swenson, Anglada-Cordero & Barone 2011; Siefert *et al.* 2013; Swenson 2014). For example, previous work found increasing functional dissimilarity among tropical tree communities along an increasing elevation gradient (Swenson, Anglada-Cordero & Barone 2011). In contrast, functional turnover along environmental gradients can sometimes be negligible (in spite of high taxonomic turnover), such as that found for fish communities along an estuarine salinity gradient (Villéger *et al.* 2012). In such cases, biotic interactions may be more important than environmental factors in shaping the functional space of communities. Overall, there is a dearth of studies on functional turnover in marine systems. Currently, we lack a clear understanding of how the distribution of species and communities along environmental gradients is mediated by their functional traits (but see Sunday *et al.* 2015; Marzloff *et al.* 2018).

The depth gradient is a major spatial gradient for which patterns of beta diversity are largely unknown due to vast swathes of the ocean remaining unexplored (McClain & Rex 2015). The deep sea is the largest habitat on earth; it is well connected and environmentally buffered (Ramirez-Llodra *et al.* 2010). Generally, as habitat is thought to become more homogenous with increasing depth, we may expect communities to be more functionally similar across large (latitudinal) spatial scales at deeper depths. However, benthic studies have shown that the deep sea can be surprisingly diverse and full of unique habitats at various spatial scales (Zeppilli *et al.* 2016). Marine fishes, which account for over half of all vertebrate diversity, and carry out key ecosystem processes such as nutrient cycling and controlling food webs (Villeger *et al.* 2017), show a decline in beta diversity with increasing depth (Anderson, Tolimieri & Millar 2013; Zintzen *et al.* 2017). Recent work suggests that fishes within a community at a specific location become more morphologically distinct from one another with increasing depth (i.e., functional alpha diversity increases), potentially driven by increasing competition for resources (Myers *et al.* in review). Investigating the link between local-level alpha patterns and the turnover of functions at larger scales (i.e., functional beta) will help to achieve three major goals: first, it will provide baseline information describing the patterns; second, it will inform development of hypotheses regarding the potential processes shaping communities; and third, it will inform better management decisions to protect key functions for fishes.

Understanding spatial patterns of beta diversity across large areas is important for conservation planning (McKnight *et al.* 2007; Buckley & Jetz 2008). In most cases, however, essential data are unavailable from remote, hard-to-access areas such as the deep sea or high-latitude regions, or for understudied taxa. Identifying areas with similar characteristics may be used to ensure adequate coverage and representativeness in choosing areas for protection. Although turnover in environmental parameters, discontinuities in habitats or species' identities, have historically been used to define and demarcate bioregions (Ferrier *et al.* 2007; Shears *et al.* 2008; Ficetola, Mazel & Thuiller 2017), other phenomena, such as functional hotspots and frontiers in phylogenetic differentiation, are increasingly being identified and used in global analyses of biodiversity for fishes (Stuart-Smith *et al.* 2013; Cowman *et al.* 2017), birds (Cooke, Bates & Eigenbrod 2019), mammals (Penone *et al.* 2016; Cooke, Bates & Eigenbrod 2019), plants (Pinto-Ledezma, Larkin & Cavender-Bares 2018), and brittle stars (O'Hara *et al.* 2019). Identifying functionally diverse regions, and specific areas with high functional turnover will help to provide a baseline against which to measure the impact of future changes in environmental conditions associated with both anthropogenic and natural disturbances.

Here, we describe patterns of functional beta diversity for assemblages of marine ray-finned fishes along large-scale depth (50–1200 m) and latitudinal (29°–51° S) gradients in New Zealand waters. We focused on the multivariate functional space defined by a suite of morphological traits for locomotion and food acquisition, calculated directly from measurements of individual fish, to identify areas of functional homogeneity and transition zones. First, we modeled the relationship between the functional dissimilarities in fish communities *vs.* absolute differences in either depth or latitude (Nekola & White 1999; Millar, Anderson & Tolimieri 2011). We hypothesised that the slopes of these relationships would be steeper for the depth gradient than for the latitude gradient, and that latitudinal functional turnover would decrease with increasing depth (hence mirroring the pattern seen in Zintzen *et al.* (2017) for taxonomic turnover). We also quantified functional turnover between adjacent (neighbouring) depth-by-latitude cells to identify the specific position(s) along each gradient at which abrupt functional changes occur. Next, we used random draws of species (from broader-scale lists) to identify particular depth-by-latitude cells where observed fish communities had functional distinctness values that deviated significantly from what would be expected under a null model of random species assembly. Finally, we used clustering and ordination tools, operating on a functional dissimilarity matrix, to propose functional “bioregions” for New Zealand’s fish assemblages.

4.3 Materials and Methods

Fish community data

Stereo-BRUVs footage was used to sample marine ray-finned fishes (Class Actinopterygii) *in situ* at off-shore locations across northern, eastern and southern New Zealand (see Fig. 1 in Zintzen *et al.* 2017 for detailed positions). The stereo-BRUVs were deployed in a stratified random sampling design at each of seven depths (50 m, 100 m, 300 m, 500 m, 700 m, 900 m and 1200 m) within each of seven locations that spanned 21° of latitude in New Zealand waters (with n = 5–7 replicate deployments per depth-by-location). Video footage was obtained from a total of 329 deployments (2 hours each) across 47 depth-by-location cells (2 cells were not sampled – White Island at 1200 m and Auckland Islands at 1200 m, due to poor weather conditions). Further details regarding the sampling design and stereo-BRUVs methodology are given in Zintzen *et al.* (2012) and Zintzen *et al.* (2017).

Functional traits

Fifteen raw morphological measurements (see Fig. S3.1 in Chapter 3) were obtained from individuals of each species of fish, *in situ*, by reviewing footage obtained from each stereo-BRUVs deployment and using the software ‘EventMeasure’ (www.seagis.com.au). For details regarding the full procedure used for video analysis and measurement, see Chapter 3. Where possible, measurements from multiple individuals of a single species within a given depth-by-location cell were obtained. A complete set of morphological measurements were not always possible to obtain, however, for every species observed in the video footage. For individuals that were missing no more than 3 (out of 15) measurements, the missing values were imputed using a random-forest machine-learning algorithm (Stekhoven & Bühlmann 2012), based on the other individuals of that species in the dataset having complete measurements. This imputation relies on the assumption that relationships among the morphological variables remain constant within a given species. In addition, to ensure we would have a full set of measured traits for every fish species, we also took raw morphological measurements directly from two preserved museum specimens (held within the National Fish Collection at the Museum of New Zealand Te Papa Tongarewa, Wellington) for every species seen in the video footage (see Chapter 3 for methodological details, and voucher registrations are provided in Table S4.6 of the Supplementary Materials). In total, there were 144 species recorded across the 47 depth-by-location cells, and 509 species-by-cell occurrences. The original dataset comprised a complete set of 15 raw morphological measurements for 722 individuals observed in video footage (140 of these required some random-forest imputation), plus 295 museum specimens.

We calculated 8 trait variables – namely: eye size, oral gape position, jaw length relative to head length, elongation, eye position, caudal peduncle throttling, pectoral fin position and total body length – each as a function of the 15 raw morphological measurements (Table S4.1). These morphological traits focused on key aspects of locomotion, visual perception and feeding for fishes and have measured functional differences in the body plan and structure of fishes across large depth gradients (Myers *et al.* 2019).

To calculate measures of functional turnover, we obtained representative trait values for every species within every cell in the study design. To compile a table of 8 unique traits (columns) for each species in each depth-by-location cell (509 rows), we randomly drew 1 individual from the list of all complete individuals for each species. Random draws were also needed in order to handle cases where more than 3 raw measurements were missing/unable to be measured for a given species (i.e., where there were too many missing values on an individual to perform data imputation) in a given cell. We drew an individual of a given species from the list of all complete individuals of that species that were (in order of preference): (i) within that depth-by-location cell, (ii) at the same depth, (iii) from anywhere within the stereo-BRUV design or (iv) from a museum specimen. We replicated this random-draw procedure 100 times to generate 100 species-cell × trait (509 × 8) data tables. By calculating beta diversity values for all 100 tables, then averaging these values, we were able to integrate the available individual (within-species) morphological variation into the study, given the logistic constraints on the number of individuals of each species we were able to measure, while also maintaining spatial variation in morphologies encountered within each species as well as possible.

Measures of functional beta diversity

Measures of functional beta diversity were obtained on the basis of a Euclidean distance matrix that was calculated between every pair of unique species occurring in each depth-by-latitude cell, using the 8 normalized continuous trait variables. We calculated the following metrics between every pair of cells: (i) mean distance in functional space between all pairs of species across the two cells (mean pairwise functional distance, MPFD; (Clarke & Warwick 1998; Somerfield *et al.* 2008; Swenson 2014), (ii) mean distance to the nearest neighbour in the other cell (in functional space) for all species (MNND; Swenson & Weiser 2014). MNND has previously been used in a functional alpha context to estimate functional originality (Mouillot *et al.* 2013b; Leitao *et al.* 2016), and can be considered an indicator of differences in niche and limiting/limits to similarity (Swenson *et al.* 2020). We computed these metrics for each of the 100 species-cell by trait (509 x 8) data matrices, then the mean (and standard deviation) values for each of MPFD and MNND were calculated across all 100 tables for subsequent analyses. The result was a 47 x 47 matrix of mean functional dissimilarities (either MPFD or MNND) among all pairs of cells in our study design.

Statistical analysis

Functional turnover vs depth and latitude

We modelled functional turnover as the change in functional dissimilarity values (based on either MPFD or MNND) versus absolute differences in either depth (in meters) or latitude (distance). Separate models were fitted to visualise functional turnover with changes in depth at each of the seven latitudes. Similarly, we fit separate models of functional turnover versus latitude for each depth stratum. We also plotted turnover (MPFD or MNND) between adjacent cells along either the depth or the latitude gradient, in order to explicitly identify particular depths and/or latitudes at which ‘breaks’ in functional space occur.

Functional distinctness and comparison with null models

We assessed observed *versus* expected functional distinctness using the TAXDTEST feature of PRIMER (Clarke & Gorley 2015a). TAXDTEST is normally used to calculate average taxonomic distinctness, but in this case was adapted to calculate the functional analogue "average functional distinctness", as suggested by Somerfield *et al.* (2008). The average functional distinctness of a depth-by-latitude cell is the average functional distance among all pairs of species in the cell, and can be considered the average *functional breadth* of a sample (also known as mean pairwise functional distance, MPFD, in Chapter 3). Note that, whereas taxonomic distinctness utilizes a taxonomic tree to calculate distances among species, it is possible also to perform these same calculations using a distance matrix among species instead. We performed the TAXDTEST algorithm separately for each depth stratum, using the mean functional distance matrix among 144 species (normalized Euclidean distance matrix based on the 8 traits). Specifically, we considered a null model that the functional distinctness obtained for the list of species observed in a given cell is within the bounds of what would be expected at that depth stratum, given the number of species observed in that cell. Thus, we generated 95% confidence bounds for the expected functional distinctness for a given number of species (from 3 species to 35 species) using 1000 random draws from the full list of species seen within each depth stratum (e.g., 50 m) across the entire study design.

Functional bioregions

To visualise functional turnover across the entire study design, we produced a non-metric multi-dimensional scaling (nMDS; Kruskal & Wish 1978) ordination plot based on functional dissimilarities between all pairs of depth-by-latitude cells. This was achieved using PRIMER v7 (Clarke & Gorley 2015a), which allows any distance matrix among species to be used (and here, we used functional distances among the species based on the 8 normalized traits, rather than a taxonomic tree) in order to define relationships among the species in the calculation of resemblances. Hence, taxonomic resemblances (called “Gamma+” in PRIMER, see Clarke, Somerfield & Chapman 2006) readily become functional resemblances (or dissimilarities in the form of MNND) using this approach. We used Gamma+/MNND instead of MPFD because of the stronger trends with differences in depth and also with differences in latitude (see Results, Fig. 4.1), making it a more natural choice for the broader ensuing analyses. In addition, a two-way crossed non-parametric ANOSIM test of the two ordered factors of depth and latitude was done on the basis of this functional resemblance matrix. This tested the null hypothesis that there was no ordered pattern of functional turnover along each gradient, independently of any potential changes along the other gradient. For further details regarding non-parametric tests of ordered changes in community structure along gradients, see Somerfield, Clarke and Olsgard (2002). For details of two-way ANOSIM tests on ordered factors, see Clarke, Somerfield and Gorley (2016).

To classify New Zealand’s fish assemblages into biogeographic groups of cells containing sets of species that collectively possess a similar suite of functional strategies/morphologies, we used *k-R* clustering (Clarke, Somerfield & Gorley 2016) on the functional (Gamma+ or MNND) resemblance matrix among the depth-by-latitude cells. We performed sequential non-hierarchical *k-R* cluster analyses for choices of *k* from 2 up to 10 clusters. The algorithm was stopped when similarity profile tests (SIMPROF, see Somerfield & Clarke 2013) indicated that no further splitting into a larger number of clusters was justifiable (i.e., when there was not sufficient structure within any of the resulting *k-R* cluster groupings to generate a statistically significant SIMPROF test-statistic). This generated k = 7 groups of cells, corresponding to what we shall refer to as functional bioregions. For each functional bioregion, we identified the individual fish species lying closest to the centroid (in 8-dimensional functional space) to provide a visual exemplar of a typical morphological body-plan for fish occurring in each group.

4.4 Results

Functional turnover vs depth and latitude

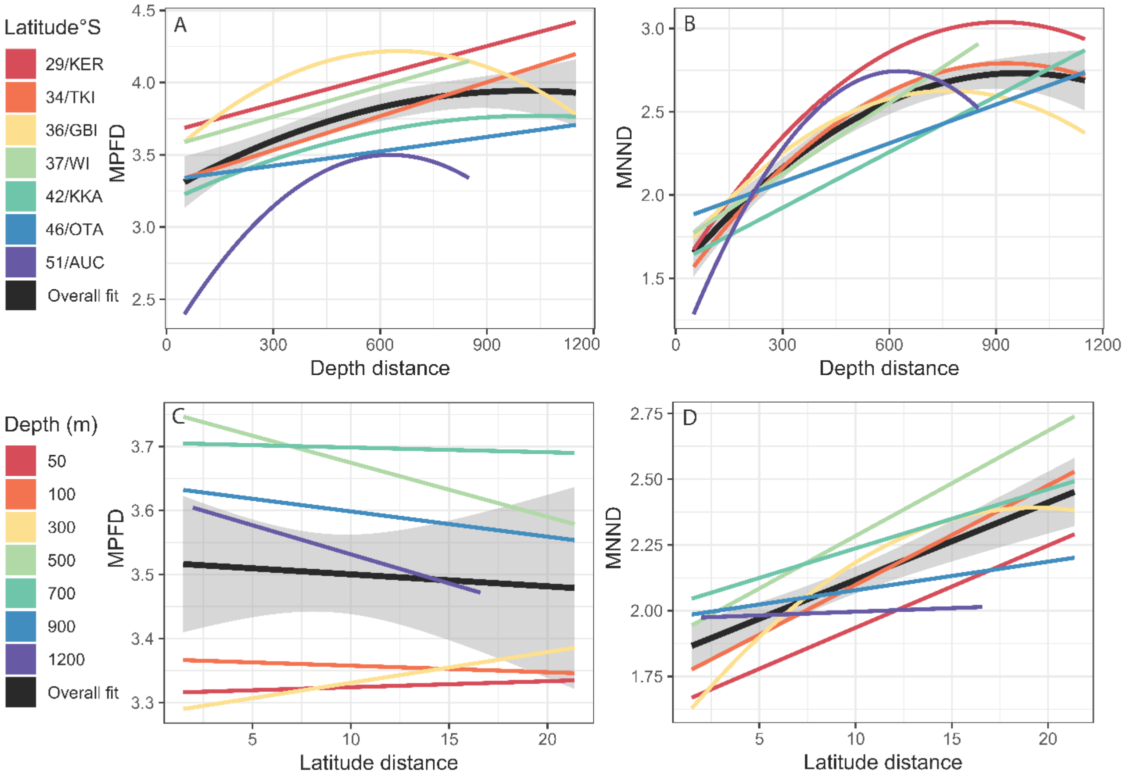


Figure 4.1. Plots showing the fitted models for the relationships between functional turnover in the morphology of fishes, measured as either MPFD or MNND, *vs* absolute differences in depth (A, B) or absolute differences in latitude (C, D). Coloured lines show the individual fitted models within each latitude (A, B) or within each depth stratum (C, D). Black lines show the best overall fitted model, with 95% confidence interval (shaded grey).

Functional turnover in fish communities, as measured by MPFD, was greater along the depth gradient than along the latitudinal gradient (Fig. 4.1A, C). The slope of the relationship between functional dissimilarity and differences in depth was steeper for smaller absolute differences in depth (50–300 m) and was also generally steeper when measured using nearest-neighbour distances (MNND, Fig. 4.1B). Generally, MPFD and MNND plateaued at absolute differences in depth of ~ 750 m or more, indicating limits to functional turnover in fish communities overall. In addition, southern latitudes generally had lower values of MPFD and MNND than did northern latitudes (i.e., a smaller intercept).

Strikingly, the mean pairwise functional distance (MPFD) between fish communities did not increase significantly with increasing latitudinal distance (the relationships remained non-significant for all depth strata; Table S4.2). Thus, functional dissimilarities appear not to be related to latitude. In addition, intermediate depths (500–700 m) consistently had the largest functional latitudinal turnover (i.e., high intercepts, see Table S4.2), followed by deep (900–1200 m) and shallow (50–300 m) depths (Fig. 4.1C). In contrast, MNND did increase with increasing latitudinal distance although the relationship became flatter for deeper depths (Fig. 4.1D). The deepest depths (700–1200 m) had a non-significant relationship, indicating that there was no increase in functional turnover of fish communities, despite increasing spatial distance (i.e., a flat relationship at 1200 m; Table S4.2).

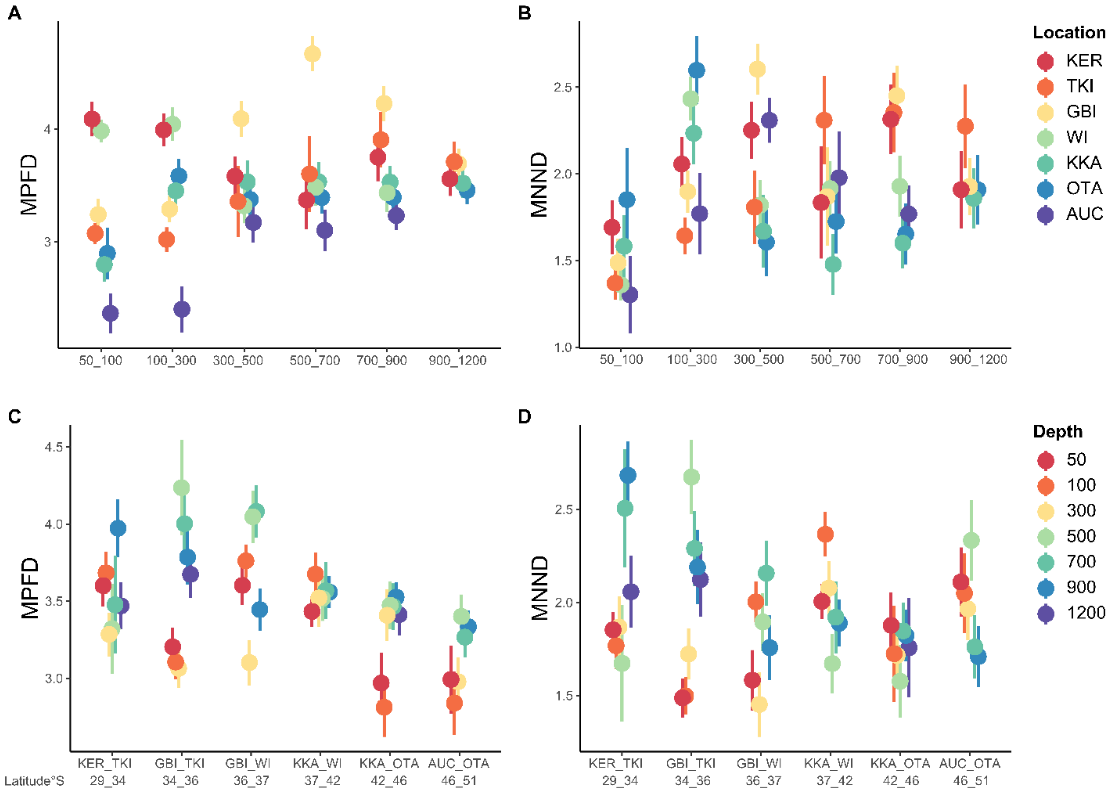


Figure 4.2. Functional turnover (measured by MPFD and MNND) between adjacent depth cells at each latitude (A, B; with coloured symbols denoting locations from KER in the north to AUC in the south), and between adjacent latitudinal cells within each depth stratum (C, D; with coloured symbols denoting depth strata from 50 m to 1200 m). The error bars give the standard deviation in MPFD or MNND values calculated across the 100 data tables drawn randomly from the complete dataset.

Peaks in turnover among adjacent depth cells depended on latitude (Fig. 4.2). For example, the greatest functional turnover was between 50 m and 100 m for the Kermadecs and White Island (Fig. 4.2A), whereas Great Barrier Island showed the highest turnover between 500 m and 700 m, and southern locations (e.g., Auckland Islands) showed very low functional turnover at shallow depths (50–100 m or 100–300 m; Fig. 4.2A). However, functional turnover from 900 m to 1200 m was very similar (MPFD ~ 3.5) for all latitudes. Similarly, turnover among adjacent latitudinal bands was depth dependent. Interestingly, for both MPFD and MNND, the greatest functional turnover between adjacent latitudes occurred at mid-to-deep depths of 500 m, 700 m and 900 m, particularly at northern locations between the Three Kings Islands, Great Barrier Island and White Island (Fig. 4.2C, D).

Functional distinctness and comparison with null models

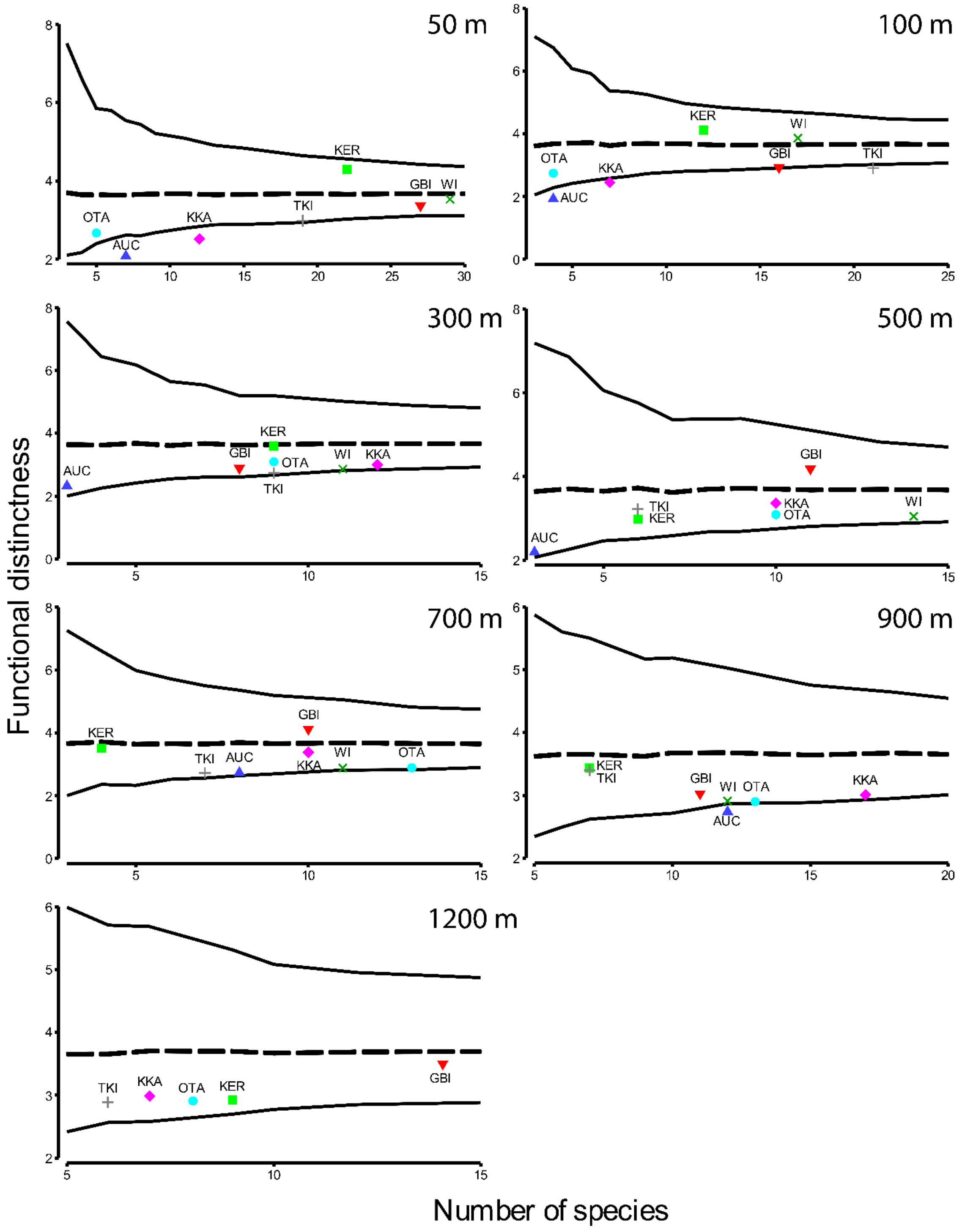


Figure 4.3. Funnel plots showing mean (dotted line) and 95% confidence bounds (solid lines) for the expected functional distinctness, given the number of species observed in each cell using random draws from the full list of species seen within each depth stratum. Coloured symbols show the observed functional distinctness values for each depth-by-latitude cell.

Observed values of functional distinctness generally fell within the 95% bounds of expected values generated from lists of species observed within each depth stratum, although many fell below the mean (mid-line ~3.8) (Fig. 4.3). The Auckland Islands, however, generally had lower than expected functional distinctness, consistently falling outside, or on the lower bounds of the funnel across all depth strata. At shallower depths, KKA (50 m and 100 m) and TKI (100 m) also had lower-than-expected functional distinctness. Generally, northern locations such as KER or GBI had greater functional distinctness compared to other locations across all depths.

Functional bioregions

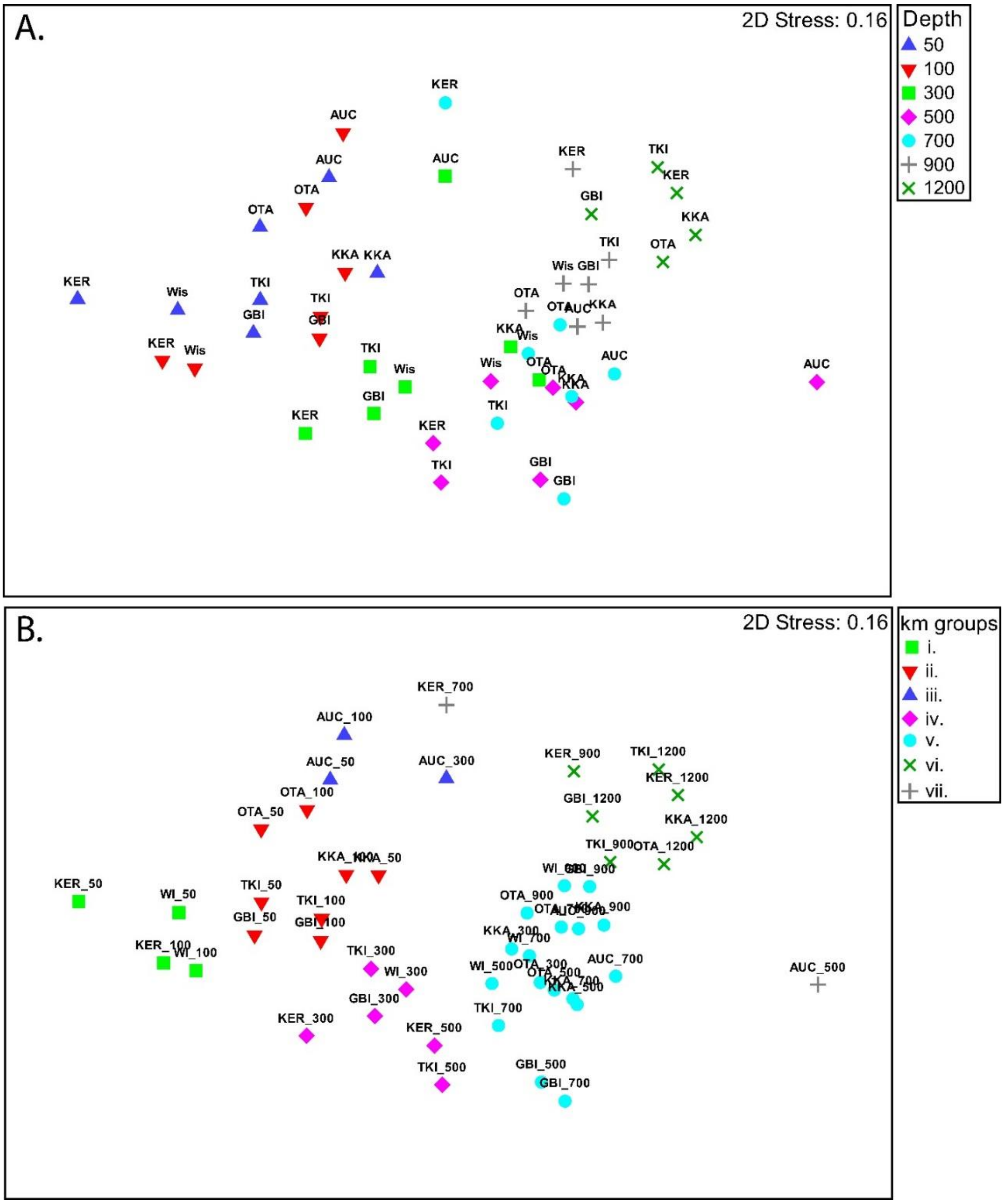


Figure 4.4 Non-metric multi-dimensional scaling (nMDS) ordination on the basis of mean nearest-neighbour functional distances (the Gamma+ dissimilarity measure in PRIMER, or MNND) among depth-by-location cells for $p = 8$ normalized functional traits, with symbols corresponding to (A) the 7 depth strata or (B) the 7 functional bioregions identified using unconstrained non-hierarchical *k-R* partitioning and associated SIMPROF tests.

There was a clear trend of functional turnover in fish communities from shallow to deep environments (i.e., from left to right on the nMDS plot; Fig. 4.4A).

There was a strong and significant pattern of sequential functional turnover in fish communities detected along the depth gradient (two-way ordered ANOSIM: R = 0.828, P = 0.0001). Significant sequential functional turnover, although less strong, was also detected along the latitude gradient (R = 0.501, P = 0.0001), although it was not apparent in the nMDS ordination plot (Fig. 4.4A).

The *k*-*R* cluster routine performed on depth-by-latitude cells with SIMPROF tests identified 7 groups, which we will refer to hereafter as *functional bioregions*. Cells within the same functional bioregion possess fish species which broadly embrace a similar area of the 8-dimensional functional morphological trait-space investigated here. Interestingly, the cells within the same cluster were generally spatially identifiable and contiguous (with few exceptions), even though no spatial constraints were imposed on the *k*-*R* partitioning algorithm (Fig. 4.5). These 7 functional bioregions were also very clearly identified as coherent groups in the nMDS plot (Fig. 4.4B).

Fish communities sampled from 50 m or 100 m at either the Kermadecs or White island comprised the first group (i). Communities at shallow depths (50 – 100 m) in mid-latitude locations (TKI, GBI, KKA and OTA) comprised a second group (ii), while shallow communities at the Auckland Islands (from 50–300 m) comprised a third group (iii). Intermediate depths were split into a northern 300 m to 500 m group (iv) and a larger, close-knit group ranging from predominantly southern 300–900 m depths (v). A deep group (vi), encompassed all 1200 m depths and fish communities at 900 m at the northern locations of KER and TKI (Fig. 4.4B; Fig. 4.5A). Finally, a seventh group included two disparate communities: 700 m at the Kermadecs and 500 m at the Auckland Islands (Fig.

4.5); however, these two cells were not located closely together, but rather appeared to be outliers on the nMDS plot (Fig. 4.4B).

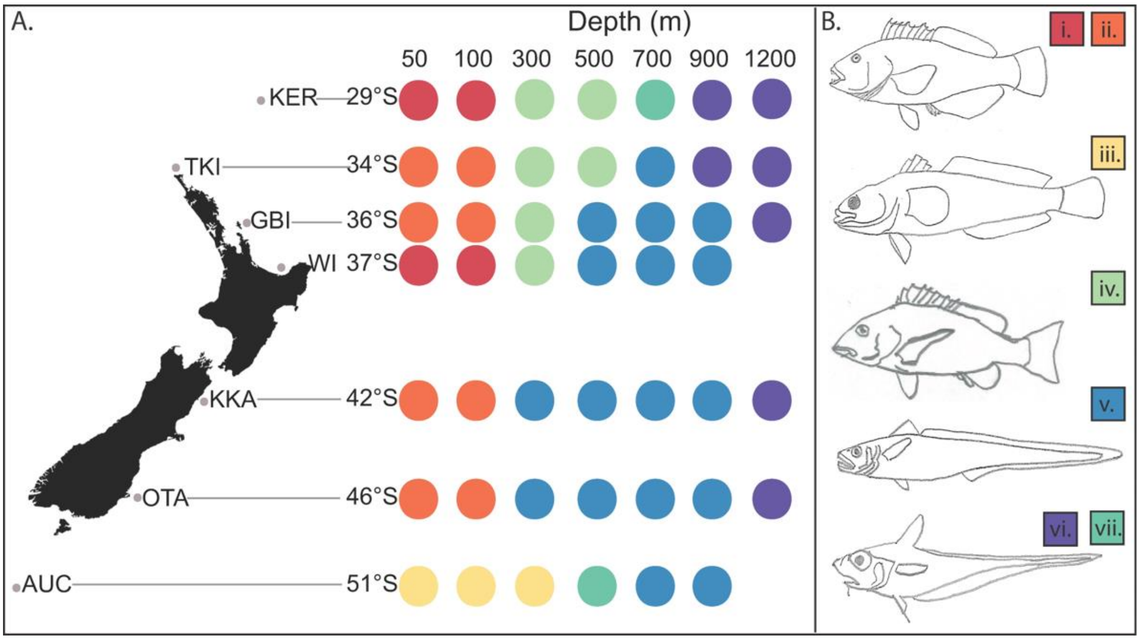


Figure 4.5. A) Schematic diagram of the cells in the study design belonging to each of the 7 functional bioregions (i)-(vii), denoted by seven colours, alongside a map of New Zealand. B) A family-level representation of the fish species closest to the centroid in the 8-dimensional trait space (i.e., an “arch-typical” species) for each functional bioregion, adapted from Roberts, Stewart and Struthers (2015): i) *Bodianus unimaculatus*, Labridae, ii) *Bodianus flavipinnis,* Labridae, iii) *Notothenia microlepidota,* Nototheniidae, iv) *Etelis coruscans,* Lutjanidae, v) *Lyconnus pinnatus,* Merluccidae, vi) *Coryphaenoides subserrulatus*, Macrouridae, vii) *Lepidorhynchus denticulatus,* Macrouridae. See Figure S4.1 for a photograph of each species.

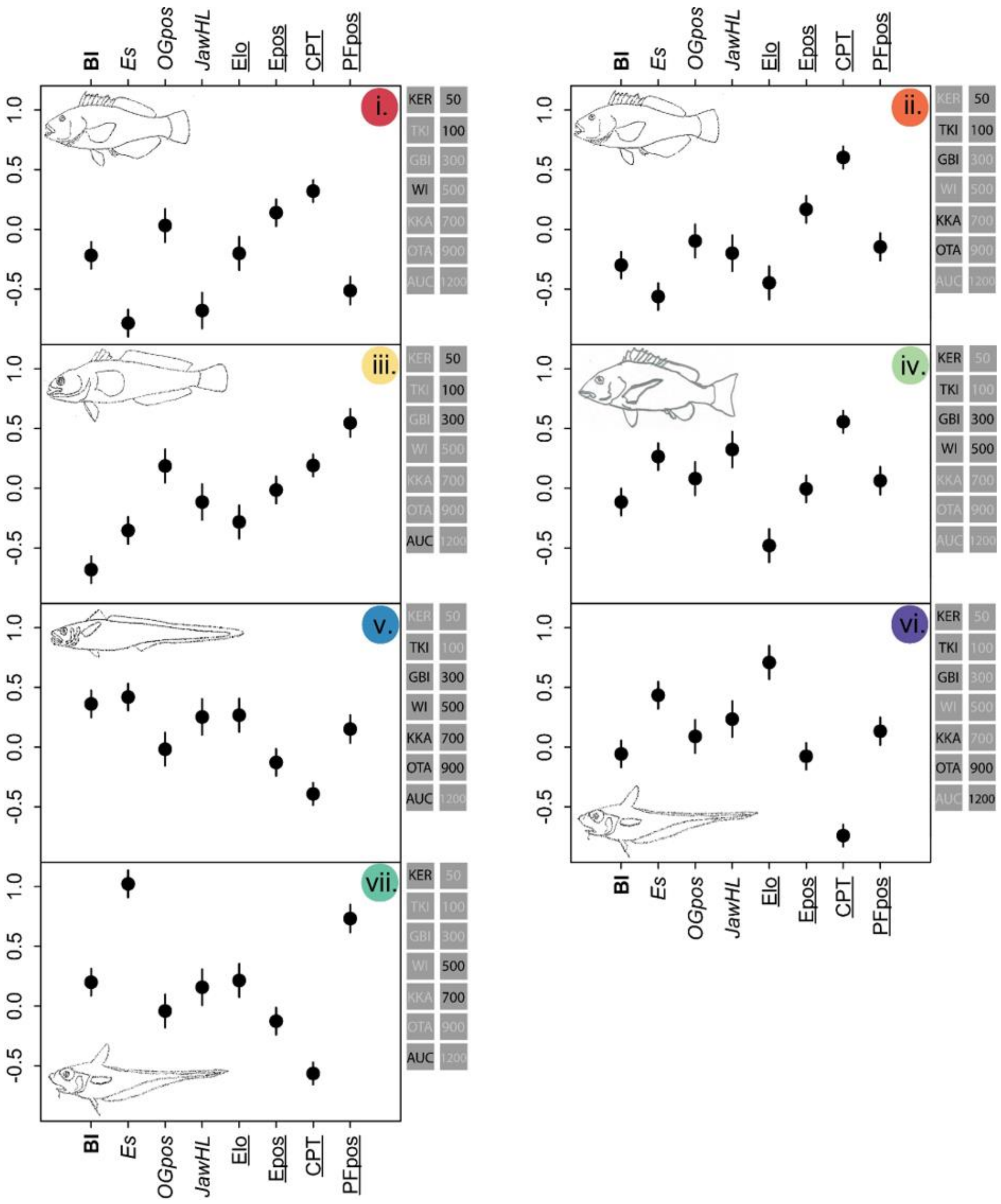


Figure 4.6. Mean ±1SE of the normalized functional trait values for fish species occurring within each functional bioregion (see Fig. 4.5). The y-axis scale is fixed for each plot to allow direct comparisons of mean trait values across the different plots. Bl = body length, Es = eye size, OGpos = oral gape position, JawHL = jaw length as a proportion of head length, Elo = elongation, Epos = eye position, CPT = caudal peduncle throttling, PFpos = pectoral fin position. Number of fishes used to calculate the SE ranged from 14 (group iii.) to 182 (group v). Trait abbreviations: **bold** represents a universal trait, *italics* represents food acquisition traits, and underlined represents locomotion traits (see Table S4.1 for a description of each trait).

The general change in fish morphology along the depth gradient shows a transition from deeper bodied, with rounded, lunate or forked tails in shallow and intermediate depths to a more elongate, slender form with a tapering tail in deeper waters (Fig. 4.5B; Fig. 4.6). Fishes that are closest to the centroid of the functional space are generally perciforms. Shallow groups (Fig. 4.6 i, ii) tended to have similar morphologies (except group ii had a greater mean jaw to head length ratio). Eye size was larger in intermediate and deep groups (Fig. 4.6 iv-vii) and was particularly large relative to body length for fishes at KER_700 and AUC_500 (i.e., group vii). Elongation was generally highest and caudal peduncle throttling was lowest at intermediate and deep depths (Fig. 4.6 v-vii), which is typical of deep-sea orders (Gadiformes, Notocanthiformes, Ophidiiformes and Anguilliformes).

4.5 Discussion

We have provided a description of the patterns of functional beta diversity for a sample of New Zealand's marine ray-finned fishes across large-scale depth and latitudinal gradients, characterising how the functional structure of communities varies according to key food acquisition and locomotion traits. We found that functional variation in fish communities was primarily structured by depth and then by latitude, and that fish communities generally became more functionally homogenous with increasing depth. More specifically, functional turnover among cells increased with increasing depth distance, but this relationship plateaued at greater depth distances (> 750 m). Functional turnover, as measured by MPFD and MNND, did not change significantly with increasing latitudinal distance for depths between 700–1200 m, suggesting that the environmental filtering of traits in the deep sea may lead to functional homogeneity among communities spread over large spatial scales. Abrupt changes in the functional structure of communities were latitude-dependent, and shallow, northern depth-by-latitude cells were most variable (MPFD and MNND), as was deeper, northern depth-by-latitude cells for MNND. Most of the observed values of functional distinctness fell within the expected bounds generated under a null model for a particular targeted depth, and that northern locations (KER and GBI) were generally more functionally distinct than southern locations (KKA and AUC), which occasionally had lower-than-expected functional distinctness. Finally, functional bioregions in shallow depth strata (50–100 m) were delineated according to latitude, whereas deeper bioregions consisted of broad groups of cells along the latitudinal gradient. Fishes in the shallows (50–100 m) had a body shape that was more conducive to efficient propulsion (a high value for Caudal

Peduncle Throttling) for both catching and eluding prey/predators (Webb 1984; Villéger *et al.* 2010), and a deep body for defence against gape-limited predators (Hodge *et al.* 2018). In contrast, fishes in deeper depths were more elongated, enabling energy efficient swimming in low-resource environments and large eyes for dimly lit intermediate depths (Neat & Campbell 2013; Myers *et al.* 2019).

Our most salient finding was that along the depth gradient, the further apart two depth-by-latitude cells were, the more functionally dissimilar they were (Fig. 4.1 A, B). We found that the *rate* of functional turnover along depth varied according to absolute depth distance at specific positions along the gradient (i.e., functional dissimilarity increased with increasing depth distance, until ~750m, and then plateaued). Functional beta diversity has previously been found to decline with increasing environmental (i.e., elevation Swenson, Anglada-Cordero & Barone 2011) and geographic (Siefert *et al.* 2013) distance in tropical (Puerto Rico) and temperate (North Eastern American) tree communities respectively. In a taxonomic context, Zintzen *et al.* (2017), found a pronounced decline in beta diversity at 700–900 m for fishes in New Zealand, owing to homogeneous environmental conditions associated with the Antarctic Intermediate Water mass (Garner 1959). Steep rates of functional dissimilarity for smaller depth distances may reflect environmental filtering according to fishes' physiological adaptations (or their lack thereof) to specific regions/sections of the depth gradient. For example, the traits that enable survival at 50 m are likely very dissimilar to the traits of a fish living at 700 m (e.g., see Myers *et al.* 2019). The rapid physical changes that occur vertically along the depth gradient, such as decreasing light, temperature, dissolved oxygen, food and increasing pressure (Priede 2017b), occur at smaller spatial scales than that of the latitudinal gradient and combine to cause functional turnover at the scale of 100's of meters as opposed to 100's of kilometres across latitude. In contrast, over deeper parts of our study (i.e., between ~700–1200 m), the traits of fishes are likely similar due to the relatively homogeneous habitat sampled (e.g., an elongated body, a tapering tail, and a large gape; Neat & Campbell 2013; Myers *et al.* 2019). Therefore, the comparison of functional traits among fishes living at 50 m *versus* 700 m, and 50 m *versus* 1200 m are similar – explaining the plateau in Figure 4.1A-B. Hence, functional turnover for fishes across depth depends on the position along the depth gradient, and more specifically, is likely influenced by the rate of environmental change along the depth gradient, which may differ among locations.

In contrast to patterns of functional turnover along the depth gradient, our functional metrics MPFD and MNND demonstrated two different types of response along the latitudinal gradient. MPFD, which is heavily influenced by species that are functionally divergent, showed little change with increasing latitudinal distance, with a slightly negative, non-significant trend (Table S4.4). This suggests that *within* each depth stratum, species that are separated by large functional distances (i.e., are functionally divergent) occur in communities spread along the entire length of the latitudinal gradient. This may be a result of functionally convergent species at the extreme ends of the latitudinal gradient carrying out similar functions, regardless of their taxonomic or phylogenetic relationship. For example, Tebbett *et al.* (2020) found that a key function - macroalgal removal - was carried out by a surgeon fish (*Naso unicorus*) on the Great Barrier Reef, and a trigger fish (*Melicthys niger*) in the Caribbean, suggesting that key functional roles traverse both classical taxonomic and biogeographic barriers as expected under a scenario of functional convergence.

In contrast, a significant linear increase of MNND (Table S4.4) was observed along the latitudinal gradient. This may indicate that the "closest functional neighbour" of fishes (i.e., fishes with similar functional strategies) in nearby latitudes tend to become increasingly dissimilar with larger geographic (latitudinal) distances. Interestingly, the increasing MNND with latitudinal distance became flatter (and non-significant) for deeper depths (700–1200m; Figure 4.1D), suggesting that the relatively high nearest-neighbour distances among deeper fish communities remain relatively constant. We considered that this pattern (which also occurs across all depths for MPFD) might be explained by a functional trait version of the "ecological village hypothesis" developed by Smith *et al.* (2014), which suggests that across regions with similar environmental characteristics, a full collection of essential ecological roles will be represented, yielding taxonomic similarity at the family level (but not necessarily at the species level) across large spatial scales. We suggest that this is also likely to be happening in the deep sea; i.e., due to homogeneous environmental conditions, the *functional* version of a butcher, a baker, and a candlestick maker (perhaps a gelativore, a scavenger, and a piscivore (Drazen & Sutton 2017)) is repeated across large spatial scales. This may contribute to the low functional turnover (beta diversity) found at deeper depths across latitude for MNND, and across all depths for MPFD. Thus, the functional organization of fishes may be intrinsically linked to not only the environmental characteristics of habitats at large spatial scales, but also through finer-scale ecological linkages among coexisting organisms within their niches.

Although the functional turnover across latitude was relatively low for deeper depth strata, the intercept, (i.e., the expected functional dissimilarity among fishes within a given cell), was higher for deeper depth strata than for shallow depth strata. We found that whilst the deeper communities were species poor, the repetition of co-occurring fishes from orders such as Anguilliformes (eels) and Gadiformes (rattails) was relatively common. We suggest that for communities containing only a handful of species, the high values of MNND may be driven by the co-occurrence of relatively ubiquitous species (from Anguilliformes and Gadiformes) and rarer, infrequent, functionally different species from a different order (for example*, Ruvettus pretiosus* order Scombriformes) in different latitudes. The MNND metric will be sensitive to the occurrence of such combinations of species. This result should be interpreted cautiously, however, as this pattern could be explained by low sampling effort and may dissolve under more intense effort.

Functionally distinct sections of the ocean are regions that hold many species that have functionally distinct traits, such as the tropical eastern Pacific Ocean (Grenié *et al.* 2018). A key question in this study was whether the observed functional beta diversity at a given depth was higher or lower than expected given a random draw of the broader species list (at a given depth) under a null model of random species assembly within a given depth stratum. We found that southern latitudes generally had lower-than-expected functional distinctness, particularly AUC and KKA in shallow (50–100 m) depths (Fig. 4.3A, B). This may indicate that the environmental filtering of traits in a homogeneous habitat (as shown in Smith & Wilson 2002), and consistent, stable environmental conditions has led to convergent functional communities (Swenson *et al.* 2012; Siefert *et al.* 2013; Pinto-Ledezma, Larkin & Cavender-Bares 2018). We found no depth-by-latitude cells with higher than expected functional distinctness, although communities at northern latitudes (KER, GBI) were generally more functionally distinct than southern latitudes (AUC, KKA). This may be tied to higher species richness in these locations, and a greater diversity of habitats as well as greater variability in marine environmental conditions in northern *versus* southern areas of New Zealand (Shears *et al.* 2008; Zintzen *et al.* 2012; Zintzen *et al.* 2017).

We found that functional turnover was stronger along the depth than along the latitude gradient – similar to patterns found in taxonomic diversity (Zintzen *et al.* 2017) – but that the functional bioregions were delineated by a combination of both of these major spatial gradients. The largest group of depth-by-latitude cells was a large cluster spanning intermediate and deep depths across the full length of the latitudinal gradient investigated here (group v; Fig. 4.5A), indicating that the ecological strategies associated with the food acquisition and locomotion traits of fishes in this bioregion were largely homogeneous at these depths. A similar large spatial cluster was also found when using phylogenetic diversity metrics for the same community dataset (see Eme *et al.* 2020). Conversely, functional bioregions in shallower depths were partitioned into 3 different groups according to latitude (groups i-iii; Fig. 4.5A). Knowledge of functional distinctiveness, turnover and bioregions can be used along with taxonomic and phylogenetic measures of diversity (e.g., Eme *et al.* 2020) to help designate areas of marine protection to help ensure that the greatest amount of regional biodiversity is protected, rather than duplicating functionally similar patches of high diversity (Stuart-Smith *et al.* 2013). Knowledge of where functional bioregion boundaries are located, and the transition zones between them may be ideal places to monitor to detect future change in response to anthropogenic change.

The turnover in morphology along the depth gradient to a body shape that was functionally convergent across latitude suggests that environmental filtering is a force of selection acting on individuals’ traits. The transition from a deeper-bodied morphology with a rounded or forked tail in shallower depths, to an elongate body shape with a tapering tail at deeper depths has been found by Neat and Campbell (2013) and Myers *et al.* (2019). This pattern, taken with the plateau of functional turnover in the deep (Fig. 4.1) suggests that the environmental filtering of traits in the deep sea is a key process structuring this community. Convergence of the elongate anguilliform body shape across multiple different orders (e.g., Ophidiiformes, Gadiformes, Notocanthiformes, and Aulopiformes) also indicates that this body shape has led to success in the deep sea. This widespread body form may also contribute to the low levels of functional turnover in the deep sea, potentially fulfilling the same function across large swathes of the study design.

Our study has provided novel insights into how functional beta diversity varies along large-scale environmental gradients. We consider future studies should examine other traits that may be responsible for similarly convergent or divergent patterns in the functional structure of the community, such as key life-history, physiological, and behavioural traits (Bellwood *et al.* 2019). Traits that can be used to detect species’ response to climate-related environmental change will be advantageous, such as size and growth rate, as well as key indicators of habitat use, such as thermal preference and water column position (McLean *et al.* 2019b). Furthermore, understanding how the turnover of functional traits covary with environmental variables (such as temperature, dissolved organic matter and particulate organic carbon) will yield additional insight into key mechanistic processes structuring functional communities (Wieczynski *et al.* 2019). Additionally, studying a greater depth range would help to model important trends of functional turnover *versus* depth. Finally, we emphasize that functional bioregion boundaries (and the species typifying each bioregion) may be constantly shifting under global-scale environmental change. Quantifying the temporal evolution of functional beta diversity will help to clarify the impacts of important future changes on ecosystem functioning (Pinto-Ledezma, Larkin & Cavender-Bares 2018; McLean *et al.* 2019b).

4.6 Conclusions

In the face of cumulative anthropogenic impacts such as climate change, overfishing, pollution and deep-sea mining, ensuring the future health of the deep ocean requires an understanding of current baseline conditions and rates of change in marine ecosystems (Danovaro *et al.* 2020). Here we have provided the first description of patterns of functional beta diversity for fishes along large-scale depth and latitude gradients in New Zealand waters, and have proposed functional bioregions for fishes based on these patterns. Representative sites from each functional bioregion, particularly from multiple areas of higher functional turnover (i.e., shallow-intermediate depths), should be prioritized for protection in order to ensure a variety of assemblages supporting many different functional traits will be conserved (Socolar *et al.* 2016). We have also proposed a “functional village hypothesis”, a natural extension of the “ecological village hypothesis” (Smith *et al.* 2014), and consider that the repetition of the same key functions making up a “village” (i.e., a community) may contribute to lower functional turnover in the deep sea. Overall, documenting the trends in large-scale patterns of functional beta diversity for marine fishes allows us to: 1) set-up baseline patterns to test for potential functional homogenization in the future that may be caused by global changes in marine ecosystems; 2) delineate biogeographic transition zones that could serve as regions to monitor for change; and 3) locate regions/depths containing key functional traits that may act as protected reservoirs of essential functions in order to maintain fundamental ecosystem processes.

4.7 Authors' Contributions

E.M.V.M., M.J.A., D.E., L.L., and C.D.R. conceived and designed the study. E.M.V.M. measured all of the traits from the stereo-BRUV footage and museum specimens. E.M.V.M, D.E. and M.J.A. analysed the data and produced the figures. E.M.V.M. drafted the initial manuscript and all authors contributed towards the interpretations of results, the initial drafting and the revisions of the final manuscript.

4.8 Supplementary Materials

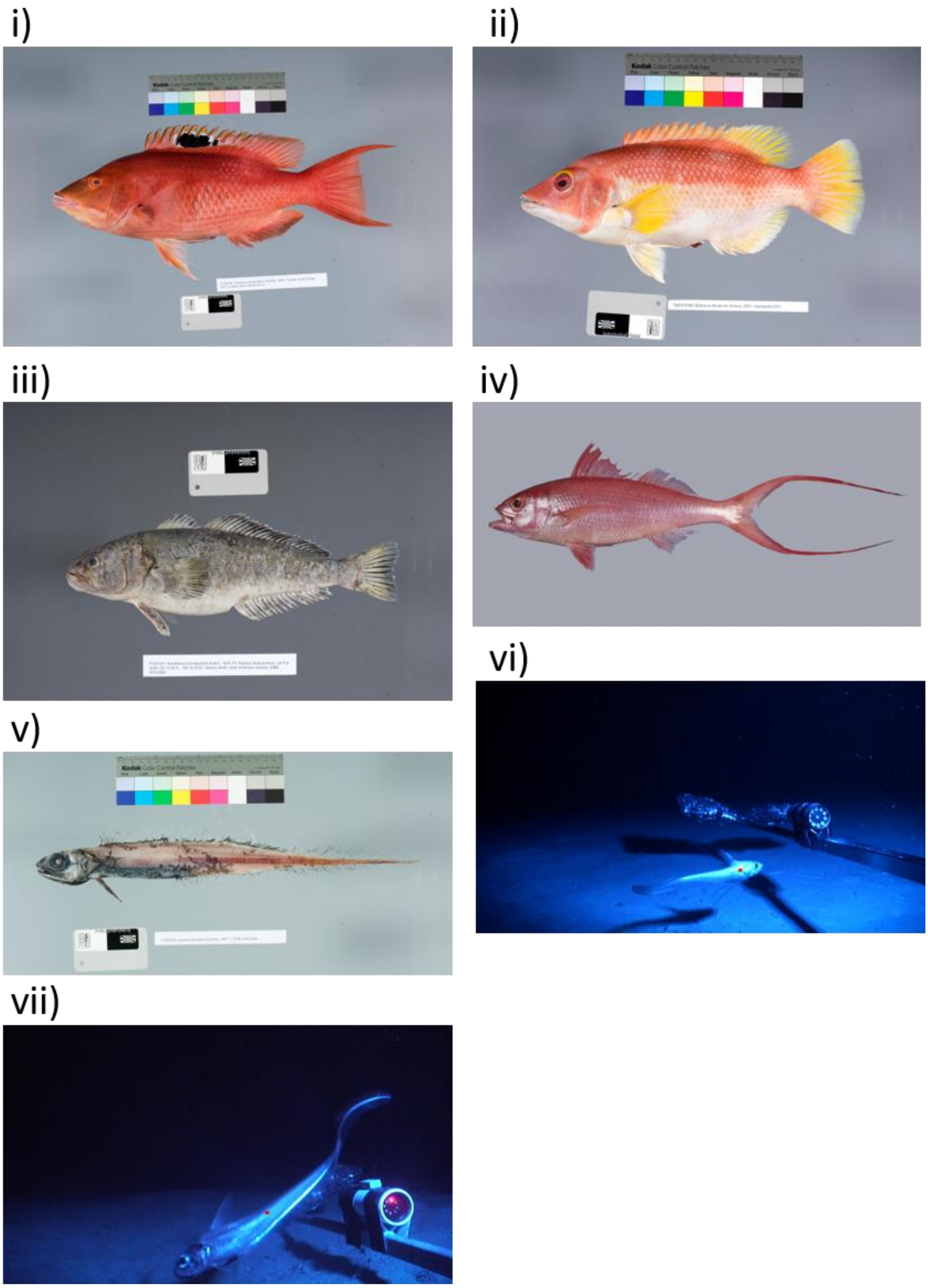


Figure S4.1. Photographic images of the species closest to the centroid (in 8-dimensional functional trait-space (i.e., the “typical” species morphology) for each functional bioregion (from Figs. 4.5-4.6). i) *Bodianus unimaculatus*, Labridae, ii) *Bodianus flavipinnis,* Labridae, iii) *Notothenia microlepidota,* Nototheniidae, iv) *Etelis coruscans,* Lutjanidae, v) *Lyconnus pinnatus,* Merluccidae, vi) *Coryphaenoides subserrulatus*, Macrouridae, vii) *Lepidorhynchus denticulatus,* Macrouridae.

Table S4.1. Functional traits derived from raw morphological length measurements of individual fishes (see Figure S3.1 in Chapter 3 for an illustration). *CFd* = caudal fin depth, *CPd* = caudal peduncle depth, *Ed* = maximum eye diameter, *Eh* = eye height, *Hd* = head depth, *Hl* = head length, *Lj* = lower jaw length, *mBd* = maximum body depth, *Mo* = mouth open, *PFb* = body depth at pectoral fin base, *PFi* = pectoral fin insertion, *TL* = total body length, *Uj* = upper jaw length. Traits adapted from Villéger *et al.* (2010) are identified by an asterisk; traits described by Myers *et al*. (2019).

	Functional Trait	**Calculation**	**Ecological relevance**
Universal trait	Total body length	*TL*	Proxy for overall body size; indicative of trophic level or relative food-web position
Food acquisition	Eye size*	*Ed / Hd*	Prey detection
	Oral gape position*	*Mo / Hd*	Feeding method in the water column
	Jaw length^	$\frac{1}{2}$ *(Uj + Lj) / Hl*	Proxy for size of oral gape; indicative of the size of potential prey
Locomotion	Elongation	*TL / mBd*	Indicative of overall body shape; greater elongation indicates steady swimming ability (Claverie & Wainwright 2014)
	Eye position*	*Eh / Hd*	Indicative of vertical position in the water column
	Caudal peduncle throttling*	*CFd / CPd*	Indicative of the efficiency of caudal propulsion; reduction of drag
	Pectoral fin position*	*PFi / PFb*	Indicative of manoeuvrability using pectoral fins

Table S4.2. Parameter estimates and statistical significance individual terms of the fitted linear models (lm) for the relationships between functional turnover in the morphology of fishes, measured as either MPFD or MNND, *vs* absolute differences in depth. A model selection is performed using AICc to choose the best model with either a linear term or a linear and quadratic term. The general relationship with absolute depth distance is modeled, with all latitudes pooled together. Non-significant *P*-values are in **bold** (at the alpha-level of *P* >0.01).

Metric	ModelType	Parameters	Estimate	Std. Error	t value	Pr(>|t|)
MPFD	lm	(Intercept)	3.24	0.11	29.74	0.00
		Depth.dist	0.00	0.00	3.21	0.00
		Depth.dist2	0.00	0.00	-1.91	**0.06**
MNND	lm	(Intercept)	1.53	0.09	17.77	0.00
		Depth.dist	0.00	0.00	7.31	0.00
		Depth.dist2	0.00	0.00	-4.54	0.00

Table S4.3. Parameter estimates and statistical significance individual terms of the fitted linear models (lm) for the relationships between functional turnover in the morphology of fishes, measured as either MPFD or MNND, *vs* absolute differences in depth. A model selection is performed using AICc to choose the best model for each individual curve fitted by latitude with a linear term or a linear and quadratic term. Non-significant *P*-values are in **bold** (at the alpha-level of *P* >0.01).

Metric	ModelType	Location	Parameters	Estimate	Std. Error	t value	Pr(>|t|)
MPFD	lm	KER/29	(Intercept)	3.65	0.11	34.21	0.00
			Depth.dist	0.00	0.00	3.74	0.00
		TKI/34	(Intercept)	3.30	0.14	24.17	0.00
			Depth.dist	0.00	0.00	3.44	0.00
		GBI/36	(Intercept)	3.48	0.27	13.13	0.00
			Depth.dist	0.00	0.00	2.22	**0.04**
			Depth.dist2	0.00	0.00	-2.11	**0.05**
		WI/37	(Intercept)	3.55	0.15	23.63	0.00
			Depth.dist	0.00	0.00	2.22	**0.04**
		KKA/42	(Intercept)	3.17	0.10	30.43	0.00
			Depth.dist	0.00	0.00	2.87	0.01
			Depth.dist2	0.00	0.00	-1.70	**0.11**
		OTA/46	(Intercept)	3.32	0.08	40.70	0.00
			Depth.dist	0.00	0.00	2.45	**0.02**
		AUC/51	(Intercept)	2.20	0.31	6.98	0.00
			Depth.dist	0.00	0.00	2.62	**0.02**
			Depth.dist2	0.00	0.00	-1.97	**0.07**
MNND	lm	KER/29	(Intercept)	1.51	0.14	10.73	0.00
			Depth.dist	0.00	0.00	6.16	0.00
			Depth.dist2	0.00	0.00	-4.16	0.00
		TKI/34	(Intercept)	1.43	0.20	7.17	0.00
			Depth.dist	0.00	0.00	3.83	0.00
			Depth.dist2	0.00	0.00	-2.54	**0.02**

		GBI/36	(Intercept)	1.62	0.15	10.51	0.00
			Depth.dist	0.00	0.00	4.44	0.00
			Depth.dist2	0.00	0.00	-3.58	0.00
		WI/37	(Intercept)	1.70	0.13	13.59	0.00
			Depth.dist	0.00	0.00	5.40	0.00
		KKA/42	(Intercept)	1.59	0.11	14.77	0.00
			Depth.dist	0.00	0.00	6.22	0.00
		OTA/46	(Intercept)	1.85	0.17	10.95	0.00
			Depth.dist	0.00	0.00	2.77	0.01
		AUC/51	(Intercept)	1.02	0.26	3.86	0.00
			Depth.dist	0.01	0.00	4.17	0.00
			Depth.dist2	0.00	0.00	-3.15	0.01

Table S4.4. Parameter estimates and statistical significance individual terms of the fitted linear models (lm) for the relationships between functional turnover in the morphology of fishes, measured as either MPFD or MNND, *vs* absolute differences in latitude. A model selection is performed using AICc to choose the best model with either a linear term or a linear and quadratic term. The general relationship with absolute latitude distance is modeled, with all depths pooled together. Non-significant *P*-values are in **bold** (at the alpha-level of *P* >0.01).

Metric	ModelType	Parameters	Estimate	Std. Error	t value	Pr(>|t|)
MPFD	lm	(Intercept)	3.52	0.06	57.48	0.00
		Lat.dist	0.00	0.01	-0.32	**0.75**
MNND	lm	(Intercept)	1.82	0.05	36.09	0.00
		Lat.dist	0.03	0.00	6.04	0.00

Table S4.5. Parameter estimates and statistical significance individual terms of the fitted linear models (lm) for the relationships between functional turnover in the morphology of fishes, measured as either MPFD or MNND, *vs* absolute differences in latitude. A model selection is performed using AICc to choose the best model for each individual curve fitted by depth with a linear term or a linear and quadratic term. Non-significant *P*-values are in **bold** (at the alpha-level of *P* >0.01).

Metric	ModelType	Depth	Parameters	Estimate	Std. Error	t value	Pr(>|t|)
MPFD	lm	50	(Intercept)	3.31	0.15	22.08	0.00
			Lat.dist	0.00	0.01	0.07	**0.95**
		100	(Intercept)	3.37	0.19	17.60	0.00
			Lat.dist	0.00	0.02	-0.06	**0.96**
		300	(Intercept)	3.28	0.14	23.13	0.00
			Lat.dist	0.00	0.01	0.35	**0.73**
		500	(Intercept)	3.76	0.16	23.86	0.00
			Lat.dist	-0.01	0.02	-0.56	**0.58**
		700	(Intercept)	3.71	0.15	24.24	0.00
			Lat.dist	0.00	0.01	-0.05	**0.96**
		900	(Intercept)	3.64	0.08	45.43	0.00
			Lat.dist	0.00	0.01	-0.51	**0.61**
		1200	(Intercept)	3.62	0.07	49.50	0.00
			Lat.dist	-0.01	0.01	-1.17	**0.28**
MNND	lm	50	(Intercept)	1.62	0.11	14.14	0.00
			Lat.dist	0.03	0.01	2.84	0.01
		100	(Intercept)	1.72	0.11	15.20	0.00
			Lat.dist	0.04	0.01	3.48	0.00
		300	(Intercept)	1.50	0.10	14.37	0.00
			Lat.dist	0.09	0.02	4.11	0.00
			Lat.dist2	0.00	0.00	-2.32	0.03
		500	(Intercept)	1.88	0.18	10.47	0.00
			Lat.dist	0.04	0.02	2.32	0.03

		700	(Intercept)	2.01	0.13	15.33	0.00
			Lat.dist	0.02	0.01	1.78	**0.09**
		900	(Intercept)	1.97	0.11	17.73	0.00
			Lat.dist	0.01	0.01	1.02	**0.32**
		1200	(Intercept)	1.97	0.08	25.33	0.00
			Lat.dist	0.00	0.01	0.33	**0.75**

Table S4.6. Museum voucher specimens of 144 New Zealand actinopterygian fish species examined. For each species there was between 1 – 4 individuals measured. See Roberts, Stewart and Struthers (2015) for details of classification, nomenclature, distribution, and biology of each species. Specimens listed in phylogenetic order, followed by unique collection registration number. Prefix: AK and MA – Tāmaki Paenga Hira Auckland War Memorial Museum, The Domain, Parnell, Auckland; P – National Fish Collection, Museum of New Zealand Te Papa Tongarewa, 169 Tory Street, Wellington.

Order	**FAMILY**	***Genus Species***	**Reg. no**
Notacanthiformes	HALOSAURIDAE	*Halosaurus pectoralis*	MA4287
		Halosaurus pectoralis	P.047357
		Halosaurus pectoralis	P.047099
	NOTACANTHIDAE	*Notacanthus sexspinis*	P.042185
		Notacanthus sexspinis	P.046667
Anguilliformes	CONGRIDAE	*Gorgasia japonica*	P.035166
		Bassanago bulbiceps	P.044020
		Bassanago bulbiceps	P.044371
		Conger verreauxi	AK135203
		Conger verreauxi	MA045555
		Conger verreauxi	P.045555
	MURAENIDAE	*Gymnothorax berndti*	P.034433
		Gymnothorax nubilus	AK655313
		Gymnothorax nubilus	P.037121
		Gymnothorax nubilus	P.052124
		Gymnothorax nubilus	P.044274
		Gymnothorax porphyreus	AK655399
		Gymnothorax porphyreus	P.044115
		Gymnothorax porphyreus	P.044077
		Gymnothorax porphyreus	P.044079
		Gymnothorax prasinus	P.044073
		Gymnothorax prasinus	P.044242
		Gymnothorax prionodon	P.004867
	OPHICHTHIDAE	*Ophisurus serpens*	AK118
		Ophisurus serpens	MA046347
		Scolecenchelys castlei	P.044497
		Scolecenchelys castlei	P.044495
	SYNAPHOBRANCHIDAE	*Diastobranchus capensis*	P.044025
		Diastobranchus capensis	P.044259
		Simenchelys parasitica	P.044094
		Simenchelys parasitica	MA180057
		Synaphobranchus affinis	P.044083
		Synaphobranchus affinis	P.044016
Argentiniformes	ALEPOCEPHALIDAE	*Alepocephalus australis*	P.046858
		Alepocephalus australis	P.047640
Stomiiformes	CHAULIODONTIDAE	*Chauliodus sloani*	P.042448
		Chauliodus sloani	P.023804

Aulopiformes	IPNOPIDAE	*Bathypterois longifilis*	P.042010
		Bathypterois longifilis	P.054527
	NOTOSUDIDAE	*Scopelosaurus hamiltoni*	P.046766
		Scopelosaurus hamiltoni	P.051901
	PARAULOPIDAE	*Paraulopus nigripinnis*	P.042473
		Paraulopus nigripinnis	P.047687
		Paraulopus okamurai	P.054938
		Paraulopus okamurai	P.051928
Polymixiiformes	POLYMIXIIDAE	*Polymixia cf. busakhini*	P.056079
		Polymixia cf. busakhini	P.056136
Ophidiiformes	OPHIDIIDAE	*Brotulotaenia nigra*	P.045943
		Brotulotaenia nigra	P.046587
		Genypterus blacodes	P.044057
		Genypterus blacodes	P.044035
Gadiformes	BATHYGADIDAE	*Bathygadus cottoides*	P.054706
		Bathygadus cottoides	P.044249
		Gadomus aoteanus	P.023310
		Gadomus aoteanus	P.047085
	MACROURIDAE	*Coelorinchus acanthiger*	P.038935
		Coelorinchus acanthiger	P.046391
		Coelorinchus aspercephalus	P.005256
		Coelorinchus aspercephalus	P.006670
		Coelorinchus biclinozonalis	P.034780
		Coelorinchus biclinozonalis	P.012997
		Coelorinchus bollonsi	P.023348
		Coelorinchus bollonsi	P.046061
		Coelorinchus fasciatus	P.023370
		Coelorinchus fasciatus	P.023372
		Coelorinchus innotabilis	P.023565
		Coelorinchus innotabilis	P.008124
		Coelorinchus kermadecus	P.038988
		Coelorinchus kermadecus	P.034014
		Coelorinchus mycterismus	P.039350
		Coelorinchus mycterismus	P.047507
		Coelorinchus mystax	P.039439
		Coelorinchus mystax	P.056089
		Coelorinchus oliverianus	P.023538
		Coelorinchus oliverianus	P.023539
		Coryphaenoides murrayi	P.046951
		Coryphaenoides murrayi	P.046941
		Coryphaenoides rudis	P.039706
		Coryphaenoides rudis	P.042706
		Coryphaenoides serrulatus	P.037130
		Coryphaenoides serrulatus	P.034596
		Coryphaenoides subserrulatus	P.021692
		Coryphaenoides subserrulatus	P.011309

		Lepidorhynchus denticulatus	P.025859
		Lepidorhynchus denticulatus	P.003549
		Lucigadus nigromaculatus	P.039606
		Lucigadus nigromaculatus	P.044565
		Macrourus carinatus	P.026961
		Macrourus carinatus	P.047145
		Malacocephalus laevis	P.034757
		Malacocephalus laevis	P.039297
		Nezumia nsp	P.034712
		Nezumia nsp	P.058241
	TRACHYRINCIDAE	*Trachyrincus aphyodes*	P.049413
		Trachyrincus aphyodes	P.014862
		Trachyrincus longirostris	P.030155
		Trachyrincus longirostris	P.047595
	MERLUCCIIDAE	*Lyconus pinnatus*	P.053343
		Lyconus pinnatus	P.045512
		Macruronus novaezelandiae	P.052479
		Macruronus novaezelandiae	P.054712
	MORIDAE	*Antimora rostrata*	P.047831
		Antimora rostrata	P.047832
		Laemonema robustum	P.044032
		Laemonema robustum	P.047299
		Lepidion microcephalus	P.047098
		Lepidion microcephalus	P.046760
		Lepidion schmidti	P.042216
		Lepidion schmidti	P.058051
		Mora moro	P.042435
		Mora moro	P.052244
		Notophycis marginata	P.023561
		Notophycis marginata	P.047618
		Pseudophycis bachus	P.049678
		Pseudophycis bachus	P.047709
		Pseudophycis barbata	P.052745
		Pseudophycis barbata	P.052585
		Tripterophycis gilchristi	P.044506
		Tripterophycis gilchristi	P.046600
	MURAENOLEPIDIDAE	*Muraenolepis orangiensis*	P.032946
		Muraenolepis orangiensis	P.045213
Beryciformes	BERYCIDAE	*Beryx decadactylus*	P.033364
		Beryx decadactylus	P.044340
		Beryx splendens	P.054054
		Beryx splendens	P.031766
		Centroberyx affinis	P.050476
		Centroberyx affinis	P.057370
	TRACHICHTHYIDAE	*Hoplostethus atlanticus*	P.041334
		Hoplostethus atlanticus	P.030202

		Hoplostethus mediterraneus	P.046055
		Hoplostethus mediterraneus	P.044529
Zeiformes	CYTTIDAE	*Cyttus novaezealandiae*	P.052391
		Cyttus novaezealandiae	P.034978
	MACRORAMPHOSIDAE	*Centriscops humerosus*	P.039438
		Centriscops humerosus	P.051937
	OREOSOMATIDAE	*Allocyttus niger*	P.053972
		Allocyttus niger	P.047035
		Oreosoma atlanticum	P.032973
		Oreosoma atlanticum	P.021264
	ZEIDAE	*Zeus faber*	P.044254
		Zeus faber	P.058529
	ZENIONTIDAE	*Capromimus abbreviatus*	P.042055
		Capromimus abbreviatus	P.032657
		Zenion sp	P.052317
		Zenion sp	P.046323
		Zenion sp	P.045238
Scorpaeniformes	PSYCHROLUTIDAE	*Psychrolutes microporos*	P.037011
		Psychrolutes microporos	P.044612
	SCORPAENIDAE	*Scorpaena cardinalis*	P.037092
		Scorpaena cardinalis	P.050229
		Scorpaena papillosa	P.048324
		Scorpaena papillosa	P.044467
	SEBASTIDAE	*Helicolenus barathri*	P.047352
		Helicolenus barathri	P.046482
		Helicolenus percoides	P.047376
		Helicolenus percoides	P.047388
	TRIGLIDAE	*Chelidonichthys kumu*	P.046491
		Chelidonichthys kumu	P.002812
		Pterygotrigla andertoni	P.046349
		Pterygotrigla andertoni	P.057368
Perciformes	ARRIPIDAE	*Arripis xylabion*	P.051988
		Arripis xylabion	P.052233
	CALLANTHIIDAE	*Callanthias australis*	P.039226
		Callanthias australis	P.046485
	CARANGIDAE	*Pseudocaranx georgianus*	P.045523
		Pseudocaranx georgianus	MA053942
		Seriola lalandi	P.044121
		Seriola lalandi	P.051966
		Seriola rivoliana	P.045522
		Seriola rivoliana	P.038264
	CENTROLOPHIDAE	*Hyperoglyphe antarctica*	P.054908
		Hyperoglyphe antarctica	P.037102
		Seriolella brama	P.003996
		Seriolella brama	P.045161
	CEPOLIDAE	*Cepola haastii*	P.053890

	Cepola haastii	P.042235
CHAETODONTIDAE	*Amphichaetodon howensis*	P.050218
	Amphichaetodon howensis	P.050513
CHEILODACTYLIDAE	*Cheilodactylus francisi*	P.041671
	Cheilodactylus francisi	P.017846
	Cheilodactylus spectabilis	P.048640
	Cheilodactylus spectabilis	P.057354
	Nemadactylus douglasii	P.046502
	Nemadactylus douglasii	P.044275
	Nemadactylus macropterus	P.037127
	Nemadactylus macropterus	P.044276
	Nemadactylus nsp	P.046489
	Nemadactylus nsp	P.046488
ECHENEIDAE	*Echeneis naucrates*	P.037943
	Echeneis naucrates	P.056993
GEMPYLIDAE	*Rexea solandri*	P.039338
	Rexea solandri	P.037665
	Ruvettus pretiosus	P.024449
	Ruvettus pretiosus	P.005343
	Thyrsites atun	P.046811
	Thyrsites atun	P.048504
GIRELLIDAE	*Girella cyanea*	P.050060
	Girella cyanea	P.056095
LABRIDAE	*Bodianus flavipinnis*	P.054009
	Bodianus flavipinnis	P.042465
	Bodianus unimaculatus	P.052742
	Bodianus unimaculatus	MA31305
	Coris picta	P.004809
	Coris picta	MA6377
	Coris sandeyeri	P.049928
	Coris sandeyeri	MA655759
	Notolabrus cinctus	P.047827
	Notolabrus cinctus	MA7307
	Notolabrus fucicola	P.053862
	Notolabrus fucicola	MA7313
	Notolabrus inscriptus	P.050183
	Notolabrus inscriptus	MA1168
	Pseudolabrus luculentus	P.049891
	Pseudolabrus luculentus	MA211270
	Pseudolabrus miles	P.046497
	Pseudolabrus miles	MA4372
	Suezichthys arquatus	P.050188
	Suezichthys arquatus	MA655308
	Suezichthys aylingi	P.053897
	Suezichthys aylingi	MA655905
LATRIDAE	*Latridopsis ciliaris*	P.032933

	Latridopsis ciliaris	P.032866
	Latridopsis forsteri	P.032932
	Latridopsis forsteri	P.032809
	Latris lineata	P.053323
	Latris lineata	P.053303
LUTJANIDAE	*Etelis coruscans*	P.034455
	Etelis coruscans	P.058272
MULLIDAE	*Parupeneus spilurus*	P.050266
	Parupeneus spilurus	P.041289
	Upeneichthys porosus	P.057407
	Upeneichthys porosus	P.057384
NOTOTHENIIDAE	*Notothenia angustata*	P.053299
	Notothenia angustata	P.053301
	Notothenia microlepidota	P.047327
	Notothenia microlepidota	P.053738
PINGUIPEDIDAE	*Parapercis binivirgata*	P.045603
	Parapercis binivirgata	P.045606
	Parapercis colias	P.046566
	Parapercis colias	P.055213
	Parapercis gilliesii	P.052402
	Parapercis gilliesii	P.045156
POLYPRIONIDAE	*Polyprion americanus*	P.056097
	Polyprion americanus	P.039477
	Polyprion oxygeneios	P.053547
	Polyprion oxygeneios	P.050479
POMACENTRIDAE	*Chromis abyssicola*	P.046274
	Chromis abyssicola	MA180391
	Chromis dispila	P.050125
	Chromis dispila	MA655437
GRAMMISTIDAE	*Aulacocephalus temminckii*	P.050123
	Aulacocephalus temminckii	P.049837
SERRANIDAE	*Caesioperca lepidoptera*	P.048552
	Caesioperca lepidoptera	MA7300
	Caprodon longimanus	P.052743
	Caprodon longimanus	MA774
	Epinephelus daemelii	P.046364
	Epinephelus daemelii	MA1389
	Hypoplectrodes spB	P.052735
	Hypoplectrodes spB	MA655928
	Lepidoperca inornata	P.052506
	Lepidoperca inornata	P.047740
	Lepidoperca inornata	P.049653
	Plectranthias bilaticlavia	P.038143
	Plectranthias bilaticlavia	P.020264
	Plectranthias maculicauda	P.053099
	Plectranthias maculicauda	MA2495

SPARIDAE	*Chrysophrys auratus*	P.048499
	Chrysophrys auratus	P.053537
TRICHIURIDAE	*Lepidopus caudatus*	P.039460
	Lepidopus caudatus	P.060720
TRIPTERYGIIDAE	*Forsterygion flavonigrum*	P.053907
	Forsterygion flavonigrum	P.053709
	Forsterygion maryannae	P.028344
	Forsterygion maryannae	P.055230
	Matanui profundum	P.052462
	Matanui profundum	P.052463
ZOARCIDAE	*Melanostigma gelatinosum*	P.046973
	Melanostigma gelatinosum	P.046779
DIODONTIDAE	*Allomycterus pilatus*	P.039274
	Allomycterus pilatus	P.035109
MONACANTHIDAE	*Meuschenia scaber*	P.054644
	Meuschenia scaber	P.046547
	Thamnaconus analis	P.050301
	Thamnaconus analis	P.049895
TETRAODONTIDAE	*Canthigaster callisterna*	P.040694
	Canthigaster callisterna	P.036663
	Lagocephalus cheesemanii	P.057045
	Lagocephalus cheesemanii	P.026922
	Torquigener altipinnis	P.052229
	Torquigener altipinnis	P.052245

4.9 DRC16 Statement of Contribution

5 General Discussion

It is widely accepted that biodiversity loss has a negative impact on humanity (Cardinale *et al.* 2012). What is less understood, however, is the extent to which the magnitude of those negative impacts are mediated by the functional traits of organisms, or how those traits may be linked to important global ecosystem services such as the provision of carbon storage, pollination, or biomass for human nutrition (Ellison *et al.* 2005; Luck *et al.* 2009; Villeger *et al.* 2017). The field of functional diversity has become a cornerstone of community ecology, by providing an estimation of what organisms do in their ecosystems, and how that relates to ecosystem functioning (Tilman 2001; Petchey & Gaston 2006). The recent development of large global trait datasets made publicly available such as “TRY”, “Coral Trait Database”, and “AmphiBIO” have helped fuel research into global patterns of functional diversity along large-scale environmental gradients for many taxa such as plants, corals, and amphibians (Kattge *et al.* 2011; Madin *et al.* 2016; Oliveira *et al.* 2017).

This thesis aimed to add to this body of knowledge by providing the first integrated analysis of how functional biodiversity changes along large-scale depth and latitude gradients for New Zealand’s marine fishes. Specifically, this work characterised variation in the traits of fishes at broad spatial scales, investigated the relative importance of environmental *versus* biotic drivers in shaping the functional space of deep-sea communities, and analysed the spatial turnover of functional traits. Building on previous work on marine fishes (Halpern & Floeter 2008; Villéger *et al.* 2010; Mouillot *et al.* 2013b; Stuart-Smith *et al.* 2013; Brandl & Bellwood 2014; Claverie & Wainwright 2014; D’agata *et al.* 2014;

Mouillot *et al.* 2014; Wiedmann *et al.* 2014; Coleman *et al.* 2015; Sunday *et al.* 2015; Brandl *et al.* 2016; Farré *et al.* 2016; Leitao *et al.* 2016; Mindel *et al.* 2016a; Mindel *et al.* 2016b; Kumar *et al.* 2017; Villeger *et al.* 2017; Grenié *et al.* 2018; Hemingson & Bellwood 2018; Hodge *et al.* 2018; Bellwood *et al.* 2019; McLean *et al.* 2019a; McLean *et al.* 2019b; Ladds *et al.* 2020), this thesis found that functional traits varied more strongly with depth than with latitude, and that morphology and associated biotic interactions reflected adaptations to life in a resource-poor environment.

Chapter Two quantified variation in several key morphological traits of fishes along broad-scale depth and latitude gradients, finding that with increasing depth, fish morphology shifted towards body shapes that enable energy-efficient undulatory swimming styles and increased jaw-length *versus* mouth width to aid opportunistic feeding, furthering understanding of fish ecology and the environmental drivers of morphological adaptations in the deep sea. Chapters Three and Four quantified functional alpha and beta diversity, respectively. Chapter Three used a number of different functional metrics to quantify the type of change occurring in the functional space with increasingly harsh environmental conditions and differentiated between underlying models of community assembly driving functional variation. I found that functional alpha diversity was unexpectedly high in deep-sea communities and decreased with increasing latitude. Chapter Four examined turnover in functional trait-space, finding that communities generally became more functionally homogenous with increasing depth. I surmise that environmental filtering may be the primary driver of broad-scale patterns of functional beta diversity into the deep sea, but that competition, both within and among species, also shapes multi-dimensional functional space for fishes at local (alpha-diversity) scales.

This thesis provides the first analysis of functional biodiversity along broad-scale depth and latitude gradients for fishes in New Zealand, extending the knowledge of global fish-trait relationships to the climatic extremes of understudied southern high-latitude regions, and the environmental extremes of the deep ocean. Much of the previous work on fishes in the deep sea have used trawl data, and have been located in the northern hemisphere (Neat & Campbell 2013; Farré *et al.* 2016; Mindel *et al.* 2016a; Mindel *et al.* 2016b; Kumar *et al.* 2017). Studies of functional diversity in shallow marine and freshwater environments have been more prevalent, and many methods developed in these systems have aided the work described in this thesis (Gatz 1979; Winemiller 1991; Villéger *et al.* 2010). Studies in shallow-water environments have investigated how environmental drivers can drive morphological adaptations (Bridge *et al.* 2016; Bejarano *et al.* 2017), how communities respond to management changes such as marine protected areas (Coleman *et al.* 2015), how to use trait-based analyses to predict future responses to climate change (Teixidó *et al.* 2018; McLean *et al.* 2019b), and document how evolutionary trade-offs are mediated by ecology (Hodge *et al.* 2018). This work adds to these findings by providing the first description of how the functional alpha- and beta-diversity of fishes changes with depth and latitude in New Zealand.

5.1 Future trajectory of the deep sea

The deep sea is facing unprecedented changes due to the cumulative impacts of pollution, overfishing, proposed deep-sea mining, and perhaps most pressing, climate change (Levin & Le Bris 2015; Rogers 2015; Danovaro *et al.* 2017). The interconnectivity between the productive surface waters and the deep sea means that climate-related changes to primary productivity (e.g., reduced abundance of phytoplankton, Hoegh-Guldberg & Bruno 2010), threaten food supply to the deep sea (Rogers 2015; Danovaro *et al.* 2017). Reduced food supply and altered food webs may lead to lower growth rates in the animals that humans rely upon for consumption (Danovaro *et al.* 2017), namely fishes, crustaceans, and cephalopods. Fishing has become increasingly common beyond the continental shelf (Morato *et al.* 2006; Levin, Kark & Danovaro 2018), with the deep sea providing a larger and larger proportion of the global catch. Fishing gear and plastic waste can now be found in benthic and pelagic deep-sea habitats, transported *via* downwelling currents and adhesion to sinking particles (Cózar *et al.* 2014; Choy *et al.* 2019; Pierdomenico, Casalbore & Chiocci 2019). The transport of microplastics to the ocean floor *via* adhesion to sinking organic matter is particularly concerning, as is its uptake by copepods and meso-pelagic fishes, and the associated bioaccumulation and assignation into the food chain (Davison & Asch 2011; Cózar *et al.* 2014; Ory *et al.* 2017). Some studies suggest that the total amount of plastic in the ocean is vastly underestimated, due to the suspended layer of sinking plastic particles between the surface and the sea floor not being accounted for in global models (Cózar *et al.* 2014). In addition to these impacts, disturbances from proposed deep-sea mining activities include habitat loss, organism removal and sedimentation, which combine to paint a bleak future for the organisms living in this understudied environment (Levin *et al.* 2016).

In most cases, the changes occurring as a result of cumulative (or synergistic) anthropogenic impacts are happening before researchers can document the distribution and ecology of the organisms living in the deep ocean (e.g., in the twilight zone; Martin *et al.* 2020). Studying the functional traits of animals provides a means to understanding how communities may adapt to rapid environmental change and provides a starting point against which to measure future change.

5.2 Implications for management

In the face of rapid and unprecedented change to deep-sea environments, adaptive and relevant management policies are essential for the ongoing health of deep-sea ecosystems. This thesis primarily consisted of documenting new patterns of functional diversity for fishes along the understudied gradients of depth and latitude in New Zealand waters. The following findings from this thesis may aid in the management of the deep sea:

Chapter Two described the adaptive morphology of fishes, and how the changes in key traits may lead to certain advantages, such as an elongate body shape that enables energy-efficient locomotion, a large gape for opportunistic feeding in a low resource environment, and an eye size that enables greater vision in dimly lit environments. This work reiterates the findings of Neat and Campbell (2013) who documented the proliferation of elongated, eel-like fishes in the deep sea. This information can be used to determine how the distribution of fishes along large-scale gradients may be mediated by their body shape, and how that might influence the assembly of communities in the deep sea. Trait information such as body and gape size can also be used to understand deep-sea food web dynamics (e.g., Ladds *et al.* 2020) and contribute to the sustainable management of commercial fish stocks.

Whereas management practices in terrestrial systems attempt to conserve the ecological strategies of many different taxa, such as birds and mammals (Penone *et al.* 2016; Cooke, Eigenbrod & Bates 2019; Pigot *et al.* 2020), most deep-sea species lack even a description of their ecological strategies. **Chapter Three** provides a first step to documenting the range of ecological strategies for fishes associated with food acquisition and locomotion, and how they vary along depth and latitude. Preserving a range of ecological strategies may be essential under future environmental change to ensure continued ecosystem functionality and resilience (Cooke, Eigenbrod & Bates 2019).

By documenting the trends in the patterns of functional beta diversity along large-scale depth and latitude, **Chapter Four** 1) has provided baseline data for the turnover of functions against which to test for the functional homogenization of communities in response to global changes to marine ecosystems, 2) delineated biogeographic transition zones of functional bioregions that could serve as regions to monitor for functional change, and 3) identified bioregions containing key functional traits that may help to create a reservoir where key functions for ecosystem processes can be protected.

Overall, this thesis supports previous work advocating for the inclusion of multiple aspects of biodiversity in the management and conservation of marine ecosystems, with a focus on linking the ecology of the animals studied to the traditional taxonomic measures *via* their functional or morphological traits (Mouillot *et al.* 2013b; Stuart-Smith *et al.* 2013; Mouillot *et al.* 2014; Stuart-Smith *et al.* 2015; Mindel *et al.* 2016a; Bellwood *et al.* 2019).

5.3 Future directions

This thesis made significant contributions to the development of new traits which capture a wider range of the morphological variability of fishes in the deep sea. It also progressed the inclusion of intra-specific trait variability in the calculation of functional alpha and beta metrics, and developed methodology to capture *in situ* functional trait information using stereo-video footage. This work adds to the growing field of functional ecology, and the exciting sub-fields of intraspecific trait variability and functional beta diversity. Based on the findings here, I highlight several avenues for future research below.

This work has provided a snapshot of the functional biodiversity of fishes across a single spatial extent within a single timeframe. The video footage analysed for this project was collected between 2009 and 2012 (Zintzen *et al.* 2011; Zintzen *et al.* 2012), and repeating the study to check for temporal variation in functional composition could yield information that may prove imperative to understanding the response of deep-sea fishes to global changes. Additionally, a comparative study at another location with a similarly structured sampling design would aid in testing the generality of the findings in this thesis.

The present work has also provided an estimation of the functional diversity in benthic, demersal habitats, however, the ocean is intrinsically 3-dimensional, and there is a strong trophic link between benthic and pelagic realms (Levin, Kark & Danovaro 2018). The inclusion of functional trait information of fishes at multiple discrete positions throughout the water column would complement the findings of this study, and contribute to a more integrative, 3-dimensional approach to management of the marine environment. Studies such as The Ocean Twilight Zone project led by Woods Hole Oceanographic Institution aim to provide important discoveries about the twilight zone between 200 – 1000 m depth that interconnects the benthic and pelagic realms (Martin *et al.* 2020). The integration of spatial and temporal components of functional diversity across a range of habitat types will provide a more holistic understanding of how the functional composition of fishes changes across large-scale gradients.

The description here of the patterns of functional biodiversity for NZ’s marine fishes are based on presence-absence data, which gives equal weighting to all species. However, it is becoming increasingly evident that the inclusion of species abundance information is important for understanding functional diversity (Violle *et al.* 2017). This is because the abundance (or biomass) of a species may be directly proportional to its ecological effect (Grime 1998). Recent studies quantifying abundance-weighted measures of functional diversity have led to the discovery of novel functional hotspots (Stuart-Smith *et al.* 2013; Tolimieri *et al.* 2015), providing new regions on which to focus adaptive management strategies. I suggest that the approaches in Chapters Three and Four were effective for generating a broad-scale biogeographic classification of functional strategies. In order to achieve finer-scale classifications within bioregions and to further develop understanding of ecological processes, the inclusion of abundance data into future analyses could provide additional important insights.

Despite advances in the calculation of functional diversity across multiple groups of taxa (Cooke, Bates & Eigenbrod 2019; Cooke, Eigenbrod & Bates

2019; Martinez-Almoyna *et al.* 2019), it is generally commonplace to investigate patterns of functional diversity for a single group (Wilcox, Schwartz & Lowe 2018). Whilst fishes occupy a key position in the ocean ecosystem, a more integrative analysis of functional diversity across multiple taxa may provide additional insights into the underpinnings of ecosystem functionality. A recent paper by Degen *et al.* (2018) describes a “road map” for studying traits across multiple groups of benthic invertebrate taxa in the rapidly changing Arctic ecosystem. A potential avenue of future research could be to integrate the fishes and elasmobranch species (excluded from the current analysis) using a set of standardised traits, to provide additional multi-trophic information to understand functional diversity in the deep sea.

Our understanding of how communities are assembled is dependent on our capacity to understand rarity, both taxonomic and functional, including the processes behind it (Umaña *et al.* 2017; Violle *et al.* 2017; Enquist *et al.* 2019). Generally, communities are composed of a few numerically abundant species, and many rare species (de Bello *et al.* 2007). It is important, however, not to understate the impact of rarity in terms of both *species* and *functional traits.* The functional space of this study was heavily impacted by species with rare combinations of functional traits (i.e., functionally rare species). Moving forward, discovering the prevalence and ecological significance of functional rarity, including its impact on community assembly in the deep sea, will be essential to understand the susceptibility of key functions to species loss.

Trait choice is an essential component of the study of functional diversity, and here I have only described trends based on food acquisition and locomotion traits. The addition of behavioural and life history traits to analyses would provide a more holistic understanding of functional diversity in the deep sea. Traits can also be pleiotropic, having multiple functions, for example body length in fishes is considered to be a “universal” trait and can be attributed to multiple functions such as nutrient cycling (Allgeier *et al.* 2014) and bioerosion (Bonaldo, Hoey & Bellwood 2014). Therefore, the attribution of a given trait to a specific function may be arbitrary. In addition, a trait may only act as a proxy for a supposed function, when, in fact, there may be no direct way to link traits to functions (Bellwood *et al.* 2019). It is therefore important to consider this when choosing and measuring traits, and when interpreting results. It is also important to consider trait variation in light of behaviour and “ecological opportunism”, whereby a function can be modified by a fish’s behaviour, such as the switching between feeding modes in coral reef fishes (i.e., from browsing herbivory to planktivory) (Bellwood *et al.* 2019).

Finally, a natural extension of this study would be to consider the degree to which the traits measured are phylogenetically conserved. Calculating the phylogenetic signal of the traits studied will help to: 1) see how conserved or labile the traits are from an evolutionary perspective; 2) disentangle the effect of the environment on the functional traits not related to phylogenetic inertia; and 3) disentangle any correlation between the dominant clades in the deep sea and the ecological variables of interest (i.e., depth and latitude). Furthermore, comparing patterns of functional and phylogenetic diversity will combine to uncover key eco-evolutionary mechanisms underlying present-day patterns in the biodiversity of marine fishes.

5.4 Perspectives

The dataset generated during this thesis will be used into the future with collaborations between myself and my supervisory panel, however, there was significant progress made for two additional chapters/publications which were not included here. Firstly, we used the n-dimensional hypervolume approach developed by Blonder *et al.* (2018) to decompose functional beta diversity into turnover and nestedness components (see Villéger, Grenouillet & Brosse 2013) in much the same way as Baselga (2010; 2012) has demonstrated in a taxonomic framework. We put this forward as a clear way to understand if the functional space of shallow communities is nested inside deeper communities (or *vice versa)* or was mostly distinct. Also, we hope to uncover and articulate how much of the observed differences in functional space was driven by functional turnover, and what functions were nested or unique to the shallow and deep communities.

Secondly, we suggest that it would be beneficial to investigate the intraspecific trait variability of key fisheries species in New Zealand across both depth and latitude. The aim of this would be to see if a) fishing-related pressure has had any impact on the morphology of these species across the depth (and latitude) gradient, and b) whether there are any morphologically distinct groups *within* species inside the spatial extent of this study. Preliminary analyses suggest that there are distinct groupings, according to a depth-by-latitude interaction, for key species such as the snapper, Tāmure, (*Chrysophrys auratus*). Understanding the trait variation of individual target species along large spatial gradients, particularly in light of fishing pressure (both locally, and globally), may contribute to a more sustainable approach to the management of fish stocks.

Additionally, in collaboration with my supervisory panel, we intend to combine this functional trait database with a phylogeny of the community generated by Dr. David Eme (co-supervisor) to gain evolutionary perspectives on the traits we have measured. We will do this by: (i) making comparisons of functional bioregions derived in this thesis with the phylogenetic bioregions derived and described in Eme *et al.* (2020) including comparisons of phylo alpha and beta alongside functional alpha and beta; and (ii) mapping functional traits obtained in this thesis onto the most recent phylogeny for NZ fishes that has been developed to date (Eme *et al.* 2019).

This work should be compared to the findings from other studies along similar broad-scale environmental gradients in different ecosystems. There may well be different patterns and processes driving changes in functional diversity for fishes in other ecosystems, such as along depth or latitude gradients in freshwater lakes, or along an elevational gradient in montane streams. Researchers should put extra effort into standardising traits and uploading their data to publicly available global trait databases in order to overcome some of the issues caused by the grand scale, and cost of sampling the deep sea, and to facilitate additional temporal, habitat, abundance, and taxa information.

In summary, this thesis has characterised the patterns of functional biodiversity for New Zealand’s marine fishes along a broad-scale depth and latitude gradient. I found that the functional and morphological traits of fishes vary according to changes in environmental conditions, the availability of resources, and the competition both between and within species for those resources. Specifically, I found that, with increasing depth, the body shape of fishes tended toward a morphology that enabled energy-efficient locomotion and opportunistic feeding, reflecting the large distances travelled to find patchy and scarce resources. The individual traits of fishes are adaptive and reflect the aspects of the deep sea that make it a unique environment to study biodiversity: its huge spatial area/size, and the low-levels of food and light. Linked to these characteristics, biotic interactions such as competition both between and within species drives increases in community-level functional alpha diversity with increasing depth. The spatial turnover of food acquisition and locomotion traits is stronger along the depth gradient than latitude, with traits becoming functionally homogeneous at the deepest depths of the study.

Overall, I found that both intra- and interspecific competition shape the multi-dimensional functional space for fishes at local (alpha-diversity) scales, but that environmental filtering may be the primary driver of broad-scale patterns of functional beta diversity into the deep sea.

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