How functionally diverse are fish in the deep? A comparison of fish communities in deep and shallow-water systems

Victoria G. Carrington | Yvan Papa | Chelsey M. Beese | Jessica Hall | Raphaël Covain | Peter Horn | Monique A. Ladds | Alice Rogers

Abstract

Aim: Functional diversity metrics inform how species’ traits relate to ecosystem functions, useful for quantifying how exploitation and disturbance impact ecosystems. We compare the functional diversity of entire fish communities in a shallow-water region with a deep-sea region for further insight into the differences between these ecosystem types.

Location: The regions compared in this study were selected to represent a shallow-water coastal region, Tasman and Golden Bays (TBGB), and a deep-sea region, Chatham Rise (CR), in New Zealand.

Methods: Functional diversity was assessed using four metrics: functional richness, evenness, divergence and dispersion. We compared these metrics across four key functions: habitat use, feeding, locomotion and life history.

Results: Our results showed that overall, the shallow-water and deep-sea ecosystems had equal diversity. When focusing on the four ecological functions, the two ecosystems exhibited equal diversity metrics across most analyses. Of the significantly different results, the deep-sea had higher functional richness for habitat use and locomotion traits, lower functional dispersion for feeding and lower functional evenness for life history.

Main conclusions: Differences across the functions highlight higher diversity of habitat utilization by deep-sea fish, while lower diversity in feeding suggests deep-sea fish tend towards generalist diets, likely driven by low food availability. Deep-sea fish displayed an increased range of locomotive traits in our analyses, but this conflicts with existing evidence and warrants further study. Life-history results suggest deep-sea fish exhibit higher clustering of traits, indicating potential under-utilization of life-history strategies in the deep-sea. Our results demonstrate that although deep-sea fish communities have similar levels of diversity to shallow-water communities, the traits that structure this diversity differ, and therefore, the systems may respond to exploitation differently.

Keywords: categorical traits, deep-sea, diversity metrics, ecosystem functions, functional diversity, fuzzy coding, New Zealand, null models, trait analysis
1 | INTRODUCTION

Overfishing is a significant concern (Frank et al., 2016) as fisheries appear to be declining globally, suggesting a need for improved monitoring and management (Bell et al., 2017; Pauly & Zeller, 2016). The goal of fisheries management should be to preserve ecosystem functionality and biodiversity (Hammer et al., 1993). Despite this, the primary tool for fisheries management continues to be single-species stock assessments, focusing on target species of economic importance (Emmerson et al., 2015; Pikitch et al., 2004). In response, researchers are challenged to establish reliable assessments of ecosystem functioning to measure impacts of exploitation (Borja et al., 2008) for the preservation of ecosystems and their services (Heymans et al., 2011; Levin et al., 2009; Long et al., 2015; Pikitch et al., 2004). As the functional entities of marine ecosystems change in response to stress from natural and anthropogenic sources (Larsen et al., 2005; Mouillot et al., 2013; Muntadas et al., 2016; Suding et al., 2008), the impact of these stresses, and thus the health of marine ecosystems, has historically been determined by measuring their effects upon the taxonomic diversity of a system (Stuart-Smith et al., 2013). However, it has been shown that taxonomic diversity has limited connection with ecosystem functionality and is therefore not a comprehensive measure of ecosystem health or diversity (Borja et al., 2008; Cachera & Le Loc’h, 2017; Halpern & Floeter, 2008; Loiseau et al., 2017; Pereira et al., 2012; Sagouis et al., 2017; Stuart-Smith et al., 2013; Törnroos et al., 2015). Research is consequently shifting towards alternative methods of measuring ecosystem health. As ecosystems rely on a diverse range of species that occupy vital roles which allow the system to function (Villéger et al., 2017), quantifying the effect of disturbance on an ecosystem may be achieved through measuring functional trait diversity (Hewitt et al., 2014; McLean et al., 2019).

Functional diversity is crucial as it is linked to ecosystem efficiency as well as being a key driver of ecosystem functioning (Cadotte et al., 2011; Stuart-Smith et al., 2013; Villéger et al., 2008). Functional diversity is defined as the distribution of species within the functional space of a community, such that it is the diversity of functional trait combinations (Mouillot et al., 2013). Functional traits can predict the composition of an ecological community (Dolédec et al., 1999; McGill et al., 2006; Webb et al., 2010) and identify functional groups (Dumay et al., 2004; Luczkovich et al., 2002; Reecht et al., 2013). Functional diversity is, however, complex and challenging to measure (Petchey & Gaston, 2002b; Tilman, 2013). There are several multidimensional metrics available to describe different aspects of functional diversity which can be estimated using traits, such as functional richness or functional entropy (Laliberté & Legendre, 2010; Laliberté et al., 2015; Petchey & Gaston, 2002b; Villéger et al., 2008). Diversity metrics can be used to inform how species traits and abundance respond to environmental conditions and disturbance (Aguilar-Medrano & Arias-González, 2018; Bremner et al., 2003; Lavorel & Garnier, 2002). The impacts of exploitation on ecosystem function can be measured with functional diversity through changes in trait composition, such as shifts in size and age structure (Rago et al., 1998; Stevens et al., 2000; Walker & Heessen, 1996). Thus, functional diversity provides a useful tool for ecosystem management by detecting change at the community level (Lechêne et al., 2018).

Fishing has historically impacted shallow-water ecosystems more than the deep-water, but as technology continues to improve, the exploitation of the deep-sea is increasing (Morato et al., 2006). Deep-sea ecosystems are often described as stable, low-nutrient environments with limited potential for diversity (Costello & Chaudhary, 2017), and generally biodiversity decreases along a depth gradient (Mindel et al., 2016; Price et al., 1999; Zintzen et al., 2011), with the exception of infauna communities (Mindel et al., 2016; Sanders, 1968). However, some research has shown that deep-sea systems can contain complex, high-diversity communities (Danovaro, 2010; Danovaro et al., 2014; Levin et al., 2002). Deep-sea ecosystems may be more sensitive to biodiversity loss, as species are more vulnerable to overexploitation due to slower life histories (Cailliet & Andrews, 2008; Juan-Jorda et al., 2015), therefore requiring careful consideration in management.

Biodiversity loss is often associated with reductions in community functionality (Danovaro et al., 2008; Snelgrove, 1999), to the extent that random extinction of only a few species can drastically reduce the functional diversity of a community (Cadotte et al., 2011) and therefore ecosystem functioning. Not only would this have significant ecological repercussions, but it is likely to impact the economic value of fisheries (Costanza et al., 1997), with the potential to cause trophic cascades that unbalance the ecosystems upon which fisheries depend (Bellido et al., 2011; Ferretti et al., 2010; Hall et al., 2000; Stevens et al., 2000). To effectively manage deep-sea fish communities, we must understand how their functional diversity and composition compared to shallow-water ecosystems, and how these differences impact ecosystem functioning or responses to exploitation. Deep-sea fish communities have been assessed using a range of continuous morphometric traits (Aneesh Kumar et al., 2017; Mindel et al., 2016) and categorical traits (Farré et al., 2016; Muntadas et al., 2016) using a subset of species within these communities. However, to date, no direct comparison of the functional diversity of entire fish communities in separate shallow- and deep-sea ecosystems has been conducted.

This study assesses the differences in functional diversity between a shallow- and deep-water ecosystem using two well-studied and exploited fisheries regions, Tasman and Golden Bays (TBGB) and Chatham Rise (CR) in New Zealand. The teleost and chondrichthyan community in each region are compared, with totals of 60 species from TBGB and 210 from CR. To further our insight into differences in shallow- and deep-sea ecosystems, we compare the functional diversity across four trait functions: habitat use, feeding, locomotion and life history. By including all observed fish species, not just dominant, commercial species, we account for the diversity of bycatch species, which has been shown to alter diversity metrics by up to 46% at a regional scale (Nash et al., 2017). We directly compare the two regions using four metrics of functional diversity (i.e. functional richness, evenness, divergence and dispersion), each providing
insight into different facets of diversity. We test the significance of the difference between regions for each metric using randomization of the trait matrix to create null models. We use a fuzzy correspondence analysis (FCA) to project species and modalities in the same trait space, providing insights into differences in the functional composition between regions.

2 | METHODS

2.1 | Study regions and species

The regions compared in this study were selected to represent a shallow-water coastal region, Tasman Bay and Golden Bay (TBGB), and a deep-sea region, Chatham Rise (CR), in New Zealand (Figure 1). Tasman Bay (41°15′S, 173°17′E) and Golden Bay (40°40′S, 172°50′E) are located on the north-western coastline of the South Island, with a depth of 0 m to 70 m (Newcombe et al., 2015). Chatham Rise (42°30′S–44°46′S, 173°30′E–174°30′W) stretches roughly 1,100 km off the east coast of the South Island, with a depth ranging from 250 m to 1,500 m, with the exception of seamounts to the west and the Chatham Islands to the east (Bowden & Leduc, 2017). The aim was to compare entire ecosystems, and these regions were selected because both have been extensively sampled in bottom trawl surveys (Stevens et al., 2018; Stevenson & MacGibbon, 2015). Trawl surveys are carried out every two years in both regions by the Ministry for Primary Industries New Zealand (MPI) and are used to inform fisheries stock assessments and management advice (Stevens et al., 2013; Stevenson, 2012).

All fish species caught in the last five MPI trawl surveys in each region were included in the analysis (MacGibbon, 2019; MacGibbon & Stevenson, 2013; Stevens et al., 2013, 2014, 2015, 2017, 2018; Stevenson, 2012; Stevenson & MacGibbon, 2015, 2018). Trawls were carried out using similar gear and trawling procedures, with the survey area divided into a two-phase stratified randomized design following Francis (1984). The specifications for each trawl survey are provided in Appendix S1, such as trawl density, depth range, mesh size and tow distance. Owing to mesh size and trawling tactic, survey data primarily identify species directly relevant to pelagic fisheries, as it may not capture species that reside in complex, benthic habitats. The TBGB trawl surveys were carried out on R.V. Kaharoa (Stevenson & MacGibbon, 2015), and the CR trawl surveys were carried out on R.V. Tangaroa (Stevens et al., 2018). Species accumulation curves were used to calculate the percentage of observed species, relative to the estimated total number of species in the system, and these showed that both systems were sufficiently sampled, such that the majority (>75%) of species were observed (Appendix S2).

In total, 239 species were included in the dataset, 210 from CR and 60 from TBGB, with 31 species occurring in both regions (Appendix S3). Particular families or genera which include difficult to distinguish species with similar ecology were grouped together and treated as groups of confamilial or congeneric species (Appendix S3). It is important to note that species abundance within each system was only recorded as absence or presence (0 or 1) as accurate abundance data were not available for many species.

2.2 | Trait selection

Ten traits (Table 1) were selected to cover four underlying functions (habitat use, feeding, locomotion and life history), prioritizing those with direct ecological importance and ensuring that at least four traits represented each function (Pease et al., 2012) (Appendix S4 contains sources explaining the ecological function of traits). To avoid trait redundancy (Laughlin, 2014), a correlation matrix of all ten traits was used to check for strongly correlated pairs of traits by their occurrence. No strong correlations were observed (i.e. all weaker than ±0.5) (Appendix S5).

Data collection primarily relied on fish guides for New Zealand (Francis, 2001; McMillan et al., 2019; Patterson, 2016) and global fish guides (Froese & Pauly, 2019). Additional trait information came
from extensive literature searches for specific species (Appendix S6 provides data sources and corresponding traits) as well as photographs from the Ministry for Primary Industries (MPI) January 2018 Trawl Survey of Chatham Rise (Ladds et al., 2018; Stevens et al., 2018). There were missing data for a number of species, and in these situations traits were determined from literature or photographs (Ladds et al., 2018). For diet and schooling behaviour, where data from literature were unavailable, expert opinion was used (fisheries scientist P. Horn, NIWA). Finally, for maximum age, and relative age at maturity, unknown values for species were estimated using the average value of the most closely related species. The possibility of diverging trait values within taxonomic groups was not considered here.

Categorical trait modalities (Table 1) were based on those commonly used in similar functional trait studies (Boyle & Horn, 2006; Farré et al., 2016; Patterson, 2016). Continuous traits, such as maximum size and age at maturity, were collected in continuous form and then transformed into categorical traits by assigning them to classes (Table 1). Maximum size in its continuous form was measured using different methods (i.e. standard length, fork length and total length), assigning them to classes reduced the impact of this. The purpose of transforming maximum age and age at maturity, as opposed to keeping them in continuous form, was to reduce the impact of unknown trait values that were estimated with trait values of close relatives. Maximum body size values were assigned to five discrete classes ranging from < 20 cm (S1) to ≥ 160 cm (S5). Maximum age values were similarly categorized in six classes ranging from “very short-lived” (< 5 years, MA1) through to “very long-lived” (≥ 65 years (MA6)) (Table 1). Relative age at maturity values was calculated as the age at maturity divided by maximum age, with five modalities from fast-maturing at < 10% of lifespan (MT1) through to slow-maturing, > 40% of lifespan (MT5).

Diet modalities were assigned by the dietary components (Table 1). Modalities most commonly used in functional trait-based studies (Albouy et al., 2011; Brandl et al., 2016; Dewi et al., 2018; Henriques et al., 2017; Valls et al., 2017; Yeager et al., 2017) were modified to best suit the range of diets in this dataset. The classical method of categorizing diet, assigning species to discrete categories (herbivore, planktivore, omnivore, invertivore, piscivore and generalist), lacks precision when species fall into multiple categories. That method separates generalist species from categories they overlap with, therefore measures of similarities, used to calculate functional

| Trait | Function | Trait modalities |
|-------|----------|------------------|
| Body shape (BdSh) | Habitat use | Cylindrical (CYLI) |
| | Locomotion | Fusiform (FUSI) |
| | | Oval (OVAL) |
| Caudal fin shape (CFSh) | Locomotion | Heterocercal (HETE) |
| | Habitat use | Lanceolate (LANC) |
| | | Truncate (TRUN) |
| | | Absent (ABSE) |
| | | Lunate (LUNA) |
| Eye position (EPos) | Feeding | Top (TOP) |
| | Habitat use | Mid (MID) |
| | | Side (SIDE) |
| Gape position (GPos) | Feeding | Terminal (TERM) |
| | Habitat use | Subterminal (SUBT) |
| | | Inferior (INFE) |
| | | Hyperprotrusible (HYPE) |
| Schooling (Schl) | Feeding | Solitary (SOL) |
| | Life history | Facultative (FAC) |
| | Locomotion | Obligatory (OBL) |
| Vertical habitat (VPos) | Feeding | Pelagic (PELG) |
| | Habitat use | Benthopelagic (BNPL) |
| | | Benthic (BNTH) |
| Maximum body size (SzCl) | Feeding | < 20 cm (S1) |
| | Life history | 20–40 cm (S2) |
| | Locomotion | 40–80 cm (S3) |
| | | ≥ 160 cm (S5) |
| Diet (Diet) | Feeding | Plants/algae (HERB) |
| | Habitat use | Plankton (PLNK) |
| | | Detritus (DETR) |
| | | Invertebrates (INV) |
| Maximum age (MxAg) | Life history | < 5 years (MA1) |
| | 5–(20) years (MA2) |
| | 20–(35) years (MA3) |
| | ≥ 65 years (MA6) |
| Relative age at maturity (RMat) | Life history | < 10% lifespan (MT1) |
| | 10–20% lifespan (MT2) |
| | 20–30% lifespan (MT3) |
| | 30–40% lifespan (MT4) |
| | ≥ 40% lifespan (MT5) |

TABLE 1 Traits used for functional diversity metrics (Appendix S3 contains sources explaining ecological function)
diversity metrics, would fail to classify similarities in diets between species accurately. This was an important consideration for this species pool, where species labelled as “generalists” showed high diversity in prey items (from amphipods to marine mammals). Diet modalities were the prey items (e.g. benthic invertebrates), and species were assigned to multiple modalities if required; this method more accurately depicts the diversity and overlap of species’ diets.

2.3 | Fuzzy coding

Since species were assigned to multiple modalities, all data were crisp-coded following van Rijckevorsel (1987). This transformation converts a factorial table into a binary table with as many columns as modalities, grouped by traits, where each species (rows) either belongs in a modality (columns) (1) or not (0). The resulting table was 239 × 55, referred to as the species by traits crisp-coded matrix (Appendix S7). The crisp-coded matrix was further transformed using the prep.fuzzy.var function from the R package ade4 (Chessel et al., 2004; Dray & Dufour, 2007; Dray et al., 2007), converting it to a fuzzy-coded form, following Chevenet et al. (1994). This makes the sum of each row, per trait per species, equal to one (Appendix S7). The fuzzy-coded matrix was the basis for both functional diversity metrics computation and fuzzy correspondence analyses (FCA).

2.4 | Functional diversity metrics

A species functional niche can be considered as its position when plotted within the community’s functional trait space, which is defined as a multidimensional space where each one of the axes is a trait (Rosenfeld, 2002; Villéger et al., 2008). These axes can be obtained from a distance-based multivariate analysis like principal coordinates analysis (PCoA) (Laliberté & Legendre, 2010). A distance matrix was created from the species by traits fuzzy-coded data set using dist.ktab function from the R package ade4 (Dray & Dufour, 2007). The distance matrix was input into the dbFD function from the R package FD (Laliberté & Legendre, 2010; Laliberté et al., 2015).

**Table 2** Definitions of functional diversity metrics derived from the function dbFD from the R package FD (Laliberté & Legendre, 2010; Laliberté et al., 2015)

| Metric   | Definition                                                                 | Ecological Interpretation                                                                                                                                 |
|----------|---------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------|
| nbsp     | Number of species                                                         | The number of unique trait combinations in the dataset. Note that the dbFD function reports this value as sing.sp.                                               |
| FE       | Number of functional entities                                             | Percentage of species with overlapping trait combinations, highlighting potential niche overlap. High percentage of functional entities indicates low species overlap. |
| %FE      | Number of FE shown as a percentage of nbsp                               | Functional richness can be an indicator for used or unused niche space, however, is easily inflated by outlier species and, if dispersion and divergence are also low, may indicate the presence of outliers in the system (Schleuter et al., 2010). |
| FRic     | Functional richness; higher values suggest species occupy a higher volume within trait space | Functional richness indicates the location of species weighted by abundance, which in this case is absence or presence data, so is simply a measure of species location relative to the centroid; high divergence suggests outlier species dominant in the system (Lechêne et al., 2018). |
| qual.FRic| Quality of the reduced-space representation                              | Functional evenness is used as an indicator of under- or overutilization of resources (Mason et al., 2005) and, since it decreases with increasing clustering of species, can be used to compare levels of clustering in a system and therefore the propensity for dominant species to be functionally similar (Lechêne et al., 2018; Schleuter et al., 2010). Low functional evenness can be interpreted as high functional dominance, which has been linked to regional species coexistence by altering metacommunity dynamics (Hillebrand et al., 2008). |
| FDiv     | Functional divergence; higher values suggest higher abundance of species with extreme trait combinations | Functional divergence indicates the location of species weighted by abundance, which in this case is absence or presence data, so is simply a measure of species location relative to the centroid; high divergence suggests outlier species dominant in the system (Lechêne et al., 2018). |
| FDis     | Functional dispersion; higher values suggest species are further from the centroid of traits within trait space | Functional dispersion measures the spread and diversity of traits in a traditional sense, by indicating how centralized species are in trait space, high dispersion infers high spread and, therefore, diversity (Laliberté & Legendre, 2010; Lechêne et al., 2018). |
null models by randomization of the binary trait matrix (species by traits), adapted from Swenson (2014). We tested the significance of each observed difference between regions (diff(TBGB – CR)) for each diversity metric (FRic, FEve, FDiv, FDIs). The randomization procedure shuffled species names of the species by trait matrix. This method was chosen to avoid changes in trait co-variance and impossible trait combinations, while also keeping species richness at each site constant. Randomization was repeated 9,999 times, and the functional diversity metrics were calculated from the randomized trait matrix to create a simulated distribution of diff(TBGB – CR) for each metric, and the observed value was added to the vector of simulated values. The p-value was calculated as the number of the absolute value of simulated diff(TBGB – CR) values that were greater than the absolute value of the observed diff(TBGB – CR), divided by 10,000. The R-code for this entire process can be found in Appendix S8.

2.6 | Fuzzy correspondence analysis

A fuzzy correspondence analysis (FCA) (Chevenet et al., 1994) was performed on the fuzzy-coded trait data using the dudi.fca function from ade4 (Dray & Dufour, 2007). This method allowed us to visualize the projection of species and modalities in trait space, while the PCoA visualization from the dbFD package only allows projection of the species in a dummy trait or distance space.

FCA 1 included all ten traits and 55 modalities. Species were plotted on the first two F-axes for each region. The convex hull of the species coordinates for each region was plotted to visualize the differences between the two regions in terms of differences in functional volume and niches occupied within regions, done using the grDevices package in R (chull function) (R Core Team, 2019). The contributions of each modality to the axes were obtained using inertia.dudi function from ade4 (Dray & Dufour, 2007).

2.7 | Function-specific analyses

The functional diversity metrics and FCA analyses were then repeated on four subsets of traits specific to each underlying ecological function (habitat use, feeding, locomotion and life history), as defined in Table 1. FCA 2 used six traits focusing on habitat use (36 modalities), FCA 3 used six traits related to feeding (29 modalities), FCA 4 used four traits linked to locomotion (23 modalities), and FCA 5 used four traits associated with life history (19 modalities).

3 | RESULTS

3.1 | Functional diversity metrics

For most metrics and functions, the two systems display similar levels of diversity, with 80% of metrics having no significant difference between the two regions (Table 3). Of the significant differences, across the community functions, 10% of diversity metrics were higher in CR and 10% were higher in TBGB, indicating the deep-sea can be equally or more diverse than shallow-water systems (Table 3). These results also highlight how functional diversity metrics are influenced by the traits and functions considered.

Comparing the two systems using the full set of traits (Table 3) showed that CR and TBGB had no significant differences in any diversity metrics (FRic, FEve, FDiv and FDIs). However, TBGB has a greater percentage of species occupying unique trait combinations (%FE), despite CR having higher species richness.
TABLE 3  Functional diversity metrics for all analyses; with 60 species in Tasman Bay Golden Bay (TBGB) and 210 species for Chatham Rise (CR)

| Metric | CR | TBGB | p-Value | CR | TBGB | p-Value | CR | TBGB | p-Value | CR | TBGB | p-Value |
|--------|----|------|---------|----|------|---------|----|------|---------|----|------|---------|
| FE     | 189| 59   |         | 149| 51   |         | 170| 57   |         | 93 | 42   |         |
| %FE    | 90.00% | 98.33% | 70.95% | 85.00% | 80.95% | 95.00% | 44.29% | 70.00% | 42.86% | 83.33% | 42.86% | 83.33% |
| qual.FRic | 0.4414 |        | 0.5808 | 0.5717 | 0.6049 | 0.6401 | 0.9093 | 0.5062 | 0.8855 | 0.9454 | 0.4132 | 0.168** |
| FRic   | 0.9093 | 0.5062 | 0.8855 | 0.9454 | 0.4132 | 0.168** | 0.9349 | 0.5445 | 0.737 | 0.9168 | 0.5445 | 0.0168** |
| FEve   | 0.8445 | 0.8997 | 0.2447 | 0.6626 | 0.7467 | 0.8119 | 0.7429 | 0.885 | 0.163 | 0.4375 | 0.6897 | 0.4558 |
| FDiv   | 0.8533 | 0.831 | 0.169 | 0.8623 | 0.8407 | 0.092 | 0.8693 | 0.8666 | 0.8506 | 0.9083 | 0.8745 | 0.0983 |
| FDs    | 0.5589 | 0.5687 | 0.2082 | 0.5476 | 0.5528 | 0.596 | 0.5293 | 0.5496 | 0.0486* | 0.5705 | 0.5877 | 0.1599 |

Note: See Table 2 for metric definitions. p-Values indicate the significance of the difference between sites for each metric in each analysis from randomization testing (Appendix S8); for example in the locomotion analysis, the difference in FEve between TBGB and CR (TBGB-CR = 0.2522) is significant with a p-value = 0.0209. See methods for p-value calculation. Bolded values highlight significant results; *p-value < .05, **p-values < .01 and ***p-value < .001.

3.2 Fuzzy correspondence analysis

The projection of all species and modalities on the first two axes of the FCAs for all traits, habitat use, feeding and locomotion (Figure 2) shows that these two regions mostly overlap within the observed difference of function space when considering all species (Figures 2a–d). When considering trait modalities, particular combinations of modalities stand out as they cluster together across multiple analyses. Across all plots, there is a clear pattern demonstrating that in the functional trait space, the combinations of trait modalities are predominantly found in sharks and chimaeras, suggesting species in CR have a greater range of trait combinations, while the two systems are minor. CR had significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional richness for habitat use (p = 0.048) and locomotion (p = 0.029), suggesting species in CR have a significantly higher functional
analysis of habitat use traits, the sharks and chimeras cluster along with the rattails, with absent caudal fins and inferior gape positions and cylindrical body shapes. For the analysis relating to life history, the modality plot shows association between size classes 4 and 5, maximum age classes 4 and 5, and maturity class 5, highlighting a group of long-lived, slow to mature, large fish, which corresponds to certain shark species in this dataset. Site comparison shows this group is reduced in TBGB within the habitat use and life-history trait space (Figure 3a,b,g,h).

In the modality plot for the habitat use FCA (Figure 3a,b), there is a correlation between compressed and oval body shapes, lunate and forked caudal fin shapes, planktivorous diet, lower jaw projecting gape position and pelagic vertical position. The species corresponding to the traits include species such as hatchetfish, discfish, roughies, big-scale pomfret, fantoosh and ragfish. The ecological link between these species is unclear; however, the group appears to be reduced in TBGB.

In the FCAs for all traits, feeding and locomotion (Figures 2 and 3c–f), modality plots show a relationship between compressed body shape, and lower jaw projecting gape, lunate and forked caudal fin shapes, size classes 1 and 2, maturity class 1 and maximum age class 1, obligative schooling, and pelagic habitats and planktonic prey. These patterns suggest that small, fast-maturing, short-lived, pelagic, schooling fishes cluster together in trait space, such as pearlside, lanternfish (myctophids), big-scale fish, hatchetfish and lightfish. This group is reduced in TBGB in comparison to CR, within all three trait spaces (Figure 3).

The projection of all species and modalities on the third and fourth axes of the FCAs are included in Appendix S11. Each axis is made of certain amounts of each trait modality; Appendix S12 contains the modality contributions on the axes for the first five axes and the projected inertia of each axis. The amount of inertia explained by each axis is low across all analyses, with a max of 12.83% for a single axis (life history), and as a consequence, the amount explained by the combination of the first two axes is low across all analyses (Figures 2 and 3, range 16.25%–22.98%). There was a high correlation between most PCoA axes, used to calculate the diversity metrics (Table 3), and FCA axes, used to project species and modalities in trait space (Figures 2 and 3); correlation plots are included in Appendix S13.

4 | DISCUSSION

As exploitation of marine ecosystems continues, understanding functional diversity is vital. Diversity contributes to the resilience of a system and is linked to ecosystem efficiency and functioning (Cadotte et al., 2011; Danovaro et al., 2008; Stuart-Smith et al., 2013; Villéger et al., 2008). By quantifying the diversity of functional entities and how they aggregate into functional groups, functional diversity is directly linked to the dynamics and resilience of an ecosystem. Monitoring the fish communities that support fisheries using functional diversity metrics can provide insights into utilization of resources, functional structure and species overlap (Lechêne et al., 2018; Mason et al., 2005; Schleuter et al., 2010). Understanding how functional diversity differs between deep-sea and shallow-water systems informs fisheries managers by providing a better understanding of ecosystem structure and allowing for more robust predictions on how ecosystems may respond to exploitation as a consequence of trait diversity (Hewitt et al., 2014).
Habitat Use

(a)

Feeding

(c)

Locomotion

(e)

Life History

(g)

(b)

(d)

(f)

(h)
Here, we explore these differences in two productive, exploited systems in the New Zealand Exclusive Economic Zone. Our results firstly demonstrate that in most instances, these two systems contain similar levels of functional diversity and plots demonstrate a high overlap in trait space. The differences in functional diversity metrics varied dependent on which ecosystem functions were considered, implying these two ecosystems may function differently or have contrasting adaptations to exploitation. Results suggest that the deep-sea can harbour equally diverse fish communities, contradicting the established axiom that deep-sea ecosystems exhibit reduced diversity due to unfavourable environmental conditions (Costello & Chaudhary, 2017; Price et al., 1999). Species richness generally decreases with ocean depth (Costello & Chaudhary, 2017; Stefanoudis et al., 2019). However, the CR deep-sea system harbours unusually high productivity (Bowden & Leduc, 2017), and our data indicate that it had greater species richness than the TBGB shallow-water system. This may be a product of different geographical scales, with Chatham Rise being 58 times larger; however, species accumulation curves were used to ensure that each region was sampled in relatively equal proportions to mitigate these effects.

The deep-sea ecosystem exhibited higher functional richness with respect to habitat use, suggesting a greater range of trait combinations. This increased diversity is driven by groups of pelagic fishes, with shared uncommon traits, such as lunate tail types, lower projecting jaws, planktivorous diet and oval body shape. Despite sharing these traits, there is no clear ecological link to explain the functional grouping within trait space. Little is known about how, and to what extent, fishes use the array of deep-sea habitats (Devine et al., 2020). Given the results of this study, we suggest that further research is needed to examine how deep-sea fish communities interact with and utilize habitat space.

Feeding traits revealed a higher functional dispersion in the shallow-water system, indicating species are less centralized in trait space and therefore utilize more specialized approaches to feeding. This corroborates evidence of low diet specialization in deep-sea species (Clark et al., 1989; Collins et al., 2005), a pattern likely driven by the lower nutrient content in deeper waters, lack of herbivores and reduced prey availability (Costello & Chaudhary, 2017; Stefanoudis et al., 2019; Thürber et al., 2014).

Locomotion results indicate deep-sea fish had higher functional richness and therefore a greater range of traits, while the shallow-water ecosystem has comparatively less niche utilization within those functions. Modality plots suggest this difference is driven by a cluster of small, schooling, pelagic fish species (Figure 3e,f), a functional group potentially reduced in the shallow-water ecosystem. However, increased diversity in locomotion traits in the deep-sea conflicts with existing evidence that fish morphology becomes increasingly similar with depth, thought to be driven by extreme environmental conditions (Myers et al., 2020). The mechanics of locomotion, and how the environment influences trait evolution, remain poorly understood for deep-sea fishes suggesting the need for further research.

Finally, life-history results suggest greater functional evenness in shallow-water, indicating the deep-sea has clusters of species with similar life-history traits. Irregularities in deep-sea life histories suggest potential under-utilization of life-history strategies in deep-sea fish communities. Gaps in functional space corroborate these results (Figure 3g,h), with more long-lived and slow-maturing species present in the deep-sea system but reduced in the shallow-water system. These results are consistent with previous studies that indicate deep-sea species tend towards slower life-history strategies (Cailliet & Andrews, 2008; Clark, 2001; Clark et al., 2016; Koslow, 2006; Kurup, 2006).

The combinations of correlated traits (Figures 2 and 3) are interesting to consider as they drive the observed diversity in each analysis and can therefore be used to identify key species groups that support community functioning. Species that regularly clustered together in trait space were as follows: (a) sharks, chimeras and rat-tails, (b) stargazers, frogfish and toadfishes, and (c) small, schooling, pelagic fishes, such as lanternfish, big-scale fish, hatchetfish, pearlside and lightfish. Differences in diversity metrics between these systems may be driven by these groups, with FCA plots demonstrating how they tend to cluster on the extremities of trait space along with the associated modalities. One example is the locomotion FCA with a distinct group of small, pelagic schooling fish dominated by deep-sea species, clustering away from the centroid of trait space and likely driving the observed higher functional richness in the deep-sea (Table 3, Figure 3a,b). Interestingly, these species contribute to the assemblage of fishes that undergo diel vertical migrations and may represent a functionally important group that are not abundant in shallow-water ecosystems (Cornejo & Koppelmann, 2006; Eduardo et al., 2020; Godé et al., 2009).

Functional diversity in the deep-sea is linked to distinct clusters of species with high niche specialization (Zintzen et al., 2011) highlighting the importance of outlier species for sustaining diversity (Leitão et al., 2016). Our results corroborate this, highlighting the influence of outlier species, with extreme trait combinations, and their contribution to the overall functional diversity in the deep-sea by
inflating functional richness and reducing evenness. Understanding the vulnerability and functional significance of these specialized outlier species is vital as we continue to exploit the deep-sea since species loss may cause trophic cascades and influence fisheries productivity (Gifford et al., 2009; Leitão et al., 2016).

Deep-sea species are understudied, and much remains unknown about their ecology (Aneesh Kumar et al., 2017; Danovaro et al., 2008). In this study, species with unknown values were estimated using the closest relatives, but incomplete data have been shown to impact all functional diversity metrics (Pakeman, 2014). This may have resulted in underestimated diversity within the feeding and life-history functions, which were especially information-poor for Chatham Rise. Low percentages of functional entities results in high species overlap within trait space, indicating high niche overlap and potential functional redundancy (Muntadas et al., 2016). Our results suggest that the deep-sea system had higher niche overlap compared to the shallow-water, disagreeing with studies that identified low niche overlap among deep-sea fishes (Aneesh Kumar et al., 2017). Thus, the observed higher overlap in the deep-sea may be caused by a lack of information.

Understanding the functional structure and diversity of the deep-sea using trait values derived from literature, as opposed to collected from recent data, portrays an abstract, unexploited view of these ecosystems, allowing insight into how fishing activity has or will shift fish communities. The observed higher trait diversity of deep-sea fish in regards to habitat use suggests that the degradation of benthos by bottom trawl fisheries may impact the ability of fish to utilize habitat; however, this impact is unknown as the functional role of habitat and fish behaviour in the deep-sea remains understudied (Alves, 2003; Devine et al., 2020; Lorance et al., 2002).

The slower life-history strategies of the deep-sea drove decreased diversity, implying that overexploitation may cause long-lasting population effects with slower recovery speed and capability than shallow-water ecosystems, a well-established trend in the deep-sea (Calliet & Andrews, 2008; Juan-Jorda et al., 2015). The lower diversity of feeding approaches in deep-sea fish suggests that most species in this study tend towards generalist diets which depend on benthic invertebrates. It is well established that deep-sea fisheries significantly impact benthic invertebrate communities in terms of composition, abundance and diversity (Clark et al., 2019; Goode et al., 2020). Fisheries exploitation likely impacts deep-sea trophic dynamics for fish communities through a bottom-up effect. Generally, it is assumed that the generalist species of deep-sea communities are less sensitive to shifts in prey abundance than specialists in shallow-water communities. However, this benefit of generalized diet is likely countered by the reduced prey availability in the deep-sea, and thus, fish communities’ feeding functionality may be equally impacted by fisheries exploitation (Costello & Chaudhary, 2017; Stefanoudis et al., 2019; Thurber et al., 2014).

There is conflicting evidence on the relationship between functional evenness and exploitation or disturbance. Some studies suggest low evenness is caused by overexploitation and disturbance (Hillebrand et al., 2008; Richardson et al., 2018), and implying the lower evenness in the deep-sea may be a consequence of overfishing. Overexploitation by fisheries has been reported in the Chatham Rise region, and deep-sea fisheries are deemed unsustainable (Clark, 2001; Clark et al., 2016). However, other studies have reported increased evenness as a consequence of environmental disturbance (Lechêne et al., 2018; Villéger et al., 2010) and fisheries exploitation (Gifford et al., 2009). This implies that this shallow-water system may have suffered greater shifts in functional composition as a result of disturbance. It is unclear whether overexploitation contributes to functional evenness in deep-sea life-history traits, highlighting the need for further research to identify links between functional diversity and species loss. Though by not incorporating measures of species abundance, the reliability of functional evenness and divergence are questionable (Anderson et al., 2011; Schleuter et al., 2010; Villéger et al., 2008). Additionally, individual niche specialization is not accounted for by using species as opposed to individuals, meaning the intra-specific diversity of these systems is ignored (Ingram et al., 2018; Salguero-Gómez et al., 2018).

This study demonstrates that functional diversity can be measured for an entire community with a dataset of categorical traits obtained from literature and expert knowledge, providing a cost-efficient framework that may benefit regions with limited research funding. The fuzzy-coding approach applied in this study demonstrates an accurate method for categorizing diets of generalist species in biological trait analyses. Studies have demonstrated the ability to track shifts in ecosystem diversity and functioning as a response to disturbance using these diversity metrics in both animal and plant communities (McLean et al., 2019; Mouillot et al., 2013; Petchey & Gaston, 2002a). We build on this knowledge by using categorical traits for fish communities and demonstrating how function-specific trait space analyses can be used to assess diversity relating to particular functions. Additionally, by incorporating physiological, behavioural and life-history traits, this research addresses concerns about gaps in the field of trait-based ecology (Luiz et al., 2019).

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DATA AVAILABILITY STATEMENT
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BIOSKETCH

Victoria G. Carrington's research interests lie in the area of fisheries and ecosystem management, focusing on using statistical modelling to understand ecosystem dynamics, the impacts of fisheries and assess long-term sustainability. Current research projects focus on the consequences of bycatch on deep-sea sharks.

Author contributions: A.R. and M.L. designed and supervised the research, V.C. and J.H. sourced data, P.H. contributed data, V.C., Y.P., C.B. and R.C. designed and ran the analyses, V.C. wrote the first draft, all authors contributed substantially to the revisions of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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