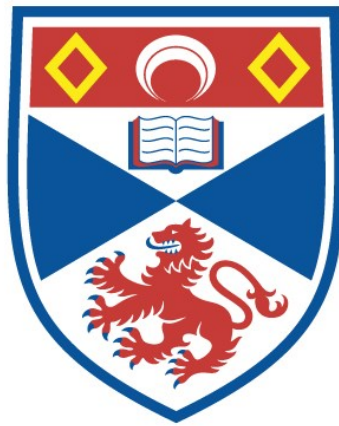


# BIODIVERSITY CHANGE IN SCOTTISH MARINE FISH ASSEMBLAGES

Faye Helen Moyes

A Thesis Submitted for the Degree of PhD  
at the  
University of St Andrews



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# Biodiversity change in Scottish marine fish assemblages

Faye Helen Moyes



University of  
St Andrews

This thesis is submitted in partial fulfilment for the degree of  
Doctor of Philosophy (PhD)  
at the University of St Andrews

May 2023

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## **General acknowledgements**

Many, many thanks to my supervisor, Professor Anne Magurran who has been an excellent mentor and who has encouraged me throughout this process. I am very grateful for all her kindness and support. I'd also like to thank my good friend and colleague, Dr Isaac Trindade-Santos for his valuable insights and comments on my work. Thanks also to all the 'Fish Lunch' people, no one could wish for a better, more supportive or encouraging lab group. Particular thanks to those who have been there for all or most of my time at St Andrews, including Professor Maria Dornelas, Dr Viviana Brambilla, Dr Alessandra Kortz and Ada Fontrodona Eslava.

I also need to thank Ian for putting up with me throughout this journey and supporting me in this adventure – for giving input on figures and colour schemes and for listening to me rambling on about fish! Thanks too to my step mum Liz and great friends, Joyce, Karen and Wendy for always being there for me and always showing interest in my work even when, as they would say, they don't really understand it.

Finally, I'd like to dedicate this to my Dad, Mum and Uncle Ronnie - I hope you would all be proud.

## **Research Data/Digital Outputs access statement**

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## Abstract

Marine fish are an irreplaceable natural resource but are currently under threat due to anthropogenic pressures. To date, most of the emphasis has been on single stocks or populations of economic importance. However, commercially valuable marine fish are embedded in assemblages of many species and there is only limited understanding of the extent to which the structure of whole communities has altered in recent years. Research suggests that recent years have seen rapid compositional and reorganisation of marine assemblages but how these taxonomic changes are related to functional diversity is less evident. Biodiversity is multifaceted but fisheries science has historically focused mainly on taxonomic diversity, for example, by taking species abundance combined with mortality rates to produce an estimate of stock size. This thesis fills a gap in marine fisheries research by using a range of different metrics to help understand diversity change in the whole assemblage from both a taxonomic and a functional perspective, and by identifying influential species in compositional change.

This thesis aims to quantify how two geographically close, but distinct ecosystems from around the Scottish coast (part of the Celtic-Biscay shelf region on the west and the North Sea region on the east), have changed over a thirty-year time frame by utilising two facets of biodiversity and analysing at a whole assemblage level. The consistent nature of the scientific trawl surveys that form the basis for this work give an ideal study system for the analysis undertaken. Moreover, the statistical bounding areas provided by the ICES rectangles allow sample-based rarefaction and enable fair comparisons between systems and latitudes. My main hypothesis is that despite the distinctions between coastal systems, their geographic proximity and similarity of species will lead to no clear difference in diversity change. This thesis will examine this biodiversity change in four main ways: spatio-temporal change in taxonomic diversity; spatio-temporal change in functional diversity; spatio-temporal change in rarity; and identification of influential species within the systems.

My results clearly indicate that it is possible to reject the null hypothesis of no difference between systems. I find contrasting patterns between the coastal systems when examining trends in both taxonomic and functional diversity, in addition to key differences between those species most influential in contributing to compositional change and the types of contributions they make. I also examine trends in rarity to ask how the different dimensions covary over time and find that the direction of temporal shifts in taxonomic rarity is consistent with a null model of change in assemblage size. However, the observed data depart from the null expectation of a decrease in functional rarity suggesting that the functional integrity of the systems is maintained, even when assemblage size increases. Gaining an understanding of the reorganisation of assemblages based on the shared dynamics of the species within them can aid with the monitoring and restoring of biodiversity.

These results underline the importance of measuring both taxonomic and functional dimensions of diversity when assessing and interpreting biodiversity change. A multidimensional, integrated approach to biodiversity assessments, as undertaken here, has an important role to play in the ecosystem-based management of fisheries. This thesis fills a gap in the current knowledge regarding biodiversity monitoring of fisheries data and as such is of potential importance to policy makers and managers.

## Table of Contents

List of figures .....	7
List of Tables .....	14
Chapter One – General Introduction.....	15
1.1 Background .....	16
1.1.1 Marine biodiversity.....	17
1.1.2 Taxonomic and functional diversity.....	19
1.2 Scottish background .....	20
1.3 Goals of this thesis .....	21
1.3.1 Taxonomic diversity – changes in diversity over three decades .....	22
1.3.2 Functional diversity – patterns of change over thirty years .....	22
1.3.3 Temporal and spatial rarity – geographical patterns and changes through time .....	23
1.3.4 Compositional change and rarity .....	23
1.4 Thesis structure .....	23
Chapter Two – General Methods and Materials.....	25
2.1 Study site and data.....	26
2.1.1 ICES scientific trawl survey – Scottish West Coast 1985 – 2014.....	29
2.1.2 ICES scientific trawl survey – North Sea 1965 – 2019.....	29
2.1.3 Sampling effort .....	30
2.2 Study species .....	31
2.2.1 Species information .....	33
2.2.2 Trait information .....	33
2.3 Biological Diversity .....	41
2.3.1 Taxonomic diversity .....	43
2.3.1.1 Alpha diversity measures .....	43
2.3.1.1.1 Species numerical abundance.....	44
2.3.1.1.2 Hill number $q_0$ – equivalent to species richness .....	44
2.3.1.1.3 Hill number $q_1$ – exponential Shannon.....	45
2.3.1.1.4 Hill number $q_2$ – reciprocal Simpson .....	45
2.3.1.1.5 Hill number $q_\infty$ – reciprocal Berger-Parker .....	46
2.3.1.2 Beta diversity measures .....	46
2.3.1.2.1 Morisita-Horn dissimilarity .....	47
2.3.1.2.2 Jaccard dissimilarity .....	48
2.3.2 Rarefaction.....	48
2.3.3 Functional Diversity.....	49
2.3.3.1 Alpha diversity .....	51

2.3.3.1.1 Functional richness.....	51
2.3.3.1.2 Functional evenness .....	52
2.3.3.1.3 Functional divergence .....	53
2.4 Data analysis methods.....	55
2.4.1 Methods used in R .....	55
2.4.2 Calculating trends, slopes and correlations .....	56
2.4.3 Tools used in ArcGIS.....	58
Chapter Three – Taxonomic diversity – changes in alpha diversity over three decades* .....	59
3.1 Introduction.....	60
3.2 Methods.....	62
3.2.1 Species numerical abundance .....	63
3.2.2 Hill number $q_0$ – equivalent to species richness.....	63
3.2.3 Hill number $q_1$ – exponential Shannon .....	64
3.2.4 Hill number $q_2$ – reciprocal Simpson .....	64
3.2.5 Hill number $q_\infty$ – reciprocal Berger-Parker.....	64
3.2.6 Dominant species.....	64
3.3 Results.....	65
3.3.1 Species numerical abundance .....	66
3.3.2 Hill number $q_0$ – equivalent to species richness.....	67
3.3.3 Hill number $q_1$ – exponential Shannon .....	67
3.3.4 Hill number $q_2$ – reciprocal Simpson.....	67
3.3.5 Hill number $q_\infty$ – reciprocal Berger-Parker.....	68
3.3.6 Dominant species.....	70
3.4 Discussion .....	74
Chapter Four – Functional diversity – patterns of change over thirty years.....	79
4.1 Introduction.....	80
4.2 Methods.....	82
4.2.1 Functional richness .....	83
4.2.2 Functional evenness .....	83
4.2.3 Functional divergence.....	83
4.2.4 Correlations with taxonomic diversity metrics .....	83
4.2.5 Decadal change .....	84
4.2.6 Decadal change in correlations between systems.....	84
4.3 Results.....	85
4.3.1 Functional richness .....	85
4.3.2 Functional evenness .....	86
4.3.3 Functional divergence.....	87
4.3.4 Correlations with taxonomic diversity metrics .....	88

4.3.5 Decadal change .....	90
4.3.6 Decadal change in correlations between systems.....	93
4.4 Discussion .....	95
4.5 Conclusion.....	97
Chapter Five - Temporal and spatial rarity – geographical patterns and changes through time** .....	98
5.1 Introduction .....	99
5.2 Methods.....	100
5.2.1 Taxonomic rarity.....	101
5.2.2 Functional rarity.....	102
5.2.3 Functional rarity (no abundance weighting) .....	103
5.2.4 Simpson’s Evenness, S and N.....	104
5.2.5 Null model .....	106
5.2.6 Slopes and correlations .....	107
5.3 Results.....	107
5.3.1 Taxonomic rarity.....	108
5.3.2 Functional rarity.....	108
5.3.3 Functional rarity (no abundance weighting) .....	109
5.3.4 Simpson’s evenness, S and N .....	109
5.3.5 Null model .....	111
5.3.6 Slopes and correlations .....	115
5.4 Discussion .....	118
5.5 Conclusion.....	120
Chapter Six – Compositional change and rarity .....	122
6.1 Introduction .....	123
6.2 Methods.....	125
6.2.1 Beta diversity approaches .....	126
6.2.2 Chao Ricotta approach.....	127
6.2.3 Gotelli framework.....	128
6.2.4 Core and transient species.....	129
6.2.5 Top quartile of rare species.....	129
6.3 Results.....	130
6.3.1 Beta diversity approaches .....	130
6.3.2 Chao Ricotta approach.....	131
6.3.3 Gotelli framework.....	135
6.3.4 Core and transient species.....	135
6.3.5 Top quartile of rare species.....	136
6.4 Discussion .....	139
6.5 Conclusion.....	143

Chapter Seven – General Discussion.....	144
7.1 Background .....	145
7.1.1 Chapter Three – Taxonomic diversity – changes in diversity over three decades .....	145
7.1.2 Chapter Four – Functional diversity – patterns of change over thirty years .....	146
7.1.3 Chapter Five – Temporal and spatial rarity – geographical patterns and changes through time.....	146
7.1.4 Chapter Six – Compositional change and rarity.....	147
7.2 Summary .....	147
7.3 Future directions for the field .....	148
References .....	151
Appendices .....	185
Appendix 2 .....	186
Appendix 2.1 Code block shows the resampling code common to all research chapters (3, 4, 5 and 6) .....	187
Appendix 2.2 List of species used in this thesis with Coast column populated according to location, and, where only found in one system, shaded by colour (blue for the east coast and green for the west). .....	191
Appendix 2.3 Table of pairwise correlations (Pearson) between trait values in functional analyses. ....	192
Appendix 3 .....	193
Appendix 3.1 Code block showing functions used in this chapter .....	195
Appendix 3.2 Table of summary statistics for slopes of change used in this chapter .....	198
Appendix 4 .....	199
Appendix 4.1 Code block for functions in this chapter .....	201
Appendix 4.2 Table of summary statistics for slopes of change used in this chapter .....	202
Appendix 5 .....	203
Appendix 5.1 Code block including null model.....	208
Appendix 5.2 Table of summary statistics .....	211
Appendix 5.3: Results of five different starting samples of the gamma assemblage .....	213
Appendix 6 .....	214
Appendix 6.1 Code block showing functions used in this chapter .....	223
Appendix 6.2 Table of species classifications by coast used in this chapter .....	232
Appendix A – Published papers .....	233

## List of figures

<b>Figure 1.1:</b> This figure outlines the aims and questions addressed in my thesis.....	24
<b>Figure 2.1:</b> Full study site showing the three ICES areas used in this thesis, they are labelled by name and filled with pale green for the West Coast and pale blue for the North Sea sites. These colours corresponding to coastal system are constant throughout this thesis. ....	26
<b>Figure 2.2:</b> ICES rectangles coloured by coastal system, pale blue for the North Sea and pale green for the West Coast survey. ....	27
<b>Figure 2.3:</b> This plot shows the mean sea surface temperatures across all latitudinal bands at each time step. An OLS regression was performed, and this trend line is added (solid line for significant as on the west coast and dashed for non-significant as on the east).....	29
<b>Figure 2.4:</b> Complete set of ICES statistical rectangles for comparison work. Each point represents a record with species, numerical abundance, date and location information and has been mapped to the ICES rectangle it falls within. ....	30
<b>Figure 2.5:</b> Phylogenetic trees for the two coastal systems. Left hand side (A) illustrates the species within the West coast (SWC-IBTS survey) and the right-hand side (B) the East coast species (NS-IBTS survey). This was generated in R using the package rotl which is an interface to the Open Tree of Life (Michonneau <i>et al.</i> , 2016). ....	32
<b>Figure 2.6:</b> Figure shows the pairwise correlations between all traits within the study fish. The Pearson correlations are calculated using the pairs.panel function in the psych package in R (Revelle, 2019), extracted and used to plot a histogram of their distribution. The values are largely uncorrelated and mainly centred around zero. The correlations represent the pairwise relationships between the values for each of the eleven traits considered in this work (growth, length at first maturity, Q/B, trophic level, maximum depth, temperature preference, generation time, swim mode, body shape, reproductive guild and position in the water column), see Appendix 2.3 for a table of all pairwise values. ....	34
<b>Figure 2.7:</b> Venn diagram showing the three facets of biodiversity – taxonomic, functional and phylogenetic. 41	41
<b>Figure 2.8:</b> This figure illustrates the difference between the components of diversity. The main map shows the full West coast survey data plotted in the 1° grid cells. Firstly, taxonomic diversity is represented by (a) which shows the rank abundance plot for the overall gamma diversity of the full area, whilst (b) and (c) show the same rank abundance plots for the smaller subsets represented by the red and blue coloured grid cells and representing alpha diversity. Functional alpha and gamma diversity are shown in (d) where the grey dots represent the position in functional space (see section 2.3.3 and Figure 2.12 for details) of the wider gamma diversity of the full area, red and blue correspond to those in only either cells (b) or (c) and purple are those appearing in both subsets. Phylogenetic diversity is represented by (e), (f) and (g) where (e) shows the phylogenetic tree for the full area (gamma diversity) and (f) and (g) refer to the phylogenetic trees for the subsets in (c) and (b) respectively (alpha diversity) and shaded accordingly. ....	43
<b>Figure 2.9:</b> A random subset of the full study data containing a 30-year time series is used to illustrate the results when using the different alpha diversity metrics featured. The metrics are computed for each time step (points) and a trend line fitted (using a simple Ordinary Least Squares (OLS) regression). These data show a slight but significant increase in both abundance (shown as log N) and species richness ( $q_0$ ) but small and non-significant declines in exponential Shannon ( $q_1$ ), reciprocal Simpsons ( $q_2$ ) and reciprocal Berger-Parker ( $q_\infty$ ). .	46
<b>Figure 2.10:</b> Illustration of changes in beta diversity, how sites become more or less similar to each other. Firstly, (A) is the visual representation of the Jaccard equation where dissimilarity is measured based on the difference between the intersect and the separate sections. (B) shows how two samples can differ in composition even when only three distinct species are involved. ....	48
<b>Figure 2.11:</b> Body shape is illustrated at the ends of different types. Length (x axis) shows the shorter bodied fish such as the pale green coloured cod-like and turquoise coloured herring-like being positioned towards zero	



whilst the longer blue coloured eel-like is much further along the axis. Height (y axis) illustrates the ‘taller’ flat fish such as the green coloured plaice-like being at the top end of the axis whilst again the cod-like and herring-like are closer to zero..... 50

**Figure 2.12:** Changes in functional richness do not need to happen in tandem with changes in species richness as illustrated in the above figure. In the first assemblage (A) there are five different species (S=5) that are distributed throughout the functional space, both on the outer edges and towards the centre. In (B and C) there are still five distinct species but since the more functionally distinct conger eel (B) or plaice (C) have been replaced by a sole (which is related to the plaice), the actual space being occupied has contracted significantly in (B) and slightly in (C). Finally, in (D) the functional space occupied is unchanged from (A) despite the decrease in S to four (S=4)..... 52

**Figure 2.13:** Each plot represents an assemblage with either high or low divergence or evenness, the position of the circles represents a species’ place in functional space whilst the size is representative of the abundance amount (larger points show higher abundance). (A) shows an assemblage with low functional evenness – species are clustered together in groups of both trait combinations and abundances. However, (B) illustrates high functional evenness where both abundance and trait combinations are regularly distributed throughout the space. (C) shows an assemblage with low functional divergence, species with distinct combinations of traits are located on the edges of the functional space and the small circles show that they contain the lowest abundances of the species, the larger circles representing the more dominant species are all towards the centre of the space suggesting similar combinations of traits (example species could be herring and mackerel). Finally, (D) illustrates an example of high functional divergence, here the more distinct species on the edges have the highest abundances whilst those in the centre of the space are less abundant..... 54

**Figure 2.14:** Mock version of typical plots showing temporal change as (A) significant positive, (B) significant negative, (C) non-significant positive and (D) non-significant negative. The x-axes are years whilst the y-axes are generic values used for illustration purposes only. .... 57

**Figure 3.1:** Simple workflow detailing the steps performed in this chapter. In a) the data is downloaded from the public website (link included) and filtered for the ICES regions studied, in b) the data are cleaned by removing non species level individuals. In c) I sum the species abundance data to year and location before d) plotting by location in ArcGIS (ESRI, 2015), the layer file for latitudinal bands is then added to the map in e). The final steps are to f) carry out a spatial join between the latitudinal bands and the species abundance records and perform rarefaction (or resampling) in g) before exporting the csv ready for analyses – h) calculating the metrics outlined in the next sections. .... 63

**Figure 3.2:** The map details the five main metrics calculated by latitudinal band and shows these in the geographic position they fall in, the numbers on the plot strips represent the mid-point of the band in decimal degrees latitude. Each metric is plotted at each time step (year) (yearly points are not illustrated here) before a simple OLS regression trend line is added, the plot panels are coloured by z score (based on the qnorm of their p-value (calculated using R)) with the following key applied. Scores -  $z \leq -4$  in darker blue,  $-4 > z \leq -1$  in light blue,  $-1 > z < 1$  in grey,  $1 > z < 4$  in light pink and (although none apply here)  $z > 4$  in dark pink. .... 66

**Figure 3.3:** This figure shows the same slopes as shown in Figures 3.2 and 3.4 but allows for a quick visual comparison both between and within the systems. Here the slopes for each metric are plotted side by side and coloured by coastal system (as with previous figures this is exemplified by green for the west coast and blue for the east). It is evident that the differences between systems are clearly visible and that the only similarity in pattern is in the case of  $q_0$  (see Figure 3.4 and legend for the results of the median absolute deviation). .... 67

**Figure 3.4:** Here the slopes of change as shown in Figures 3.2, 3.3 and 3.5 are plotted against latitude. This suggests a clear latitudinal signal on the east coast for all metrics, but no pattern is evident for the west coast system. The east coast exhibits a decreasing trend in the strength of slopes towards the higher latitudes in all measures except N (numerical abundance) which appears to be increasing towards the north. .... 69

**Figure 3.5:** Slopes of change (OLS regression) as density plots coloured by coastal system. Each plot is centred around zero, represented here by a dotted line. The distinction in variation is clear with particular emphasis on the differences for N,  $q_2$  and  $q_\infty$ . I also computed the Median absolute deviation for each system using the mad

function in base R (RCoreTeam, 2021). These results are as follows: east coast – N=3375,  $q_0=0.2$ ,  $q_1=0.04$ ,  $q_2=0.03$ ,  $q_\infty=0.02$ . West coast - N=1863,  $q_0=0.18$ ,  $q_1=0.04$ ,  $q_2=0.05$ ,  $q_\infty=0.03$ ..... 70

**Figure 3.6:** This plot shows the trend in relative dominance by year. The relative dominance of the most dominant species is calculated across all latitudes with an OLS regression trend line added, represented as a solid line for a significant slope and dashed for non-significant. The trend is increasing in both systems but only significantly on the west coast. .... 71

**Figure 3.7:** Figure showing the spatio-temporal changes in dominants (by both identity and amount). The map illustrates changes in the dominance of the most dominant species by latitudinal band. Each pie summarises a ten-year period and is colour coded to show the relative dominance of the most dominant species, the key to species identity is included at the top left corner. The three columns on each coast are not situated longitudinally but only according to decade (decade 1 – 3 left to right on each coast). .... 72

**Figure 3.8:** The pairs plot shows the scatter plot and densities of the slopes (as in Figure 3.3) alongside the correlations between each of the pairs of metrics. Here the overall correlation is shown in grey whilst the green and blue are representative of the coastal systems as previously (west = green and east = blue). The asterisks indicate strength of correlation from . to \*\*\* where \*\*\* is the strongest. Asterisks represent p-values ( $. < 0.1$ ,  $* < 0.05$ ,  $** < 0.01$ ,  $*** < 0.001$ ). .... 73

**Figure 3.9:** Each metric (slope of change) is connected to the others within their coastal system, the strength of correlation is based on Pearson’s correlation coefficient and ranges from -1 to +1 where -1 is strongly negative related and +1 is strongly positively related. A white or near invisible link indicates no correlation or only very weakly correlated..... 74

**Figure 4.1:** Workflow diagram illustrating the steps carried out within this chapter and where to find further details on each. In a) the data is downloaded after filtering for the ICES regions and trawl methods, in b) the data is cleaned by removing any zero abundances or any non-fin fish/unidentified species. In c) the individual species records are plotted in ArcGIS (ESRI, 2015) and allocated to the latitudinal band layer before d) resampling is carried out. In e) the selected traits are extracted from FishBase and matched to the species identities before calculating the chosen functional diversity metrics in f). In g) a pairwise matrix is created by combining with taxonomic results from Chapter 3 before finally h) comparative pairs plots and dendrograms are built..... 82

**Figure 4.2:** The map shows the changes in the three functional diversity metrics plotted through time. The plots are overlaid on the map at approximately the latitude and coastal system they are located in, with the exact central latitude of each plot row labelled on the left. From left to right on each coast the panels show functional richness, functional evenness and functional divergence. Lines connect the yearly points, and a linear regression is added, coloured and shaded red for significantly negative, blue for significantly positive and grey for non-significant. .... 86

**Figure 4.3:** This figure shows the latitudinal trend of the slopes for each of the three metrics. The y-axes represent the slopes of the named metric. On the west all three metrics show steeper increasing slopes northwards (although only significantly so for functional divergence ( $p\text{-value}=0.04$ ). In contrast, the east coast slopes tend to become shallower towards the northern latitudes for functional richness and functional evenness whilst functional divergence is increasing as the bands move north. All trends on the east coast are significant (FR  $p\text{-value}=0.01$ , FE  $p\text{-value}=0.004$ . FD  $p\text{-value}=0.001$ )..... 87

**Figure 4.4:** This figure shows the slopes of temporal change for each metric by coastal system (these are the same slopes as represented in Figure 4.2). The black lines denote the overall trend, significant as solid and non-significant as dashed. This figure helps to clarify the distinctions in slope variability between the systems for each metric..... 88

**Figure 4.5:** This figure illustrates the relationship between functional and selected taxonomic metrics. The west coast system is shown in green, whilst the east coast is blue. The plots represent the yearly values for a functional metric plotted against a taxonomic metric, a simple linear regression (OLS) is then added, solid lines indicate a significant trend whilst dashed lines are non-significant. For all three functional metrics the two systems behave in a similar manner, functional richness is increasing in line with  $q_0$  (species richness) and both

coasts show strong significant trends (West -  $p$ -value<0.0001, Adj. $R^2$ =0.72; East -  $p$ -value<0.0001, Adj. $R^2$ =0.79). Although both coasts show a very weak negative slope for functional evenness when  $q_\infty$  increases this is non-significant and the adjusted  $R^2$  very close to zero suggesting no linear relationship between the two variables exists. Functional divergence is increasing as  $N$  increases for both systems, but this relationship is a weakly significant one on the east coast ( $p$ -value<0.0001, Adj. $R^2$ =0.05). ..... 89

**Figure 4.6:** This plot shows the correlations between the slopes of change of the pairs of metrics grouped by coastal system. The west coast plots and correlations are shaded in green with the east coast in blue. The overall correlation for both systems is shown in dark grey. The strength of the correlation is indicated by the ., \*, \*\* or \*\*\* shown alongside (no symbol = weak or no correlation). Asterisks represent  $p$ -values (. <0.1, \* <0.05, \*\* <0.01, \*\*\* <0.001). ..... 90

**Figure 4.7:** This shows the linear relationship between functional and taxonomic richness ( $q_0$ ) and how this relationship changes for a single assemblage by decade. Here I take the assemblages at the latitudinal band centred around 58 degrees from each coastal system (with the west represented by green and the east by blue). The points represent the yearly values of each metric and the lines the linear trend (simple OLS regression), these are solid for significant trends and dashed for non-significant (West latitude 58: Decade 1 –  $p$ -value=0.14, Adj.  $R^2$ =0.16, Decade 2 –  $p$ -value=0.05, Adj.  $R^2$ =0.31, Decade 3 –  $p$ -value=0.001, Adj.  $R^2$ =0.7; East latitude 58: Decade 1 –  $p$ -value=0.01, Adj.  $R^2$ =0.54, Decade 2 –  $p$ -value=0.05, Adj.  $R^2$ =-0.07, Decade 3 –  $p$ -value=0.24, Adj.  $R^2$ =0.05). ..... 91

**Figure 4.8:** This shows the linear relationship between functional evenness and  $q$  infinity and how this relationship changes for a single assemblage by decade. Here I take the assemblages at the latitudinal band centred around 58 degrees from each coastal system (with the west represented by green and the east by blue). The points represent the yearly values of each metric and the lines the linear trend (simple OLS regression), these are solid for significant trends and dashed for non-significant (West latitude 58: Decade 1 –  $p$ -value=0.47, Adj.  $R^2$ =-0.05, Decade 2 –  $p$ -value=0.04, Adj.  $R^2$ =0.34, Decade 3 –  $p$ -value=0.5, Adj.  $R^2$ =-0.06; East latitude 58: Decade 1 –  $p$ -value=0.79, Adj.  $R^2$ =-0.12, Decade 2 –  $p$ -value=0.32, Adj.  $R^2$ =0.01, Decade 3 –  $p$ -value=0.6, Adj.  $R^2$ =-0.07). ..... 92

**Figure 4.9:** This shows the linear relationship between functional divergence and  $N$  (shown as  $\log_{10} N$  for ease of visualisation and comparison) and how this relationship changes for a single assemblage by decade. As with previous examples I take the assemblages at the latitudinal band centred around 58 degrees from each coastal system (with the west represented by green and the east by blue). The points represent the yearly values of each metric and the lines the linear trend (simple OLS regression), these are solid for significant trends and dashed for non-significant (West latitude 58: Decade 1 –  $p$ -value=0.54, Adj.  $R^2$ =-0.07, Decade 2 –  $p$ -value=0.7, Adj.  $R^2$ =-0.1, Decade 3 –  $p$ -value=0.75, Adj.  $R^2$ =-0.11; East latitude 58: Decade 1 –  $p$ -value=0.18, Adj.  $R^2$ =0.12, Decade 2 –  $p$ -value=0.63, Adj.  $R^2$ =-0.09, Decade 3 –  $p$ -value=0.03, Adj.  $R^2$ =0.37). ..... 93

**Figure 4.10:** Tanglegram showing the difference between the three decades. The dashed lines indicate distinct edges in those trees whilst the coloured lines connecting the two represent subtrees that are common to both systems. ..... 94

**Figure 5.1:** Workflow diagram illustrating the steps carried out within this chapter and where to find further details on each. In a) I download the data from DATRAS as described in Chapter 2.2 before cleaning in b) and plotting in ArcGIS (ESRI, 2015) to c) allocate latitudinal bands. In d) I resample the data as previously before e) matching fish to FishBase (Froese & Pauly, 2019) and assigning trait values. In f) I perform the rarity analyses as described in section 5.2 before g) running the null models and h) calculating assemblage level metrics and slopes. Finally in i) I examine the correlations between measures. ..... 101

**Figure 5.2:** Simplified 2-D example of species position in functional space and the calculation of functional rarity. This herring like fish is represented by the medium sized point shown by the green arrow, whilst the black arrows indicate the distances between this fish and all others within the assemblage. Each point is weighted by abundance with the larger dots indicating a higher number of individuals. ..... 103

**Figure 5.3:** Simple pictorial representations of the rarity metrics. Taxonomic rarity is shown in a) as a mock assemblage where level of abundance is the main influence of rarity. Three species are shown here with

differing abundances (size of the dot indicates abundance), the skate type, of whom there is only one will be the rarest, the herring type which is the most dominant and has six individuals will be least rare and the flat fish of whom there are three will be central to the other two. In b) functional rarity is illustrated, here the species with more unusual combinations of traits will be located on or close to the border of the functional space, this version of the rarity calculation takes abundance into account, so the size of the dot is increased with the number of individuals per species. The rarity of a species will depend on how different they are in terms of both abundance and trait combinations from the other fish in their assemblage. Here the skate and shark types which are low in abundance and have more unusual trait combinations will be the rarest, whilst the herring type which has a common combination of traits and is very abundant will be least rare. In this example the flat fish is rarer than the haddock type despite the fact that it has a more unusual combination of traits, this is due to the higher number of individuals in this representation. In c) functional rarity with no abundance weighting is shown, this example is identical to b) except there are no abundances counted, this results in a slight shifting of the ordering, namely, the flat fish is now higher (rarer) than the haddock type..... 104

**Figure 5.4:** Simple pictorial illustration of assemblages exhibiting high and low evenness. In a) the herring type fish is the most dominant and all other species have relatively low abundances leading to an uneven pattern of distribution of individuals among species suggesting low evenness. In b) the distribution of individuals among species is very even consisting of two per fish, this suggests a high level of evenness in the assemblage..... 105

**Figure 5.5:** Simple workflow showing the steps performed in the null model. After selection of initial 50 species from the gamma pool the traits are shuffled before the selection of ~55 random species with abundances. At each iteration of the loop, n individuals are selected (with sequential increases until total N for the assemblage is reached) and the community metrics are calculated and stored. Then the matrix is re-shuffled, and the process repeated (for a total of 1000 iterations). ..... 107

**Figure 5.6:** Figure showing the direction and significance of slopes of change in the latitudinal bands. .... 108

**Figure 5.7:** Slopes of change (using ordinary least squares regression) of latitudinal bands for each metric through time coloured by coastal system. The darker line is the common trend (computed as the OLS regression of all the time series) and the lighter lines the individual latitudinal bands. The figure shows the greater heterogeneity of slopes on the east coast as compared to the west. All slopes are listed in Table 1 and full summary statistics can be found in Appendix 5.2. All overall trends are shown as solid lines, indicating significance. .... 110

**Figure 5.8:** Output of the null model showing the relationship between species richness (S) and numerical abundance (N). The flattening curve of S v N is consistent with the pattern typically seen in empirical data sets. .... 112

**Figure 5.9:** The null model shows that a positive change in assemblage size is expected to have a direct effect on both evenness and taxonomic rarity (in opposing directions). In turn these structural changes should result in a decrease in the functional rarity of the assemblage. However, in the observed results I find that although evenness and taxonomic rarity behave as expected, functional rarity is increasing, albeit very slightly, in line with assemblage size and taxonomic rarity. .... 112

**Figure 5.10:** Relationship between null and observed. Observed values (yearly results by latitudinal band) are shown as solid points, with the distribution of null results indicated by the shaded area. In both cases trends are indicated using a loess fit, computed using the `stat_smooth(method="loess")` option in `ggplot2`. West coast results are shaded green, and east coast blue, with the observed loess as a pale dashed line and the null as a darker solid line. .... 113

**Figure 5.11:** Relationship between null and observed. As with Figure 5.10, observed values are shown as solid points, with the distribution of null results indicated by the shaded area and trends shown using a loess fit. The west coast results are shaded green, east coast blue, with the observed loess as a pale dashed line and the null as a darker solid line. .... 114

**Figure 5.12:** The boxplots show the distributions of kurtosis and skewness when viewing the null by the observed. Medians are as follows: West kurtosis: null=2.08, observed=3.5. West skewness: null=0.18, observed=0.1. East kurtosis: null=2.12, observed=3.45. East: skewness null=0.07, observed=-0.2. .... 114

**Figure 5.13:** Pearson correlations between slopes of change for all metrics. The asterisks indicate strength of correlation from . to \*\*\* where \*\*\* is the strongest. Asterisks represent p-values (. <0.1, \* <0.05, \*\* <0.01, \*\*\* <0.001). The correlations and plot figures are coloured by coastal system, green for west and blue for east as previous figures with the overall correlation results shown in grey. Here Functional P/A refers to the functional rarity measure with no abundance weighting. .... 116

**Figure 5.14:** The plots represent the change in the relationship between functional and taxonomic rarity over the three decades of this study. The west coast band (55.5 degrees latitude) is shown in the upper panel and coloured green whilst the east coast band (60.5 degrees latitude) is coloured blue and shown in the lower panel. Slopes are calculated using OLS and are shown as solid lines if significant and dashed if non-significant. West coast – Decade 1: p-value=0.01, Adj. R<sub>2</sub>=0.61; Decade 2: p-value=0.18, Adj. R<sub>2</sub>=0.12; Decade 3: p-value=0.74, Adj. R<sub>2</sub>=-0.11. East coast – Decade 1: p-value=0.71, Adj. R<sub>2</sub>=-0.12; Decade 2: p-value=0.97, Adj. R<sub>2</sub>=-0.13; Decade 3: p-value=0.01, Adj. R<sub>2</sub>=0.5. For full summary statistics of these and other results see Appendix 5.2. .... 117

**Figure 5.15:** Historic catch data sourced from the Sea Around Us (Pauly & Zeller, 2015b) project. Catch is represented as tonnes and the area is the full Large Marine Ecosystem for each coastal system (West coast – Celtic Biscay Shelf, East coast – North Sea). These catch data are compiled from multiple fisheries sectors (artisanal, industrial, subsistence, recreational) and include discards. The dashed line represents the start point of this study (1985). These data are not partitioned by the latitudinal band system used elsewhere in this analysis but can give some insight into fishing practices in the regions..... 118

**Figure 6.1:** Workflow diagram illustrating the steps carried out within this chapter and where to find further details on each. Following on from the steps in earlier chapters I first a) import the resampled data for coastal and latitudinal band level assemblages before b) running code to implement the Chao-Ricotta approach. Using the same input, I c) run code to assign species classifications according to the Gotelli framework and then d) assign the core or transient status to each species according to temporal occupancy of coastal system. The next step is to e) allocate rare/common designations to each species using the output from Chapter 5 before f) calculating the two dissimilarity measures (by coast and latitude). I then g) identify species that are the greatest contributors to change according to the approaches developed by Chao-Ricotta and Gotelli et al. Finally in h) I examine the connections between rarity and these influential species. .... 126

**Figure 6.2:** The figure shows toy examples of each form of classification with species presence coloured by category and absence in white. Whitespace is left after the first year of the time series to highlight the converging/diverging nature of the directional change categories. .... 128

**Figure 6.3:** The figure shows log<sub>10</sub> total abundance of all species by the number of years appearing in the system. The dashed lines represent the cut-off point used to designate a species with either core or transient, the paler shades represent the core species, persistent for at least twenty years. As throughout the left panel and green colours show the west coast system whilst the right panel and blue shades are the east. .... 129

**Figure 6.4:** Yearly dissimilarity measured against the baseline first year of the time series. As throughout this thesis the points are coloured according to coastal system – blue for the east and green for the west. Each point represents the dissimilarity at that time step when compared to the baseline (here the first year of the time series). Points are fitted with a simple linear regression (Ordinary Least Squares) and the lines are solid in the case of a significant trend and dashed for non-significant. Jaccard dissimilarity: west coast – p-value=0.05, Adj. R<sup>2</sup>=0.1; east coast – p-value=0.3, Adj. R<sup>2</sup>=0.01. Morisita-Horn dissimilarity: west coast – p-value=0.17, Adj. R<sup>2</sup>=0.03; east coast – p-value=0.46, Adj. R<sup>2</sup>=-0.02. .... 131

**Figure 6.5:** Plots showing the contributions that each species is making to compositional change (Jaccard type dissimilarity) when looking through the lens of the Hill numbers, q<sub>0</sub>, q<sub>1</sub> and q<sub>2</sub>. Upper panel shows the west coast, and the lower panel shows the east. The top ten contributors for each system as outlined in Table 6.1 can be identified by the height of the visible columns in the q<sub>1</sub> and q<sub>2</sub> plots. .... 133

**Figure 6.6:** The pie charts show the proportions of each classification separately for each system. In both systems the random category holds the largest proportion, but this is slightly larger on the east coast whereas the west coast makes up this deficit by holding increased proportions of recurrent and no change species. Although for both coasts the directed change categories consist of approximately 10% of species, there are slight

differences between them, whereby the west coast includes only diverging decreasing species and the east coast only converging decreasing species..... 135

**Figure 6.7:** Venn diagram showing the overlap of core species common to both systems, most core species (64%) are persistent through time for both coasts. West coast shown in green and east in blue. .... 136

**Figure 6.8:** Figure shows the east and west coast systems with species split into core and transient based on the criteria in the methods section (6.2.4). Here the darker shades represent the transient species (with lower total abundances), and the black lines denote the linear regressions by group. Dashed lines are non-significant and solid significant. .... 136

**Figure 6.9:** The left panel Venn diagram shows the numbers of species found in the upper quartile for functional rarity in each system. There is a small overlap (39%) where a species is rare in both systems. The right panel shows the overlap between the systems for taxonomic rarity (restrictedness), only 6% of species are taxonomically rare (upper quartile) in both systems..... 137

**Figure 6.10:** The alluvial plots represent the connections between the different Gotelli classifications. The numbers of species falling into the category combinations is used to create ‘flows’ between the columns. The west coast is on the left and east coast on the right. Upper panel represents functional rarity whilst the lower panel is taxonomic rarity in the form of restrictedness. The flows are coloured according to their core status, ‘Core’ in dark blue and ‘Transient’ in plum. .... 139

## List of Tables

<b>Table 2.1:</b> Description of the reproductive strategies of study fish with species examples. ....	37
<b>Table 2.2:</b> Body shape descriptions with illustrations and examples from the study fish.....	38
<b>Table 2.3:</b> descriptions and examples of study fish for position in the water column. ....	39
<b>Table 2.4:</b> Details and examples of the different swimming modes utilised by the study fish .....	40
<b>Table 2.5:</b> Table listing the main diversity indices used throughout this thesis, fuller descriptions of the methodology and equations found in the relevant sections. ....	55
<b>Table 4.1:</b> Results of correlation measures of similarity between systems through the decades. The cophenetic correlation and Baker’s Gamma metrics are scaled between -1 and 1 with values close to zero indicating little or no statistical similarity between trees whilst the entanglement measure ranges from 0 to 1 with values close to zero representing no entanglement (or similarity). ....	93
<b>Table 5.1:</b> Regression slopes (OLS) for each metric are shown by latitudinal band, here they are ordered by coast and latitude with the more northerly latitudes being listed first. These slopes are the same as the ones illustrated in Figure 5.7 and the full set of summary statistics for metrics provided in Appendix 5.2. ....	111
<b>Table 5.2:</b> This table shows mock changes to evenness, mean functional and taxonomic rarity and the rarity values for the most and least distinctive fish in the assemblage. This toy example contains the same ten species and always has 100 individuals – the only change is the distribution of these individuals amongst species. These are extreme and unlikely scenarios but illustrate how abundance changes to certain species can affect the collective rarity of the assemblage.....	115
<b>Table 6.1:</b> The top ten contributors to change in Jaccard type dissimilarity for both Chao-Ricotta $q_1$ and $q_2$ , shown here alongside the different categories from other sections, namely the Gotelli classification and the upper quartile (top 75%) of rare species from the functional and taxonomic rarity metrics, (see Appendix 6.1 for details and values of all species).....	134
<b>Table 6.2:</b> Table showing the species in the upper quartile for both systems for functional and taxonomic rarity and the Gotelli categories they fall into for each coastal system. ....	138

## Chapter One – General Introduction



*Anstruther Harbour, circa 1860.*



## Chapter One - General Introduction

### 1.1 Background

Biodiversity is changing at unprecedented rates across the planet (Crutzen, 2006; Pereira *et al.*, 2010), and these changes can have severe impacts on species populations (Barnosky *et al.*, 2011; Dirzo *et al.*, 2014; Cafaro, 2015; Ceballos *et al.*, 2015; Briggs, 2017; Ceballos *et al.*, 2017) and consequently on human well-being (Shivanna, 2020). The threat of mass extinction is, however, not without precedent (MacArthur & Wilson, 1967; Jablonski, 2001; Benson *et al.*, 2021); previous changes in the world's landscape have resulted in the loss of multiple species from dinosaurs (Gould, 1992) to the dodo (Strickland & Mellville, 1848) and the evolution of many new species, not least of these being *Homo sapiens* (Stringer, 2016). This current biodiversity crisis (Pimm *et al.*, 2014; Steffen *et al.*, 2015a) is widely assumed to be the consequence of a combination of anthropogenic impacts including over exploitation (Trindade-Santos *et al.*, 2020), human impacts (Pimm *et al.*, 2006; Pievani, 2014; Pecl *et al.*, 2017; Bernardo-Madrid *et al.*, 2019; Ellis, 2019; Bowler *et al.*, 2020) such as change in land use and climate change (Hampe & Petit, 2005; Lavergne *et al.*, 2010; Ellis, 2011; Newbold, 2018). These factors can be seen as important drivers of community reorganisation and better understanding of these trends can contribute to improved conservation and management policies (Brondízio *et al.*, 2019; Brondizio *et al.*, 2019; Rosa *et al.*, 2020; Ruckelshaus *et al.*, 2020). Furthermore, studies have shown that the changes to biodiversity differ between the realms (Bowler *et al.*, 2017), particularly when comparing the marine and terrestrial realms (Bowler *et al.*, 2018; Pinsky *et al.*, 2019). Blowes *et al.* (Blowes *et al.*, 2019b) found that compositional change in the marine realm exceeded the global average and could be up to four times more than the terrestrial realm, particularly in the tropical regions (Antão *et al.*, 2020).

Much of marine fisheries research to date has focused on single stock assessments (Branch *et al.*, 2011; Cadrin & Dickey-Collas, 2014) rather than revealing diversity change from a whole assemblage approach. This thesis takes a different, and integrated, approach to assessing and monitoring fish diversity. It does so by examining a range of methods that quantify change from an assemblage point of view and identify influential species in the change process. These analyses are carried out on two consistently sampled time series of thirty years duration. Any formal analyses of time series data benefit from longer length as a larger sample size will lead to more robust results (Wauchope *et al.*, 2019; Harvey *et al.*, 2020)

In the terrestrial realm projections suggest that if no action is taken then there are numerous species at risk of decline and even extinction (Powers & Jetz, 2019), mainly as a result of substantial increases in land use (Morelli *et al.*, 2017; Oliveira Hagen *et al.*, 2017; Maskell *et al.*, 2019; Daskalova *et al.*, 2020), including permanent deforestation for commercial gain (Curtis *et al.*, 2018) and habitat degradation (Li *et al.*, 2022), particularly over the last 200 years (Narisma & Pitman, 2003). This has consequences for the species traditionally occupying these habitats (Betts *et al.*, 2017). Alongside the devastation these environmental changes can have on species loss are the effects on human welfare (Bond *et al.*, 2019). Landscape transformation and the agricultural repurposing of many traditional habitats is a complex issue, which has multiple effects, not only on biodiversity, but also on those peoples occupying the areas (Blaikie & Jeanrenaud,

1997; Wilkie *et al.*, 2006; Chan *et al.*, 2007; Nguyen *et al.*, 2019; Kendal *et al.*, 2020; Shivanna, 2020) and it is sometimes difficult to successfully combine approaches to reach positive outcomes for both society and biodiversity (Kremen & Merenlender, 2018; Nguyen *et al.*, 2019). The actions taken now can affect the future well-being of both society and biodiversity (Pyron & Pennell, 2022).

In the freshwater realm, biodiversity change can have severe consequences (Albert *et al.*, 2021; Su *et al.*, 2021). Freshwater systems provide important resources for society, including transportation, recreation, waste disposal and human food, water and energy provision (Hoekstra & Mekonnen, 2012). Furthermore, although freshwater systems represent only around 0.8% of the earth's surface (Dudgeon *et al.*, 2006), they contain around one third of vertebrate species (Strayer & Dudgeon, 2010), including around 12% of all identified species (Albert *et al.*, 2021). Human interference has resulted in much greater loss of habitat here than in the terrestrial realm (Tickner *et al.*, 2020). Additionally, both human impact and biodiversity loss are occurring at faster rates than in the terrestrial realm (Turak *et al.*, 2017; Reid *et al.*, 2019).

Similarly, the marine realm is changing at unprecedented rates, often more rapidly than in the terrestrial realm (Blowes *et al.*, 2019b). These changes are driven by a combination of factors (Jennings *et al.*, 2009; Kaiser *et al.*, 2011), including habitat loss (Kaiser *et al.*, 2002; McCauley *et al.*, 2015; Yan *et al.*, 2021), over exploitation of fish stocks (Ye & Gutierrez, 2017; Trindade-Santos *et al.*, 2020), warming waters (Perry *et al.*, 2005; Hiddink & Ter Hofstede, 2008; Brander, 2010a; Pörtner & Peck, 2010; Quentin Grafton, 2010; Rogers *et al.*, 2011; Poloczanska *et al.*, 2013; Engelhard *et al.*, 2014; Cheung, 2018; Wabnitz *et al.*, 2018; McLean *et al.*, 2019c; Fredston-Hermann *et al.*, 2020; Chaikin *et al.*, 2021; Stuart-Smith, 2021; Zhao *et al.*, 2022) and pollution (Shahidul Islam & Tanaka, 2004). Worldwide, the fishing industry supports around 12% of the population (Garibaldi, 2012) as well as being the main source of protein to around three billion people (WFP & UNICEF, 2022). It is therefore important (Bridgewater, 2016) that we balance the realities of human impact and human needs (Steffen *et al.*, 2015b) in order to protect our lands, rivers and oceans and ensure they remain sustainable. However, there are still substantial knowledge gaps about the extent of biodiversity change, and about the consequences of this change (Pereira *et al.*, 2012). Addressing these gaps means taking into account differences between realms and geographic regions, and balancing biodiversity conservation with societal well-being, particularly in areas of deprivation (Pecl *et al.*, 2017).

### **1.1.1 Marine biodiversity**

Marine biodiversity is a field in itself with its own challenges (Gray, 1997). There have been numerous studies looking at the recent temporal and spatial changes in fish diversity (Bremner *et al.*, 2003; Beaugrand *et al.*, 2015; Elahi *et al.*, 2015; Kowalewski *et al.*, 2015; Dencker *et al.*, 2017; Wabnitz *et al.*, 2018; Rogers *et al.*, 2019; Myers *et al.*, 2021; Eme *et al.*, 2022). Many marine communities have undergone significant change over recent times, often taking place over just decades (Magurran *et al.*, 2015b), and these changes can be driven by both natural and anthropogenic drivers (Kowalewski *et al.*, 2015). Nevertheless, it is widely recognised that human impacts can be responsible for the exacerbation of these changes (Harley *et al.*, 2006; Hoegh-Guldberg & Bruno, 2010; Gilarranz *et al.*, 2016; Poloczanska *et al.*, 2016), whether directly, as with overfishing (Beamish

*et al.*, 2006; Yan *et al.*, 2021) and climate change (Perry *et al.*, 2005; Hiddink & Ter Hofstede, 2008; Bruno *et al.*, 2018; Maureaud *et al.*, 2021; Stuart-Smith, 2021; Santana-Falcón & Sférian, 2022) or indirectly (Scheffer *et al.*, 2005), as a result of the dynamics of ecological communities. For example, the introduction of invasive species (Edelist *et al.*, 2013), species range shifts (Perry *et al.*, 2005; McHenry *et al.*, 2019; Stuart-Smith, 2021), changes to trophic structure (van der Veer *et al.*, 2015), energy availability (Woolley *et al.*, 2016) or alteration of predator-prey interactions (Frank *et al.*, 2005; Ellingsen *et al.*, 2015b; Ellingsen *et al.*, 2020) which can have cascading effects on assemblages (Corrales *et al.*, 2017). Increases in water temperatures can result in unexpected distributions of species (Perry *et al.*, 2005), some of whom adapt well (Sguotti *et al.*, 2016; Fredston-Hermann *et al.*, 2020; Chaikin *et al.*, 2021), and others, such as the common dab, *Limanda limanda*, (Linnaeus, 1758), which can be constrained by their adaptability to depth (Rutterford *et al.*, 2015).

Overexploitation of marine fish has been taking place over centuries (Jackson *et al.*, 2001; Jackson, 2008) with often catastrophic effects on fish stocks (Harris, 1999) such as the collapse of the Norwegian herring, *Clupea harengus* (Linnaeus, 1758) (Lorentzen & Hannesson, 2006) in the 1960s and 1970s. Despite the long term trends of overexploitation (Holm *et al.*, 2019), the advent of steam trawlers, followed by diesel vessels and further advances in gears and technology meant that the twentieth century saw increased demands on the marine realm (Garstang, 1900, 1919; Knauss, 2005; Thurstan *et al.*, 2010). However, the last sixty years have seen huge declines in fish stocks (Roberts, 2007) with total collapse of some important commercial species such as Atlantic herring, *Clupea harengus* (Linnaeus, 1758) and Atlantic cod, *Gadus morhua* (Linnaeus, 1758) (Drinkwater *et al.*, 2018; Trochta *et al.*, 2020). Furthermore, it is now recognised that the depletion of commercially important species is not the only concern for this marine biodiversity, as many of the methods used, particularly in subsistence fishing areas, have implications for other marine life (Northridge *et al.*, 2016) such as marine mammals (Burgess *et al.*, 2018) and seabirds (Grémillet *et al.*, 2018; Fayet *et al.*, 2021). There is also an increasing awareness of the cascading effects on marine assemblages when key species are removed (Frank *et al.*, 2005; Scheffer *et al.*, 2005; Casini *et al.*, 2009), in addition to the broadening of fisheries targets to include previously commercially unattractive species such as monkfish (or angler), *Lophius piscatorius* (Linnaeus, 1758) (Government, 1922 - 2015). Recent work has also identified the increase of functionally diverse species (Trindade-Santos *et al.*, 2020; Dulvy *et al.*, 2021) being targeted, which can have implications for fish communities (Dee *et al.*, 2016; Rincón-Díaz *et al.*, 2021).

Overexploitation is not the only human impact threatening the marine world; other anthropogenic factors such as climate change and water pollution contribute to the challenges fish face (Halpern *et al.*, 2008). Warming sea temperatures can often have severe implications for marine fishes, leading to range shifts (Hiddink *et al.*, 2014; Poloczanska *et al.*, 2016; McHenry *et al.*, 2019; Stuart-Smith, 2021), decreases in body size (Brander, 2010b; Genner *et al.*, 2010; Rogers *et al.*, 2011), compositional reorganisation of assemblages (Magurran *et al.*, 2015b; Gotelli *et al.*, 2021) and even complete collapses of fish stocks (Hutchings & Reynolds, 2004; Pershing *et al.*, 2015; Drinkwater *et al.*, 2018) such as the Atlantic cod, *Gadus morhua* (Linnaeus, 1758). It is clear that climate change impacts upon the fishing industry (Brander, 2010a; Pörtner & Peck, 2010; ter Hofstede & Rijnsdorp, 2011; Engelhard *et al.*, 2014; Schartup *et al.*, 2019; Pinnegar *et al.*, 2020; Zhao *et al.*, 2022) both directly and indirectly, often leading to an increased negative influence on the biodiversity of fish communities (Planque *et al.*, 2010). By attempting to understand how climate change can impact marine assemblages and as a result

interpret the implications for fisheries (Jennings & Brander, 2010) it is possible to tailor management policies more accurately and efficiently rather than using a ‘one size fits all’ approach (Smith & Link, 2005; Hilborn *et al.*, 2020). In developing future management plans it is important to maintain and sustain these important marine systems whilst taking account of the consequences of the combination of climate change and fishing (Perry *et al.*, 2010; Weatherdon *et al.*, 2016).

Despite the apparent gloomy outlook (Garcia & Grainger, 2005), the introduction of sustainable fishing policies (Benson & Stephenson, 2018; Froese *et al.*, 2018; Gordon *et al.*, 2018) and marine protected areas (Rodríguez-Rodríguez *et al.*, 2016) has led to revitalised fish stocks in many parts of the world (Davies *et al.*, 2022). However, these do not always focus on whole assemblage assessments and as such may not always effectively protect the most vulnerable species (Trindade-Santos *et al.*, 2022). This reinforces the need for ecosystem-based approaches towards fisheries management (Serpetti *et al.*, 2017; Nielsen *et al.*, 2018a; Trochta *et al.*, 2018; Piet *et al.*, 2019), or an integrated system (Hammer *et al.*, 1993) evaluating the assemblage and not only the population.

### **1.1.2 Taxonomic and functional diversity**

Biodiversity can be challenging to define (Hamilton, 2005) but captures a number of different elements including numbers and types of species, and the interactions within community groups. Biodiversity is multifaceted and here I focus on two dimensions, namely taxonomic and functional diversity.

Taxonomic diversity investigates the diversity of species within a site, this uses species identities and/or abundances to examine the contents of an assemblage at a given time point. Taxonomic diversity can be considered as alpha diversity, which measures a single site at a particular time, or beta diversity which compares between different sites or the same site at different time points. Alpha diversity can be measured using numerous techniques (Magurran, 2013b; Santini *et al.*, 2017; Moreno *et al.*, 2018) ranging from a simple count of the number of distinct species found, to complex statistical frameworks such as the MoB (McGlinn *et al.*, 2019) method developed by McGlinn *et al.* The concept of beta diversity was first introduced by Whittaker (Whittaker, 1960) but Paul Jaccard (Jaccard, 1912) had already developed his index of comparison of fauna between sites in 1908 (Jaccard, 1908). The Jaccard metric takes no account of species abundances, only presence/absence but, as with alpha diversity, there are numerous methods available to calculate the beta diversity of sites, both including and excluding abundance (Wilson & Shmida, 1984; Koleff *et al.*, 2003; Magurran, 2013b; Magurran *et al.*, 2019).

It is becoming more evident that the quantification of biodiversity change is more than just taxonomic analysis and ecologists are now examining functional diversity much more frequently in their work (Laureto *et al.*, 2015). Functional diversity evaluates the diversity of traits within a site or assemblage. As with taxonomic diversity, there are multiple methods available to quantify changes in functional diversity, once again, both including and excluding species abundances (Mouillot *et al.*, 2013a; Villéger *et al.*, 2017; Magneville *et al.*,

2021). Although functional beta diversity can also be quantified, in this thesis I focus only on alpha functional diversity measures.

The use of functional diversity in addition to taxonomic diversity can add a further layer of information regarding an assemblage (Cadotte, 2011; Cadotte *et al.*, 2011; Gagic *et al.*, 2015). For example, considering a small local fish assemblage with one hundred individuals belonging to a total of six species, it is possible to see very different types of communities if trait combinations are also considered (see Chapter 2.3 for details). Additionally, functional diversity can help us understand how species respond to their environments given their traits and trait combinations. This approach can reveal a more mechanistic view of the structures underlying the way biodiversity responds to environmental changes. Furthermore, it reveals how different combinations of species can affect ecosystem functioning (Petchey & Gaston, 2006; Villéger *et al.*, 2010). Assemblages exhibiting decreases in functional diversity are less likely to be able to respond positively to environmental change (Mouillot *et al.*, 2011b; Mouillot *et al.*, 2013b).

## **1.2 Scottish background**

My interest is in the marine diversity of the fish assemblages around Scotland and how these have changed over the last thirty years. My data come from two systematic scientific trawl surveys undertaken by the International Council for the Exploration of the Sea (ICES) (ICES, 2014) and are mapped by location to twenty latitudinal bands (see Chapter 2.1 and 2.2 for further details). These data represent two distinct ecosystems to the west and east coast of Scotland and belong in part to the large marine ecosystems: the North Sea (east coast) and the Celtic-Biscay Shelf (west coast). As such the systems consist of different habitats and tidal currents (Heessen *et al.*, 2015; ICES, 2018c, 2019) although the fish populations are largely similar (see Appendix 2.2 for full species list).

Scotland has a long tradition of fishing (Museum), and indeed the industry still contributes substantially to the economy (Government, 2021). However, the strength of the fishing industry has declined significantly over the last two centuries, particularly since public awareness of declining fish stocks grew in the mid-1970s. The East Neuk of Fife was a particularly rich source of fish and in fact, King James VI coined the phrase ‘a beggars mantle fringed with gold’ to describe the Fife area because of the rich seam of fish around the coast. In the 19<sup>th</sup> century, Anstruther was an important port and trading centre for fisheries, particularly the herring industry which was significant at the time. It was the richest town in Scotland at the height of the herring boom and the Dutch, who were prominent in the herring industry of the time, influence is evident in some of the architecture even today. The decline of the fishing industry in these regions, particularly on the east coast of Scotland has had implications for the socio-economics of the areas (Government, 2002; Stead, 2005). These implications are evident in the changing face of these harbour ports, which, in many cases, have moved from vibrant fishing villages to mainly retirement and holiday homes (Museum). The fishing villages on the west coast of Scotland appear to have fared rather better than those on the east coast, apart from the areas at the Firth of Clyde. Most of the fisheries to the west coast have historically been smaller scale operations (Museum), often family led, and as such they appear to have adapted to change somewhat more successfully than their east coast counterparts.

Many of the smaller west coast fisheries diversified to inshore creel fishing for shellfish such as the European lobster, *Homarus gammarus* (Linnaeus, 1758) or Dublin Bay prawn, *Nephrops norvegicus* (Linnaeus, 1758) and fishers here appear to be more amenable to change (McGoodwin, 2001; Ford & Stewart, 2021) particularly with the introduction of co-operative management trials (Noble, 2003; Nielsen *et al.*, 2019).

Although it is likely that overexploitation of fish has contributed to some of the changes in the assemblages in these systems, there are other possible drivers such as climate change (Baudron *et al.*, 2013; Magurran *et al.*, 2015b; Moyes & Magurran, 2019). It seems likely that a combination of anthropogenic factors has led to the changes found in Scottish waters, for example, the comparison of the abundance of demersal fish catches in the North Sea and other UK waters (Rijnsdorp *et al.*, 1996; Rogers & Ellis, 2000) from the early twentieth century to the latter part and the history of two hundred years in the Firth of Clyde (Thurstan & Roberts, 2010). However, it is not only changed abundances that are noted, changes in body size are also recorded (Baudron *et al.*, 2013; Hunter *et al.*, 2016) and range shifts and community reorganisation documented (Magurran *et al.*, 2015b; McLean *et al.*, 2019a; Moyes & Magurran, 2019; Murgier *et al.*, 2021b).

The fisheries management policies and procedures that have been in place since the mid to late twentieth century (Government, 2013, 2014; Commission, 2015; Government, 2021) have gone some way to alleviate the pressures on this valuable natural resource but until recently these have been largely based on the quantification of individual populations and recruitment/spawning (Government, 2013, 2014; Froese *et al.*, 2018; Government, 2021), and current thinking suggests that an ecosystem based approach could provide a better strategy (Trochta *et al.*, 2018; Piet *et al.*, 2019). This ecosystem based approach includes functional and taxonomic aspects and can provide a valuable indicator of resilience (Rincón-Díaz *et al.*, 2021). Changes within a fish community are not only dependent upon the fish occupying the assemblage but also on the interactions between the inhabitants, so taking account of these important factors (Aune *et al.*, 2018; McLean *et al.*, 2019c; Pecuchet *et al.*, 2019) could be beneficial when designing any type of marine or fishing policy.

Despite this increased awareness towards fisheries management policy there is a fundamental need to quantify trends in biodiversity at the assemblage level as this is something that has historically received little interest due to a greater focus on population-based assessments rather than ecological communities. I hope that by creating a clearer picture of trends in Scottish marine fish diversity over recent decades, with the focus on whole assemblage assessment, my work can aid policy makers in their decision-making process.

### **1.3 Goals of this thesis**

My main aim in carrying out this research is to provide an informed analysis of spatial and temporal variation in Scottish marine fish biodiversity, and to document the patterns found. My work takes an integrative approach to quantifying biodiversity change by involving both taxonomic and functional diversity (Devictor *et al.*, 2010). My overarching question in this work is to ask how the biodiversity of marine fish assemblages around Scotland has changed over the last 30 years. I am also interested in change in spatial biodiversity patterns. For example, are the changes I find consistent for the ecosystems to the east and west coast of Scotland, and are there latitudinal trends in patterns of change? Because I investigate biodiversity change using both taxonomic and

functional metrics, I am also keen to ascertain whether there are correlations between the different measures and, once again, if these are consistent across systems. Additionally, as I am interested in the identities of the fish species driving compositional change, I ask which species make the greatest contributions to compositional reorganisation, and whether the same species are influential drivers of change in the different systems.

### **1.3.1 Taxonomic diversity – changes in diversity over three decades**

My first research chapter (see Chapter Three) investigates changes in taxonomic diversity over the last thirty years. Here my primary question is to ask how the taxonomic diversity of the two distinct coastal systems to the east and west of Scotland has changed. Here I also examine the identities of the dominant species and ask if these have changed over time. To quantify these changes, I adopt a statistical framework of diversity measures based on the Hill (Hill, 1973) numbers and use these, coupled with numerical abundance and relative dominance, to classify assemblage level change in diversity as well as identifying the most dominant species in each system for each decade (and latitude). This chapter investigates the assemblage level changes in numerical abundance, relative dominance and four orders of Hill numbers,  $q_0$ ,  $q_1$ ,  $q_2$  and  $q_\infty$  (see Chapter 3.2 for details on these methods).

The heterogeneity of the coasts suggests that I will be able to reject my null hypothesis of no difference in diversity trends between the systems. The North Sea system has historically experienced more intensive fishing practices (Stamoulis & Torreale, 2016; ICES, 2018a) in the past (see Chapter 5.3, Figure 5.15 for details) and has undergone greater sea surface temperature warming (Baudron *et al.*, 2013; ICES, 2018c, 2019) (see Chapter 2.2 for further details) which leads me to expect more change in the northerly latitudes for the east coast system as rising sea surface temperatures can lead to greater range shifts among fishes (Perry *et al.*, 2005; Dulvy *et al.*, 2008; Fredston-Hermann *et al.*, 2020).

### **1.3.2 Functional diversity – patterns of change over thirty years**

In my second research chapter (see Chapter Four) I quantify the changes in functional diversity using three well studied metrics (Villéger *et al.*, 2017; Magneville *et al.*, 2021): functional richness, functional evenness and functional divergence. I identify temporal change within and between the coastal systems before examining the correlations between these and the taxonomic results from Chapter Three. I then investigate the correlations between these functional diversity measures and the taxonomic metrics discussed in Chapter Three. I do this with the aim of gaining a better understanding how connected these facets of biodiversity are to each other as this can be helpful in the overall understanding of these systems (Cilleros *et al.*, 2016; Morelli *et al.*, 2017; Morelli *et al.*, 2018; Lamothe *et al.*, 2020; Baker *et al.*, 2021; Mattos *et al.*, 2022). In the final section of this chapter, I look at the hierarchical clustering for each system and quantify how related the systems are. I do this by decade to give an overall view of the changes found. As in Chapter Three, I expect to reject the null hypothesis of no difference between coastal systems, I also expect to find strong correlations between taxonomic and functional metrics.

### **1.3.3 Temporal and spatial rarity – geographical patterns and changes through time**

In my third research chapter (see Chapter Five) I examine rarity from a taxonomic and functional viewpoint using well established methods (Grenié *et al.*, 2017). The main purpose of this chapter is to investigate how rarity is changing over the three decades of my study system. I focus on trends in rarity to ask how taxonomic rarity and functional rarity covary over time and how these perform against a null expectation. My prediction in this chapter is that despite the distinctions between systems, the similarity of the species pools for the coasts makes it unlikely that patterns of rarity will be substantially different. A second aim is to link any changes in rarity with the structural changes in the underlying assemblages and trait distributions (Gross *et al.*, 2021). Again, my approach is to ask if I can reject the null hypothesis of no difference between east and west systems.

### **1.3.4 Compositional change and rarity**

The fourth research chapter (see Chapter Six) focuses on the compositional changes found in the coastal systems. Here I investigate compositional change and use a range of approaches, including both classical beta diversity indices (Jaccard, 1908; Morisita, 1959) and two recently developed methods (Chao & Ricotta, 2019; Gotelli *et al.*, 2021), to identify those species contributing most to change. I also categorise each species according to the role they play within the assemblage (their functional rarity), their spatial distribution (their taxonomic rarity) and their temporal persistence (core/transient). My expectation, based on Gotelli *et al.* (Gotelli *et al.*, 2021), is that only a few species will be influential in driving change, but that the identities of the species will differ between the systems. In identifying species contributions to change in these ways, I hope to gain a better understanding of how species' losses, or replacements are influencing the functioning of the overall systems (Basile, 2022).

In examining the individual strands within these chapters I aim to identify linking factors which produce a clear picture of the temporal changes (Rijnsdorp *et al.*, 1996) in Scotland's fish assemblages. A better understanding of how fish communities change through time can contribute to the broader picture needed for the successful maintenance of a sustainable (Sinclair *et al.*, 2002) fishing industry. I hope that my work might further better relationships (Mackinson, 2001) and links between science and industry.

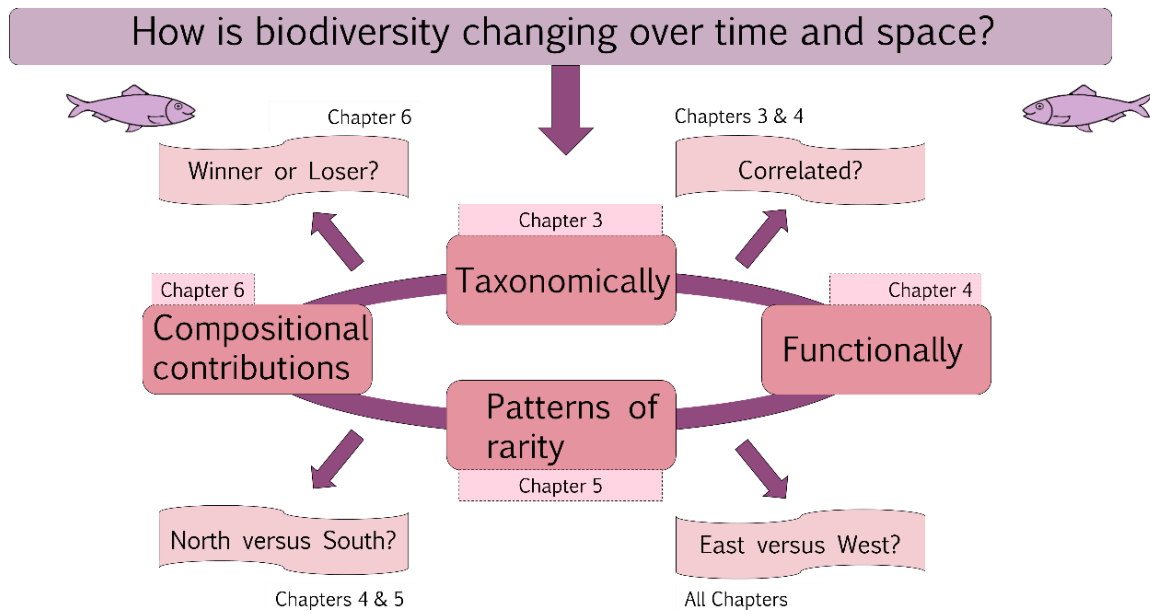
## **1.4 Thesis structure**

The overarching question within my thesis is “how is the biodiversity of these Scottish fish assemblages changing over both time and space?” and as such I address different aspects of this theme in each chapter. A broad overview of my thesis structure is as follows:

- I. Chapter One – General Introduction (this chapter)
- II. Chapter Two – General Methods and Materials
- III. Chapter Three - Taxonomic diversity – changes in diversity over three decades
- IV. Chapter Four - Functional diversity – patterns of change over thirty years



- V. Chapter Five - Temporal and spatial rarity – geographical patterns and changes through time
- VI. Chapter Six - Compositional change and rarity
- VII. Chapter Seven – General Discussion



**Figure 1.1:** This figure outlines the aims and questions addressed in my thesis. The overarching question in this thesis is “how has the spatial and temporal biodiversity of two distinct systems changed over time?” This initial question leads into several secondary questions on the topic, which are addressed in separate chapters examining taxonomic change, functional change, patterns of rarity and contributions to compositional change. The thesis further identifies several supplementary themes which are explored in one or more chapters, namely, the relationships between the east coast and west coast systems; the variation from north to south through the medium of latitudinal bands; how correlated the dimensions of diversity are and which species are ‘winning’ and ‘losing’ over time.

## Chapter Two – General Methods and Materials



*Lower Largo Harbour, circa 1860*

## Chapter Two – General Methods and Materials

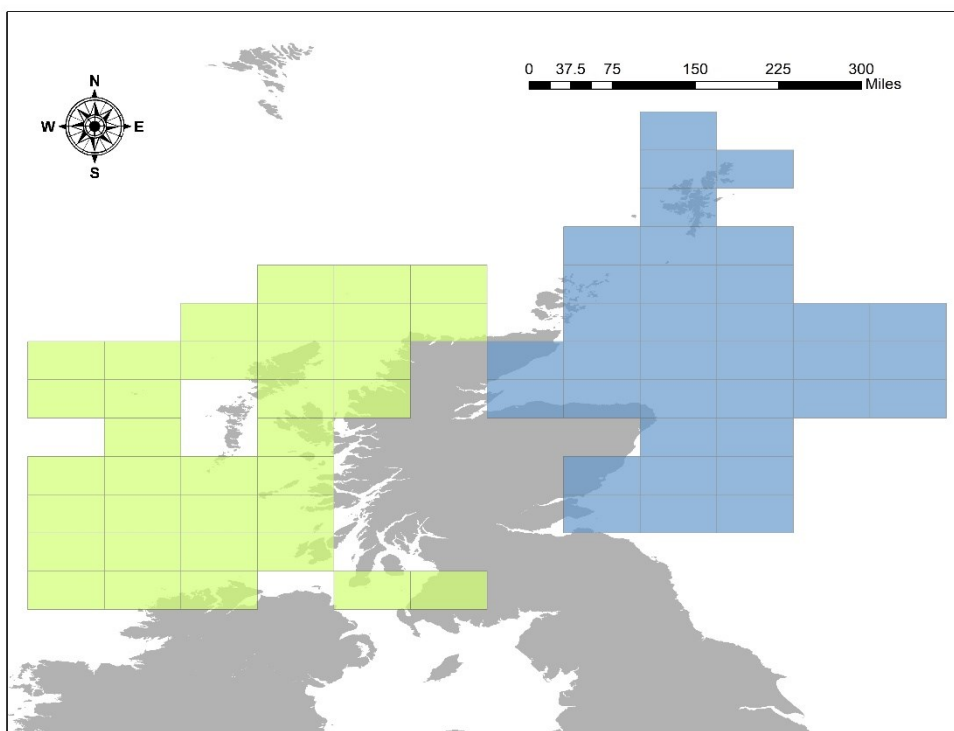
This chapter details the main materials and methods used throughout this thesis; more specialised methods not included here will be described in the relevant chapters.

### 2.1 Study site and data

Many of the underlying data used in this thesis were sourced from the International Council for the Exploration of the Sea (ICES). Their scientific surveys and spatial information are freely available on their website (<https://www.ices.dk/data/maps/Pages/default.aspx>), and the research data underpinning this thesis are available at <https://doi.org/10.17630/d4c3ab21-b14b-4365-8d67-c27c998e5a29>. There is also a large selection of associated spatial information available from ICES including the ICES ecoregions, ICES statistical areas and ICES statistical rectangles. Here I chose those areas (see Figure 2.1) most closely aligned to the scientific trawl survey data available. My work in research chapters three, four and five focus mainly on the ICES statistical rectangles (see Figure 2.2). These rectangles represent 30' latitude by 1° longitude grid cell and can also be downloaded from the ICES website (ICES, 2014). I use the rectangles as a basis for my study sites by merging them longitudinally to create 'latitudinal bands' for each coastal system.



**Figure 2.1:** Full study site showing the three ICES areas used in this thesis, they are labelled by name and filled with pale green for the West Coast and pale blue for the North Sea sites. These colours corresponding to coastal system are constant throughout this thesis.



**Figure 2.2:** ICES rectangles coloured by coastal system, pale blue for the North Sea and pale green for the West Coast survey.

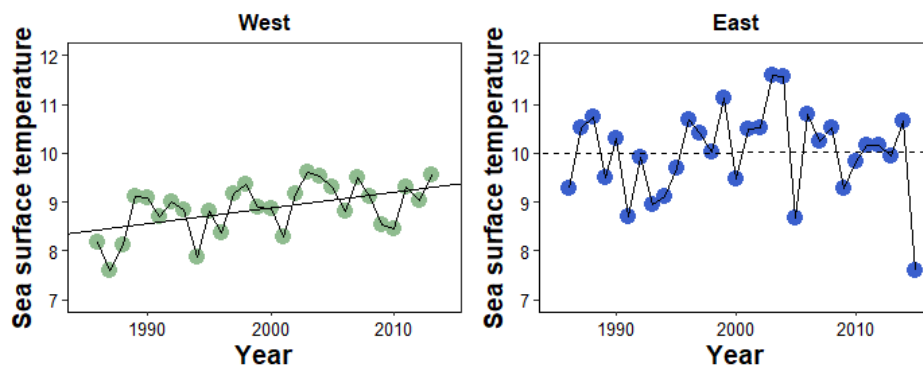
Species abundance data were also sourced from the ICES portal (ICES, 2014). These data come from two standardised scientific surveys incorporating the ICES areas VIa (West Coast), IVa and IVb (North Sea) (see Figure 2.1). My work draws on the full datasets available but not all years and/or locations are utilised in all chapters. Each species record contains a precise geographical location and numerical species abundance represented by CPUE (catch per unit effort) which in this instance refers to the number of individuals of a given species caught per hour using a tow duration of half an hour. Trawl speed is measured as 4 knots and although there are various gears in use in the North Sea surveys, this thesis focuses only on the Grande Overture Verticale (GOV) gear, a type of bottom trawl net with a small mesh which is the gear in use for the west coast surveys. The GOV trawl method is now the recommended gear for all bottom trawl surveys carried out by ICES. There are numerous gears available for industrial fishing (Greenstreet *et al.*, 1999; Sala *et al.*, 2015), most of which are specifically tailored to the target catch, for example, the pelagic pair trawl is often used when targeting shoaling species such as herring, *Clupea harengus* (Linnaeus 1758), mackerel, *Scomber scombrus* (Linnaeus 1758) or sprat, *Sprattus sprattus* (Linnaeus 1758). The use of a multispecies gear such as the GOV trawl is beneficial when performing scientific surveys as this means more species can be identified and recorded, than when using more species-specific gears such as the purse seine for Atlantic salmon, *Salmo salar* (Linnaeus 1758) or gillnets for European hake, *Merluccius merluccius* (Linnaeus, 1758). The consistency of use is also important for ease of comparison between areas and/or time periods. A full description and figures detailing the gear can be found in the ICES Manual for the International Bottom Trawl Surveys (ICES, 2022). Additionally, a comparative study carried out in 2012 (Reid *et al.*, 2012) showed that the results of trawling using this gear performed similarly to

that done using a standard commercial trawl. Although the earlier surveys in the North Sea ICES area use a variety of different gears, in this thesis I focus primarily on the years with the GOV trawl gear.

There are distinct coastal ecosystems to the east and west of Scotland. The West Coast system (part of the overall Celtic Seas ecoregion) is mostly relatively shallow particularly in the Irish Sea area where depth is typically < 100 metres. The different components of the system (e.g. Malin Sea, Irish Sea, Rockall Trough) with diverse structures such as sandbanks and rocky outcrops lead to a variety of habitats (Heessen *et al.*, 2015). The system is largely sheltered from the winds and currents of the North Atlantic and water circulation patterns are influenced by freshwater discharge from rivers such as the Severn and the Shannon as well as the many sea lochs found on the west coast of Scotland (Nolan & Lyons, 2006). Long term datasets (ICES, 2019) indicate an overall rise in both temperature and salinity, however, these trends appear to peak in 2006 and subsequently show slight but steady declines. The North Sea system in contrast exhibits temperature trends that appear to be linked to seasonal ecosystem changes (ICES, 2018c) in addition to the effects of the Multidecadal Oscillation of the Northern Atlantic. The North Sea system is semi enclosed and includes the Norwegian Deeps in the north-eastern portion where depths can be up to 700 metres. Much of the remainder of the ecosystem is relatively shallow with large estuarine areas. This system is affected by several currents bringing Atlantic water, and the major currents involved form a clockwise type pattern (Otto *et al.*, 1990) leading to heterogeneity of depth, temperature, salinity and substrate. The habitats are dominated by sand, mud and some harder grounds around the Orkney and Shetland islands and fluvial input includes that from major rivers such as the Rhine, Thames, Humber and Tees (Heessen *et al.*, 2015). These differences are important as the possible disparity between the two systems can have consequences for fisheries; for example, TACs (Total Allowable Catch) may not take into account that species abundances can be hugely variable between the east and west coasts (Heessen *et al.*, 2015; ICES, 2018c, 2019).

Although this work does not examine shifts in climate change in any detail as this is a complex science in itself with many dedicated papers on the subject, e.g., (Edwards & Richardson, 2004; Perry *et al.*, 2005; Harley *et al.*, 2006; Brander, 2010a; Burrows *et al.*, 2011; Philippart *et al.*, 2011; Comte & Olden, 2017; Bruno *et al.*, 2018; Cheung, 2018; Burrows *et al.*, 2019; Antão *et al.*, 2020; García Molinos, 2020), to provide context I do include sea surface temperatures sourced from the DATRAS portal. These temperature data are collected from a variety of monitoring vessels and consist of water surface temperatures taken from a depth of less than 10 m and measured in degrees Celsius. Temperatures are given at precise geographical points which are then mapped to their associated ICES (ICES, 2014) rectangle and corresponding latitudinal band. I calculate the mean temperature for each year across all the latitudinal bands separately for the two systems before calculating the slopes of change using a simple Ordinary Least Squares (OLS) regression.

Figure 2.3 reinforces the differences between the two coastal systems as mean sea surface temperatures across all latitudes increased through time by 1.3° C on the west coast. In contrast, change on the east coast was more muted with a mean increase of only around 0.7° C, only the west coast trend is significant (p-value=0.013, OLS regression).



**Figure 2.3:** This plot shows the mean sea surface temperatures across all latitudinal bands at each time step. An OLS regression was performed, and this trend line is added (solid line for significant as on the west coast and dashed for non-significant as on the east).

### 2.1.1 ICES scientific trawl survey – Scottish West Coast 1985 – 2014

The Scottish West Coast (SWC-IBTS) Groundfish Quarter 1 (DATRAS, 2015) survey takes place annually in January, February and March and spans 1985 to 2014. The available data were plotted by geographic location and mapped to the ICES statistical rectangles they fall within (see Figure 2.4). The ICES rectangles illustrated are those with the most consistently sampled trawl data available for all years of the study. This results in a set of 35 ICES rectangles from the West coast system featuring the most consistent examples of community time series (Magurran *et al.*, 2015a). Consequently, the resultant time series runs from 1985 to 2014 and spatial coverage is from latitudes at 55.5 degrees to 59.5 degrees.

### 2.1.2 ICES scientific trawl survey – North Sea 1965 – 2019

The North Sea International Bottom Trawl Survey (NS-IBTS) (DATRAS, 2019) is carried out biannually in the first and third quarters (first quarter being January, February and March and the third quarter July, August and September). The NS-IBTS spans 1965 – 2019 although gears and sampling effort are not consistent through time. My analyses focus mainly on those time series from 1985 to the present and from the first quarter as they are comparable with the West Coast survey in both gear utilisation and sampling effort. As before, each point is plotted to the precise geographic location given and subsequently mapped to the ICES statistical rectangle it falls within. The rectangles shown here are those chosen for the location and sampling consistency with the West Coast area.

The focus of my work is the portion of the North Sea (NS-IBTS) data that are directly comparable in years, sampling methods and gears used, to the West Coast (SWC-IBTS) survey data. In the North Sea system only data from Quarter 1 - 1985 to 2014 are used as both areas were surveyed consistently between these dates. This gives 35 consistently sampled ICES rectangles ranging from latitudes of 56.5 degrees to 61.5 degrees. These are subsequently used as a comparison for those 35 rectangles in the West Coast ecosystem.



The trawl surveys provide a sample of a wide range of species and sizes; the complete list of fish can be seen in Appendix 2.2. ICES surveys adhere to strict protocols (ICES, 2022) with all species within a haul identified to the lowest taxonomic level possible. Additional information is also recorded in these surveys, where possible, for length, age, sex and maturity, though these data are not used in this analysis.

Electronic equipment is used to monitor net geometry during all trawls; this allows for the appropriate adjustment of sweep length according to water depth (ICES, 2022). The depths where hauls are recorded range from 10m to 250m.



**Figure 2.4:** Complete set of ICES statistical rectangles for comparison work. Each point represents a record with species, numerical abundance, date and location information and has been mapped to the ICES rectangle it falls within.

All chapters feature latitudinal strips created by merging the ICES rectangles longitudinally, resulting in thirteen ‘bands’ across the region which can be subdivided into east and west coast areas (see Chapter 3 Figure 3.1).

### 2.1.3 Sampling effort

In some biodiversity studies, mainly those from the terrestrial realm such as the Barro Colorado Forest Census (Hubbell *et al.*, 2005) there is constant sampling effort throughout the project. A plot or sample site will have all individuals recorded at a given time and the same plot will be examined and recorded repeatedly for the duration of the project. Sampling effort between the two trawl surveys, and between sites (ICES rectangles, coastal systems or latitudinal bands) or years, however, is not constant. This would be a difficult task using trawls and

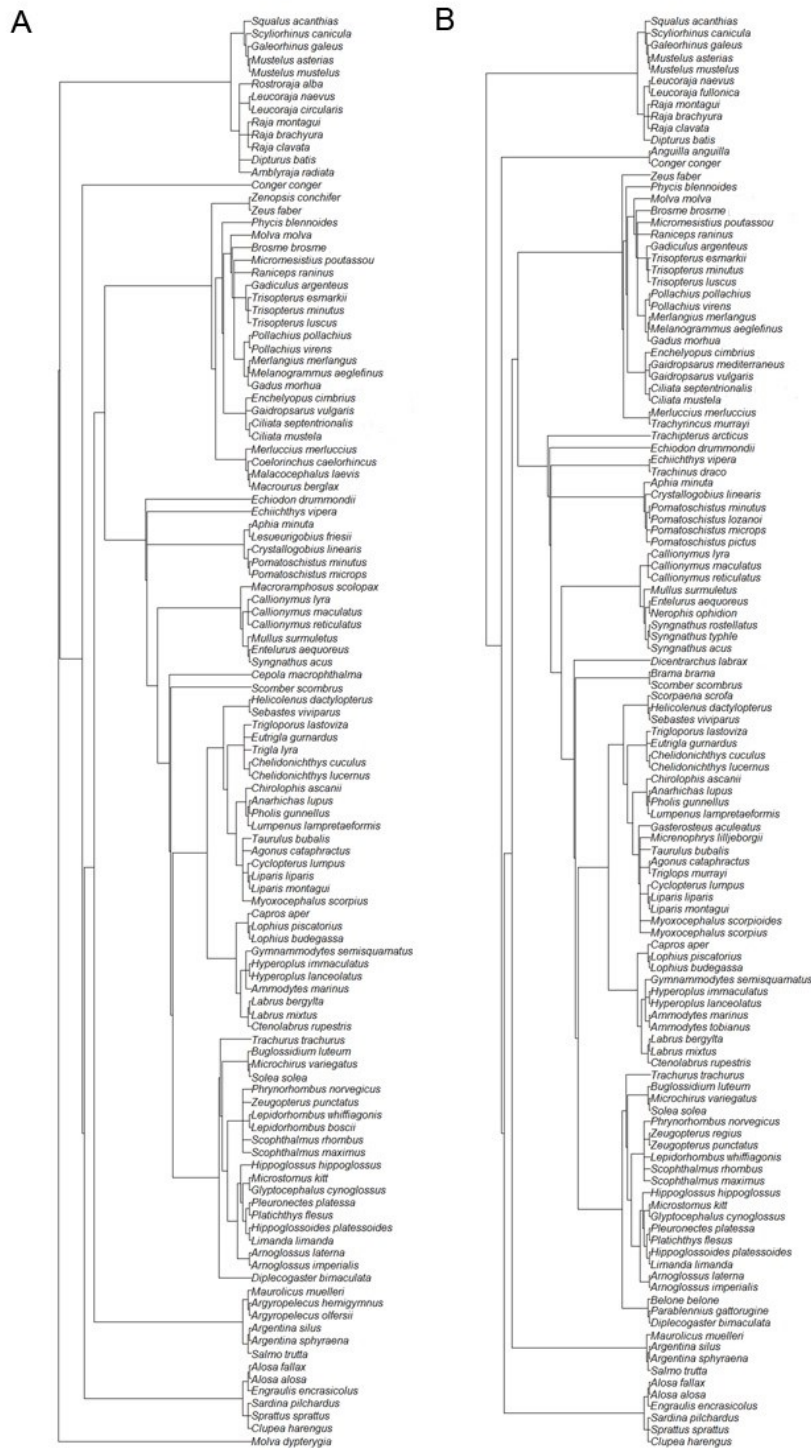
CPUE as it would be hard to revisit the same place for a trawl repeatedly. Although the geographic coordinates of the trawl position start are recorded on each occasion, these coordinates are not subsequently revisited deliberately on future trawls. The use of sample sites such as the ICES rectangles make it easier to group single locations into a larger area, but this still does not always give a consistent resampling effort through time (or between sites). To combat this problem and allow for a fair comparison between sites and/or years I use rarefaction techniques as detailed in section 2.3.2.

## **2.2 Study species**

The available data from DATRAS can be sourced using a variety of filters; here I select for all species to ensure that I have included both commercial and non-commercial fishes. Initial analyses in Chapter 3 include a few macroinvertebrates such as the European common squid *Alloteuthis subulata* (Lamarck, 1798) but subsequent work excludes these due to the lack of appropriate trait information available for the functional analyses. Most species can be found in both systems although there are several that are only located in one of the areas. Species all fall into one of two classes – Actinopterygii (ray-finned fish) and Elasmobranchii (cartilaginous fish, comprising mostly of sharks and rays). In both systems Actinopterygii make up most of the species list; on the West Coast there are 104 ray-finned fishes and 12 sharks and rays whilst the North Sea comprises 111 ray-finned fishes with 10 sharks and rays.

Although this thesis does not feature any phylogenetic diversity analyses (but see Chapter 7.3 for suggestions on future work), I produced the phylogenetic tree information for both coastal systems to illustrate similarities and differences in their phylogenetic diversity (see Figure 2.5).





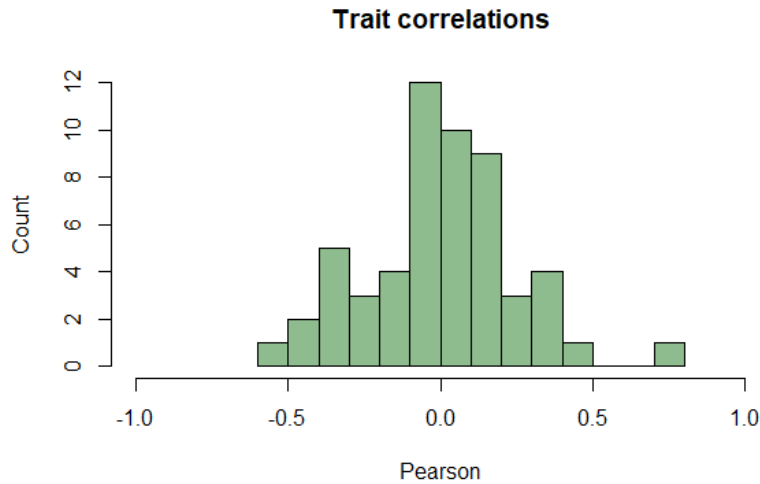
**Figure 2.5:** Phylogenetic trees for the two coastal systems. Left hand side (A) illustrates the species within the West coast (SWC-IBTS survey) and the right-hand side (B) the East coast species (NS-IBTS survey). This was generated in R using the package rotl which is an interface to the Open Tree of Life (Michonneau *et al.*, 2016).

### 2.2.1 Species information

As with the ecosystems themselves, there are some differences in the species found in each system; these differences may be influenced by disparity in fishing pressure but may also be linked to ecological factors (Heessen *et al.*, 2015; ICES, 2018c, 2019). Additionally, temperature can affect recruitment, migration, spawning and distribution of selected species such as blue whiting *Micromesistius poutassou* (Risso 1827), Atlantic mackerel *Scomber scombrus* (Linnaeus 1758), horse mackerel *Trachurus trachurus* (Linnaeus 1758) and some gadoids (ICES, 2019). The North Sea system is characterised by episodic changes in productivity which can lead to cyclical increases and decreases in abundances of many species and associated prey (ICES, 2018c). Additionally, there have been shifts in production from pelagic to benthic noted (ICES, 2018c) with many flat fish species such as the European plaice *Pleuronectes platessa* (Linnaeus 1758) increasing at unprecedented rates.

### 2.2.2 Trait information

I chose a combination of eleven traits, both continuous and categorical. In order to ensure there were no gaps in the values for the community species I included only those that could be identified using the information available on FishBase (Froese & Pauly, 2019). This process provided data for a total of 116 finfish for the west coast system and 121 for the east coast system. The traits were chosen as ones which were relatively independent of each other (see Figure 2.6).



**Figure 2.6:** Figure shows the pairwise correlations between all traits within the study fish. The Pearson correlations are calculated using the `pairs.panel` function in the `psych` package in R (Revelle, 2019), extracted and used to plot a histogram of their distribution. The values are largely uncorrelated and mainly centred around zero. The correlations represent the pairwise relationships between the values for each of the eleven traits considered in this work (growth, length at first maturity, Q/B, trophic level, maximum depth, temperature preference, generation time, swim mode, body shape, reproductive guild and position in the water column), see Appendix 2.3 for a table of all pairwise values.

### Traits used in functional analyses

All trait values are sourced from the most recent release of FishBase (Froese & Pauly, 2019). FishBase provides trait information based on a combination of observed values (generally given as averages) and estimated values calculated from associated data, often from multiple sources.

#### *Continuous or quantitative traits*

Continuous traits are those containing a range of numeric values. Each species will fall at a particular point on the distribution of the entire range of continuous trait values, for example, with length at first maturity across an assemblage each species within that community has a position on the distribution.

### Growth (k)

Growth rate is derived from the Von Bertalanffy (Von Bertalanffy, 1938) growth function -

$$l_t = L_\infty(1 - e^{-k(t-t_0)})$$

where  $l$  is length,  $k$  is growth rate and  $L_\infty$  is the asymptotic length (length reached if a fish was to keep growing indefinitely) at which growth is zero.

The values for  $k$  were extracted from the 'Growth' table in FishBase (Froese & Pauly, 2019). Higher  $k$  values are generally associated with faster growth rates (Froese *et al.*, 2000) in that  $k$  describes the speed of attainment of maximum expected length. It should not be confused with an absolute growth rate.

### **Length at first maturity (L<sub>m</sub>)**

This is calculated as the average length (in mm) at which at least half of all fish belonging to a specific species enter their reproductive phase. This value was taken from the 'Matrix' table in FishBase (Froese & Pauly, 2019) and is calculated based on an empirical relationship between the asymptotic length ( $L_{\infty}$  - see above) and length at which maturity is attained (Froese & Binohlan, 2000). This trait is important as length at first maturity can be a critical transition period due to the possible conflict between allocation of resources, production and survival (Wootton, 2012). This makes it a valuable tool for fisheries management and stock control as it can assist with the avoidance of over exploitation leading to a decline in spawning stock (Mateus & Penha, 2007).

### **(Q/B)**

This refers to the ratio between food consumption (Q) and biomass (B) and it is relevant as a measure of trophic interaction within a community or system. Previous work from the FishBase and SeaLifeBase (Palomares *et al.*, 2019) creators suggests that this ratio can be correlated with both water temperature and asymptotic weight (Pauly, 1989; Palomares & Pauly, 1998). This possibility points to environmental change leading to variation in the functioning of the assemblage. The value here is extracted from the 'Matrix' table in the FishBase database (Froese & Pauly, 2019).

### **Trophic level**

This represents the position in the food chain and is calculated based on the mean trophic value of the diet items of a fish (Pauly *et al.*, 1998). The values extracted from FishBase (Froese & Pauly, 2019) for use here are estimated values from the 'Estimate' table based on the 'Feeding' and 'Diet' tables elsewhere in the database. This trait can be informative about predator-prey interactions and trophic cascades. Additionally, it can be affected by growth and diet specialisation; purely herbivorous fish will have a low trophic level throughout their lives, whilst juveniles of certain piscivorous species such as the European plaice *Pleuronectes platessa* (Linnaeus, 1758) can increase their trophic level as they grow (Kostecki *et al.*, 2012) and diet is expanded to include shellfish and fish. Variation in trophic level can also be introduced with environmental change and as with Q/B above these differences can affect ecosystem functioning (Thébault & Loreau, 2006).

### **Maximum depth**

This refers to the maximum depth in which a species is located and is measured in metres. This value is based on the range of the deepest occurrence found of any given species (taken from the 'Species' table) and where no such data is available an estimate is based upon habitat zones ('Estimate' table) (Froese & Pauly, 2019). The

maximum depth at which a fish can exist is significant as it plays a critical role in species distribution and how both individuals and assemblages react to environmental influences from pressures such as climate change and over exploitation (Dulvy *et al.*, 2008; Simpson *et al.*, 2011; Rutterford *et al.*, 2015).

### **Mean temperature preference**

The thermal preferences of a fish species can help identify tolerance to temperature change. This value refers to the mean temperature at which a species is located, measured here in °C. The temperature ranges for each species are taken from Aquamaps (Kaschner *et al.*, 2016) and the mean calculated in the 'Estimate' table in FishBase (Froese & Pauly, 2019). As with depth preferences (see Maximum depth), a species thermal tolerance can play an important part in any alteration or redistribution of assemblages as a result of climate change (Dulvy *et al.*, 2008; Cheung *et al.*, 2013; Givan *et al.*, 2018; Pinsky *et al.*, 2020).

### **Generation time**

This is an estimate of the average age at which species give birth. It is found in the 'Matrix' table in FishBase (Froese & Pauly, 2019) and is based on age at first maturity which is also within the 'Matrix' table and associated data located in the 'Maturity' table. This trait provides an insight into how quickly a species may be able to recover stocks. Fish with short generation times rebuild stocks more quickly although there is a balance involved with this and the fact that many species with briefer generation times are also shorter lived (Pinsky & Byler, 2015). Thus, generation time can be a relevant and informative aspect in fisheries management and stock control (Babcock *et al.*, 2007).

*Categorical or discrete traits*

Categorical traits are usually text based and each species within an assemblage is assigned a value from a list of possibilities, for example, in this system, body shape can be elongated, fusiform normal, eel like, and so on.

**Reproductive guild**

This describes those species sharing similar reproductive strategies, the fish from my study fall into eight categories which are shown in Table 2.1.

**Table 2.1:** Description of the reproductive strategies of study fish with species examples.






Strategy	Sub-strategy	Description	Examples
Bearers	external brooders	Fish who deposit clutches of eggs to external pouches	Greater pipefish <i>Syngnathus acus</i> (Linnaeus, 1758)
	internal live bearers	Fish who retain eggs inside their body and give birth to live young	Tope shark <i>Galeorhinus galeus</i> (Linnaeus, 1758)
Guarders		Parental care given post spawning	Transparent goby <i>Aphia minuta</i> (Risso, 1810)
	clutch tenders	Parental care by tending to clutches until hatching	Atlantic wolffish <i>Anarhichas lupus</i> (Linnaeus, 1758)
	nesters	Eggs laid in a nest (often of algae) and guarded	Cuckoo wrasse <i>Labrus mixtus</i> (Linnaeus, 1758)
Non-guarders		Eggs are deposited and left	European conger (eel) <i>Conger conger</i> (Linnaeus, 1758)
	brood hiders	Eggs are deposited and hidden – often by covering with fine sand or gravel	Sea trout <i>Salmo trutta</i> (Linnaeus, 1758)
	open water substratum	Eggs are scattered and deposited in open water	Haddock <i>Melanogrammus aeglefinus</i> (Linnaeus, 1758)

This trait value is found in the ‘Matrix’ table and is a combination of reproduction related data retrieved from the ‘Families’, ‘Reproduc’ and ‘Spawning’ tables in the FishBase database (Froese & Pauly, 2019). Fish have a broad range of reproductive strategies (Perrone Jr & Zaret, 1979; Jakobsen *et al.*, 2016). Reproductive approach can have an effect on population dynamics leading to changes in the resilience of species to environmental and anthropogenic factors such as overfishing and climate change (Winemiller, 2005). This therefore has relevance for fisheries management (Winemiller, 2005).

## Body shape

Body shape features can influence some ecological aspects of fish behaviour including migration patterns and possible habitats occupied (Wiedmann *et al.*, 2014). The trait values described here are taken from the ‘Species’ table and are a combination of information on the lateral body shape and cross section of body at maximum width data found in the ‘Morphdat’ table, both tables are from the FishBase database (Froese & Pauly, 2019). All the study fish can be classified into the sixteen body shapes shown in Table 2.2.

**Table 2.2:** Body shape descriptions with illustrations and examples from the study fish

Lateral body shape	Body cross section	Illustration	Examples
eel like			European conger (eel) <i>Conger conger</i> (Linnaeus, 1758)
	circular		European eel <i>Anguilla anguilla</i> (Linnaeus, 1758)
elongated			Lesser sandeel <i>Ammodytes marinus</i> (Raitt, 1934)
	circular		Blue whiting <i>Micromesistius poutassou</i> (Risso, 1827)
	compressed		Picked dogfish <i>Squalus acanthias</i> (Linnaeus, 1758)
	oval		Cusk <i>Brosme brosme</i> (Ascanius, 1772)
Fusiform/normal			Cuckoo wrasse <i>Labrus mixtus</i> (Linnaeus, 1758)
	circular		Haddock <i>Melanogrammus aeglefinus</i> (Linnaeus, 1758)
	compressed		Atlantic herring <i>Clupea harengus</i> (Linnaeus, 1758)
	oval		Atlantic cod <i>Gadus morhua</i> (Linnaeus, 1758)
other			Starry ray <i>Amblyraja radiata</i> (Donovan, 1808)
	flattened		Shagreen ray <i>Leucoraja fullonica</i> (Linnaeus, 1758)
short and/or deep			John dory <i>Zeus faber</i> (Linnaeus, 1758)
	angular		Lumpfish <i>Cyclopterus lumpus</i> (Linnaeus, 1758)
	compressed		European flounder <i>Platichthys flesus</i> (Linnaeus, 1758)
	flattened		Common sole <i>Solea solea</i> (Linnaeus, 1758)

### Position in water column

This refers to the vertical position in the water column that is generally occupied by a given species. This is calculated based upon the environment preferred by a given species and is taken from the ‘Species’ table in FishBase (Froese & Pauly, 2019). The study fish fall into the seven categories shown in Table 2.3.

**Table 2.3:** descriptions and examples of study fish for position in the water column.

Position	Description	Examples
Reef associated	Fish associated with coral or seaward reefs	Grey triggerfish <i>Balistes capricus</i> (Gmelin, 1789)
Pelagic neritic	Fish occupying pelagic (open sea, neither close to the bottom or too near the top) waters close to the shore	Atlantic mackerel <i>Scomber scombrus</i> (Linnaeus, 1758)
Pelagic oceanic	Fish occupying pelagic waters in the open ocean	Silvery pout <i>Gadiculus argenteus</i> (Guichenot, 1850)
Benthopelagic	Fish occupying pelagic waters in the mid depths, opportunistic feeders who may feed close to ocean floor or shore as well as mid-range	Atlantic cod <i>Gadus morhua</i> (Linnaeus, 1758)
Bathypelagic	Fish mainly occupying deeper pelagic waters towards ocean floor often move vertically through the water column	Blue whiting <i>Micromesistius poutassou</i> (Risso, 1827)
Demersal	Fish living and feeding close to the ocean floor	Lemon sole <i>Microstomus kitt</i> (Walbaum, 1792)
Bathydemersal	Fish occupying deeper waters and living and feeding on the ocean floor	Shagreen ray <i>Leucoraja fullonica</i> (Linnaeus, 1758)

A species’ position in the water column can suggest its likely feeding habitat (Pauly *et al.*, 1998). This, in turn, can influence the allocation of nutrients around the system (Raghukumar & Anil, 2003; O’Leary & Roberts, 2018).



## Swim mode

The mobility strategies developed by a species of fish combine different aspects of its ecology. Energy needs and interactions between habitats can be influenced by swim mode. The values here are those of the main modes of swimming by the adults of each species and are taken from the ‘Families’ table in FishBase (Froese & Pauly, 2019). This trait has numerous categories, the study fish fall into those listed in Table 2.4.

**Table 2.4:** Details and examples of the different swimming modes utilised by the study fish

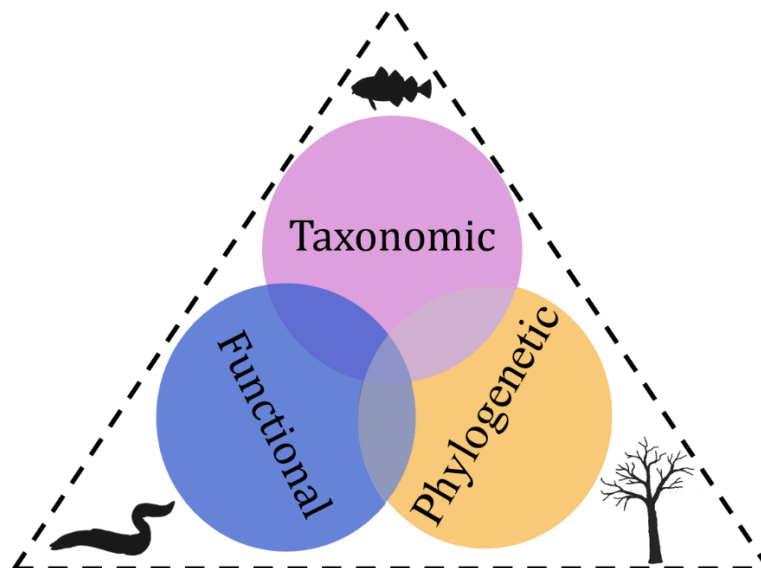
Form of propulsion	Swim mode	Description	Examples
Body/caudal fin	anguilliform	Long, slender fish who generate a constant flexion wave along their bodies	European conger (eel) <i>Conger conger</i> (Linnaeus, 1758)
	carangiform	Most movement is concentrated in the rear of the body and tail	Atlantic herring <i>Clupea harengus</i> (Linnaeus, 1758)
	ostraciiform	Tail fin oscillates rapidly, creating thrust	Silvery lightfish <i>Maurolicus muelleri</i> (Gmelin, 1789)
	subcarangiform	Flexion wave moves slowly along body with most work occurring in the rear portion	Atlantic cod <i>Gadus morhua</i> (Linnaeus, 1758)
	thunniform	Sideways motion of the tail and peduncle allowing fast forward movement	Atlantic mackerel <i>Scomber scombrus</i> (Linnaeus, 1758)
Median paired fin	amiiform	Straight body combined with undulations of dorsal fin	Snake pipefish <i>Entelurus aequoreus</i> (Linnaeus, 1758)
	balistiform	Undulations of both dorsal and anal fins to propel forward	John dory <i>Zeus faber</i> (Linnaeus, 1758)
	diodontiform	Fish generate undulations along pectoral fins	Lumpfish <i>Cyclopterus lumpus</i> (Linnaeus, 1758)
	labriform	Propulsion generated by ‘rowing’ or ‘lifting’ movement of pectoral fins	Ballan wrasse <i>Labrus bergylta</i> (Ascanius, 1767)
	rajiform	Vertical undulations of large pectoral fins promote thrust	Thornback ray <i>Raja clavata</i> (Linnaeus, 1758)
	tetraodontiform	Dorsal and anal fins are ‘flapped’ either in unison or opposingly	Tub gurnard <i>Chelidonichthys lucerna</i> (Linnaeus, 1758)

Different methods of propulsion, mainly due to body and fin morphologies, combined with individual swimming modes lead to a wide variation in swimming ability (Breder, 1926; Webb, 1984; Videler, 1993; Webb, 1994). Swimming capabilities can also be influenced by other factors or traits. Migratory fish who perform long migrations in fast flowing water or currents will generally have a better swimming performance than more sedentary fish inhabiting shallow substrate or rocky pools (Peake *et al.*, 1997; Castro-Santos, 2002).

## 2.3 Biological Diversity

The term biodiversity, a contraction of the words ‘biological diversity’ is believed to have been coined in 1985 by Walter G. Rosen, prior to a National Forum in 1986 (Harper & Hawksworth, 1994; Magurran, 2013b). Biodiversity can be difficult to define (Norton, 2008) but in this thesis I use a simple definition based on the ideas outlined in ‘Measuring biological diversity’ (Magurran, 2013b); biodiversity is the variety and abundance of taxa within a system or assemblage. There can sometimes be confusion around the terms used to describe groups of taxa or species, particularly in the usage of ‘communities’ and ‘assemblages’ (Fauth *et al.*, 1996; Stroud *et al.*, 2015). Stroud’s 2015 paper (Stroud *et al.*, 2015) differentiates between the two by suggesting that assemblages are essentially subsets of communities. For example, a wood or forest could be considered a community as there are groups of interacting species within the same space whilst an assemblage would constitute a taxonomically related subset of these species, i.e., a transect plot of terrestrial plants inside the forest. In this work I use the term assemblage to describe the marine fish species found within a given area.

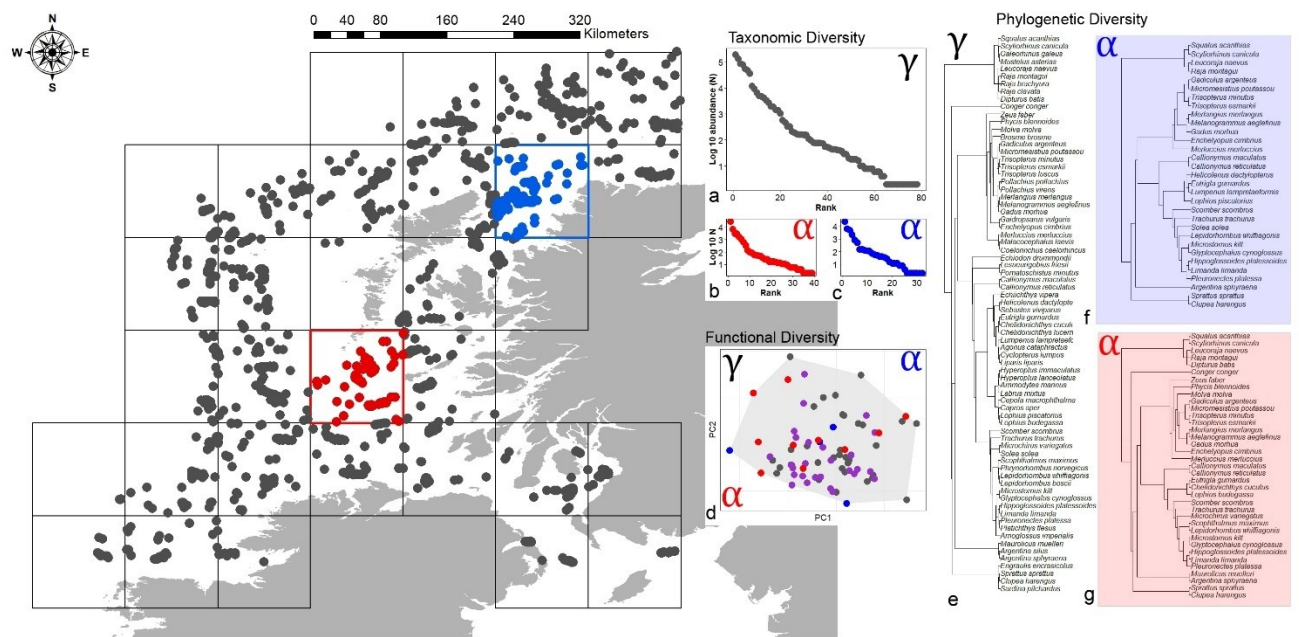
Biodiversity is multifaceted, consisting of taxonomic diversity, functional diversity and phylogenetic diversity (Jarzyna & Jetz, 2016). Taxonomic diversity considers the number of species or other taxonomic units found within a particular assemblage or system and can be measured in a number of different ways (Magurran, 2013b, a), some of which are expanded upon in the sections that follow. Functional diversity considers the traits that species possess and the ecological role that they play within their community. In the past functional diversity was less studied than taxonomic diversity, particularly in the marine realm, but the availability of trait databases such as FishBase (Froese & Pauly, 2019), TRY (Kattge *et al.*, 2011) and AnimalTraits (Herberstein *et al.*, 2022) has led to a greater focus on functional work (McGill *et al.*, 2006; Messier *et al.*, 2010; Cadotte, 2011), particularly since the mid-2000s as evidenced by Figure 1 in the work by Cadotte et al (Cadotte *et al.*, 2011).



**Figure 2.7:** Venn diagram showing the three facets of biodiversity – taxonomic, functional and phylogenetic.

By using these different facets (see Figure 2.7) to investigate biodiversity change it is possible to uncover a more complete view of what is happening in species assemblages than by looking only at one aspect. As biodiversity is multifaceted (Craven *et al.*, 2018), it is difficult to quantify change using a single unit or metric (Purvis & Hector, 2000). Utilising a variety of methods and facets provides a clearer snapshot of a system and how it may be shifting in time and/or space. This thesis focuses only on taxonomic and functional diversity. I chose these two facets as there are parallels between metrics (for example, species richness and functional richness) allowing comparisons between dimensions within assemblages, and because I wished to test predictions about the extent to which change in the two dimensions is linked.

Diversity itself can also be split into three parts, Whittaker (Whittaker, 1972) designated these as: alpha diversity, beta diversity and gamma diversity. Alpha diversity relates to the diversity of a single community within one site or at one time step or as indicated by Whittaker “the species richness of a place”. Alpha diversity is often measured by calculating the number of different species (species richness  $q_0$  – see section 2.3.1.1.2 for more details), but there are many other methods available (see chapter three in ‘Measuring biological diversity’ (Magurran, 2013b) and Thukral’s review paper (Thukral, 2017) for some examples). An example from these systems could be the number of distinct fish species found within an ICES rectangle in any given year. Beta diversity quantifies compositional changes between systems rather than within systems (Whittaker, 1960); this can be either between sites (spatial) or between time periods (temporal). Beta diversity can also be measured using a variety of methods (Anderson *et al.*, 2011) and see chapter six in ‘Measuring biological diversity’ (Magurran, 2013b). Continuing the example of an ICES rectangle in any given year, it is possible to calculate the beta diversity between years (or time periods) by comparing the numbers and/or abundances of different fish species found at each time step. This calculation can be done as a pairwise comparison, for example, by comparing each time step with the time step immediately preceding it or, as is done in this work, by comparing each time step with the baseline year. Gamma diversity refers to the overall diversity within a region or geographic area, this could be global or a regional pool of smaller assemblages (Whittaker, 1960; Whittaker, 1972). In this illustration the gamma diversity of the system would be the total number of species found across all years in the time frame.



**Figure 2.8:** This figure illustrates the difference between the components of diversity. The main map shows the full West coast survey data plotted in the  $1^\circ$  grid cells. Firstly, taxonomic diversity is represented by (a) which shows the rank abundance plot for the overall gamma diversity of the full area, whilst (b) and (c) show the same rank abundance plots for the smaller subsets represented by the red and blue coloured grid cells and representing alpha diversity. Functional alpha and gamma diversity are shown in (d) where the grey dots represent the position in functional space (see section 2.3.3 and Figure 2.12 for details) of the wider gamma diversity of the full area, red and blue correspond to those in only either cells (b) or (c) and purple are those appearing in both subsets. Phylogenetic diversity is represented by (e), (f) and (g) where (e) shows the phylogenetic tree for the full area (gamma diversity) and (f) and (g) refer to the phylogenetic trees for the subsets in (c) and (b) respectively (alpha diversity) and shaded accordingly.

In the sub-sections that follow I expand on the individual methods used within the broader sections of alpha and beta diversity.

## 2.3.1 Taxonomic diversity

### 2.3.1.1 Alpha diversity measures

There are numerous methods available to measure biodiversity generally (Magurran & McGill, 2011a; Magurran, 2013b; McGill *et al.*, 2015), and a large number of ways to calculate alpha diversity in particular (Gotelli & Colwell, 2011; Magurran & McGill, 2011b; Dornelas *et al.*, 2013). It is for this reason that in my work I have chosen to structure the taxonomic diversity metrics around Hill numbers (Hill, 1973) as this provides a clear framework and a sound mathematical group of indices that incorporate relative abundances as

part of their structure. Hill's approach showed that common methods of measurement could be placed in a unified statistical framework, with a variable (illustrated by  $a$  in the equation below) used to reflect the extent to which the measure tracks evenness. When  $a=0$  every species has the same importance (see  $q_0$  for species richness) (Hill, 1973; Magurran, 2013b).

$$q_a = (p_1^a + p_2^a + \dots + p_n^a)^{1/(1-a)}$$

where  $q_a$  is the  $a^{th}$  order of diversity and  $p_n$  the relative abundance of the  $n^{th}$  species

Equation adapted from Hill (Hill, 1973) and Magurran (Magurran, 2013b)

As the power  $a$  increases the sensitivity towards abundant species of the metric also increases, thus as  $a$  tends to  $-\infty$ , the sensitivity towards rare species is increased (Morris *et al.*, 2014). Although it is possible to use any order  $a$  of  $N$  from  $-\infty$  to  $\infty$  this work I use only four of the better understood methods (see Table 2.5). The most well-known of these metrics are Hill numbers (Hill, 1973)  $q_0$ ,  $q_1$  and  $q_2$ ; it is possible to view the increase in power as turning up the 'dial' on the emphasis upon abundance (Magurran, 2013b) and this idea is discussed in later chapters.

#### **2.3.1.1.1 Species numerical abundance**

Although not itself a Hill number, I also examine species numerical abundance as it provides context for the interpretation of change in the Hill numbers used. Species numerical abundance indicates the number of individuals found belonging to each identified species group. This thesis draws on the scientific trawl survey which uses the Catch Per Unit Effort (CPUE) to reflect observed abundances. This refers to the number of individuals counted in a single trawl (here this is 0.5 hours) event. Species abundances can change independently of species richness ( $q_0$ ) but are often closely correlated with other alpha metrics, particularly those which incorporate some element of abundance data. Species abundances ( $N$ ) are counted to reflect the number of individuals per species identified at a particular point in time and/or space. In this thesis, as only length of species rather than weight is included in the survey data used, all work is based on numerical abundance (number of individuals) but for many of the metrics considered here it is equally possible to use biomass (weight of individuals). However, using a different currency in this way can produce variation in results (Fontrodona-Eslava *et al.*, 2021), so consistency across metrics is key.

#### **2.3.1.1.2 Hill number $q_0$ – equivalent to species richness**

Species richness refers to the number of distinct species found within a site at a particular point in time; it takes no account of the abundance of the species observed, only the presence of the species themselves, and is dependent upon sampling effort. It is simple to perform and easy to understand which makes it a popular metric to use. Consequently, it has become one of the most commonly used metrics in biodiversity but although it can be informative it can also be problematic (Gotelli & Colwell, 2001; Fleishman *et al.*, 2006; Chao *et al.*,

2014) on two main counts: 1) it is strongly influenced by sampling effort; and 2) as it does not incorporate any abundance data per species it does not differentiate in any way between rare and common species.

$$q_0 \equiv S$$

where S is the total number of species found

### 2.3.1.1.3 Hill number $q_1$ – exponential Shannon

The Shannon index (also known as the Shannon-Weiner index) is another commonly used diversity metric which takes account of both the identities and abundances of species within an assemblage (Pielou, 1975). Hill used the exponential of the Shannon index as this gives an estimate of how many species the assemblage would contain if all were equally abundant (Daly *et al.*, 2018).

$$q_1 = \exp - \sum_{n=1}^n (p_i \ln p_i)$$

where  $n$  is the number of samples,  $p_i$  the relative abundance of sample  $i$  and  $\ln$  is the natural logarithm although in practice any log can be used

Equation adapted from Hill (Hill, 1973) and Magurran (Magurran, 2013b).

### 2.3.1.1.4 Hill number $q_2$ – reciprocal Simpson

Simpson's index is an informative measure of how even an assemblage is (Magurran, 2013b). Species evenness refers to how evenly balanced the species found within a community are. For example, if most fish species within an assemblage each consist of 10 individuals and the final fish has 11, the assemblage can be regarded as even but if the final species had 100 individuals this would no longer hold true. This metric is closely related to Hurlbert's PIE (Hurlbert, 1971)) which measures the probability that two individuals, selected at random, will be different species. In the Hill framework, the reciprocal form of Simpson's index is used. The Simpson index is a valuable tool for capturing the variance of a species abundance distribution (Magurran, 2013b) and when used, as here, as the reciprocal it will return higher values as evenness increases.

$$q_2 = 1/\sum p_i^2$$

where  $p$  represents the proportion of individuals in the  $i^{th}$  species

Equation adapted from Hill (Hill, 1973) and Magurran (Magurran, 2013b)

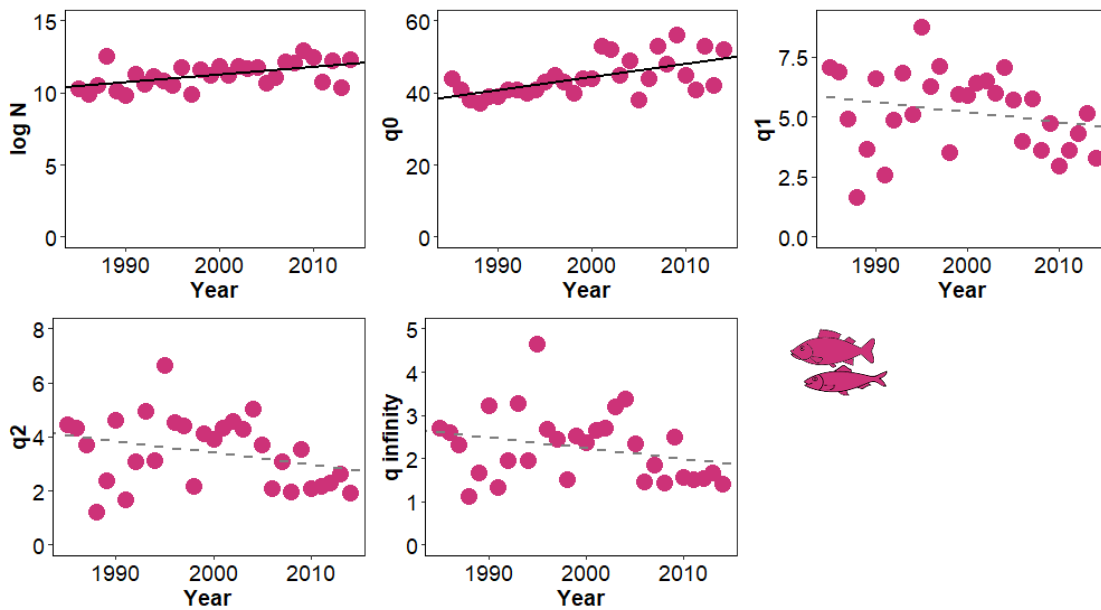
### 2.3.1.1.5 Hill number $q_\infty$ – reciprocal Berger-Parker

The Berger-Parker index (Berger & Parker, 1970) is a simple metric used to calculate how dominant a species is within an assemblage. It represents the relative abundance of the most dominant species found within an assemblage. In the Hill framework, the reciprocal is used, thus a greater value is associated with higher diversity and a decrease in dominance. In Chapter Three, in addition to  $q_\infty$  I quantified the percentage of relative dominance and the identities of those dominants.

$$q_\infty = \frac{1}{\frac{Ab_d}{Ab}}$$

where  $Ab$  represents total abundance and  $Ab_d$  is the abundance of the most dominant species found

Equation adapted from Hill (Hill, 1973) and Magurran (Magurran, 2013b)



**Figure 2.9:** A random subset of the full study data containing a 30-year time series is used to illustrate the results when using the different alpha diversity metrics featured. The metrics are computed for each time step (points) and a trend line fitted (using a simple Ordinary Least Squares (OLS) regression). These data show a slight but significant increase in both abundance (shown as log N) and species richness ( $q_0$ ) but small and non-significant declines in exponential Shannon ( $q_1$ ), reciprocal Simpsons ( $q_2$ ) and reciprocal Berger-Parker ( $q_\infty$ ).

### 2.3.1.2 Beta diversity measures

Beta diversity was described by Whittaker (Whittaker, 1972) as “the extent of species replacement or biotic change along environmental gradients”. It refers to the composition of the species within an assemblage and can be calculated as a dissimilarity measure of how composition has changed either through time or through

space. Beta diversity can be seen as the difference between sites or time steps and is often referred to as ‘species turnover’. Whittaker (Whittaker, 1972) defined beta diversity in several ways, the simplest and most intuitive of which was to simply divide gamma diversity by mean alpha diversity. This method has some limitations (Tuomisto, 2010b, a), however, but in this basic form it is easy to understand and explain making it a popular choice for many (Jost, 2007; Jost *et al.*, 2011; Chao & Ricotta, 2019).

$$\beta = \gamma / \text{mean}(\alpha)$$

Beta diversity describes the relationship between local (at site/sample or time step) and regional ( $\gamma$ ) diversity as well as defining the level of distinction between those sites/samples/time steps (Baselga, 2010). Beta diversity, as alpha diversity, is sensitive to both sample size and scale so these factors should be considered carefully before choosing an appropriate index to calculate change. Indices such as Jaccard (Jaccard, 1912) that focus on presence-absence data only will not differentiate between levels of abundance, thus, a singleton species found within an assemblage will be treated in the same way as an extremely abundant one. The limitations of this approach led to the development of a range of metrics weighted by species abundance. As with alpha diversity, there are several different metrics available to calculate (dis)similarity between samples, in this work I focus only on two, one using abundance data (see 2.3.1.2.1 Morisita-Horn dissimilarity) and one based on presence-absence data only (see 2.3.1.2.2 Jaccard dissimilarity).

### 2.3.1.2.1 Morisita-Horn dissimilarity

The Morisita-Horn dissimilarity index is based on the premise that the probability of any individual being chosen from a community is likely to belong to a different species than that of a single individual being picked from a different assemblage (or time period). An advantage of Morisita-Horn is that it is not as strongly influenced by species richness or sample size as many other abundance-based (dis)similarity metrics (Wolda, 1981). One potential disadvantage, however, is that it is sensitive to the abundances of the most abundant species (Magurran, 2013b), nevertheless, this can be a useful choice when used to quantify overall compositional change, particularly when examining dominance alongside. For temporal analyses I compare each year to the first year of the time series and in the case of spatial analyses I carry out pairwise comparisons between sites.

$$MH_{Diss} = 1 - \frac{2 \sum x_i y_i}{\left( \frac{\sum x_i^2}{x^2} + \frac{\sum y_i^2}{y^2} \right) XY}$$

where  $x_i$  and  $y_i$  represent the abundances of species  $i$  in sites  $X$  and  $Y$

and  $X$  and  $Y$  represent total abundances in each site

Equation adapted from Magurran (Magurran, 2013b)



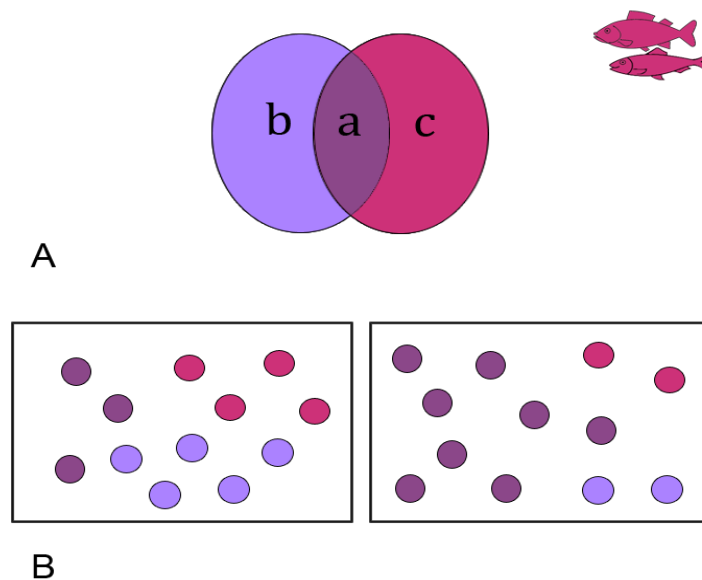
### 2.3.1.2.2 Jaccard dissimilarity

The Jaccard index is another example of a method used to calculate the similarity and diversity of different sites or time steps or how distinct one sample is from another. This was first developed by Paul Jaccard in 1908 (Jaccard, 1908; Jaccard, 1912) to compare regional flora and is simple to understand. It is rooted in the idea that the more species two sites have in common, the more alike in composition they will be, however, as Jaccard uses a binary input taking no regard of species abundance it is appropriate only for presence-absence data.

$$Jacc_{Diss} = \frac{b + c}{a + b + c}$$

where  $a$  represents the species in a pair of sites and  $b$  and  $c$  the species in each site only

Equation adapted from Jaccard (Jaccard, 1912), Koleff et al (Koleff *et al.*, 2003), Magurran (Magurran, 1988) and Southwood & Henderson (Southwood & Henderson, 2000)



**Figure 2.10:** Illustration of changes in beta diversity, how sites become more or less similar to each other. Firstly, (A) is the visual representation of the Jaccard equation where dissimilarity is measured based on the difference between the intersect and the separate sections. (B) shows how two samples can differ in composition even when only three distinct species are involved.

### 2.3.2 Rarefaction

Many metrics used to calculate biodiversity are sensitive to sampling effort (see section 2.1.3). This is particularly true in the case of species richness. Problems with bias in sampling effort need to be accounted for when calculating diversity; it is sensible to assume that the larger the area, greater the number, or wider the range that is sampled will lead to a larger number of species found. Rarefaction is a statistical method of making

fair comparisons between years, sites, or samples. A curve representing the number of species as a function of the number of samples taken is created. Generally, this curve will increase extensively at first as the common species are recorded but will plateau when there are only rare species left. By re-sampling individuals (or samples) randomly from the overall pool of samples a number of times, rarefaction curves can be generated by plotting the average per sample (Gotelli & Colwell, 2001). Sanders (Sanders, 1968) first developed a technique to deal with this issue when he wished to compare different sample sizes. This technique of creating and comparing rarefaction curves has been refined and revised many times over the years (Hurlbert, 1971; Heck Jr *et al.*, 1975; Chao *et al.*, 2014) and is now used not only to measure species diversity but to produce robust statistical estimates of biodiversity change.

Rarefaction can be either individual-based or sample-based (Gotelli & Colwell, 2011). In individual-based rarefaction data are collected from observed individuals and species identities are recorded. This means that it is only possible to plot a rarefaction curve by randomly selecting species with no sample or site information included.

Alternatively, in sample-based rarefaction, a defined number of sites or years are randomly sampled multiple times. The number to sample is usually based on the smallest count from the full assemblage. Diversity trends are calculated based on each individual site that is sampled and then the mean or median is extracted from the distribution.

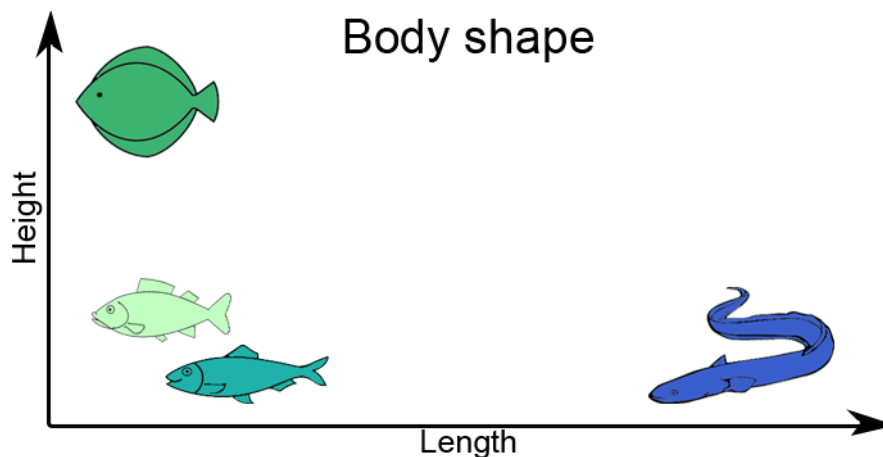
### 2.3.3 Functional Diversity

One generally used definition of functional diversity is “the value and the range of those species and organismal traits that influence ecosystem functioning” (Tilman, 2001). In any fish community there will generally be a range of species, each of whom have different combinations of traits. These combinations may be closely aligned, for example, pollack *Pollachius pollachius* (Linnaeus, 1758) and saithe *Pollachius virens* (Linnaeus, 1758) have mainly very similar traits, whilst other species, despite similarities in common names may be very different with regard to many of their traits, i.e., solenette or yellow sole *Buglossidium luteum* (Risso, 1810) and lemon sole *Microstomus kitt* (Walbaum, 1792).

The functioning of an ecosystem will depend on the combination of species found within it. Each species brings its own unique combination of traits to an assemblage which play specific roles within the system. For example, Atlantic herring *Clupea harengus* (Linnaeus, 1758) are a forage fish who play a vital role in the marine food web by transferring energy from their food to their predators (Thayer *et al.*, 2020). However, often a number of species within an assemblage will possess very similar traits leading to functional redundancy (Rosenfeld, 2002). A simple analogy to this is a small village. There may be 50 people living in the village, each of them performing a different task in their community – for example, there could be a doctor, a minister, some nurses, teachers, bakers, grocers, farmers and fishers. Each person, in their individual role, brings something to the effective running of the village. However, people are not static and may move away, and although a new person may then move into the village, thus retaining the initial 50, if they have a different role or job to perform then it can affect everyone. A doctor being replaced by a teacher will have a major effect whereas the substitution of

grocer for a general shop keeper would have little real influence on the functioning of the community, mirroring the functional redundancy effect. The same is true in the fish world, species richness may remain the same, but the actual functioning of the community can change dramatically if the replacement species have very different combinations of traits.

In order to calculate functional diversity metrics, it is first necessary to generate the multi-dimensional functional space occupied by the assemblage being analysed. I built the functional space occupied by the species in each system using the R function (*quality\_funct\_space()*) developed by Maire, Villéger and colleagues (Maire *et al.*, 2015) to calculate the optimal pairwise functional coordinates for each fish using Gower distance (Gower, 1971), this method is needed as I have a combination of categorical and continuous traits. I then used another of the functions provided by the Villéger team (*multidimFD()*) to compute various functional diversity indices (Violle *et al.*, 2007). To calculate the functional space, I first convert the traits (see section 2.2.2) for each species in the community for analysis into a species by trait matrix. I then combine this matrix with the species by abundance matrix for the relevant assemblage before running the code. In this thesis I mainly focus on only three indices, namely functional richness, functional evenness and functional divergence. Functional space across multiple dimensions can be difficult to envisage but a simple two-dimensional illustration helps to clarify how the trait analysis works. In the example in Figure 2.11 body shape is represented on a two-dimensional graph and it is clear that species with very different body shapes will be further apart from each other than those with similar ones.



**Figure 2.11:** Body shape is illustrated at the ends of different types. Length (x axis) shows the shorter bodied fish such as the pale green coloured cod-like and turquoise coloured herring-like being positioned towards zero whilst the longer blue coloured eel-like is much further along the axis. Height (y axis) illustrates the ‘taller’ flat fish such as the green coloured plaiice-like being at the top end of the axis whilst again the cod-like and herring-like are closer to zero.

### 2.3.3.1 Alpha diversity

#### 2.3.3.1.1 Functional richness

Functional richness, as used in this work, refers to the proportion of space occupied by the species present in an assemblage. Species with similar traits will be clustered together whilst unusual or uncommon fish within that assemblage will generally be located around the outer perimeter of the space.

$$FR_{tc} = SF_{tc}/R_t$$

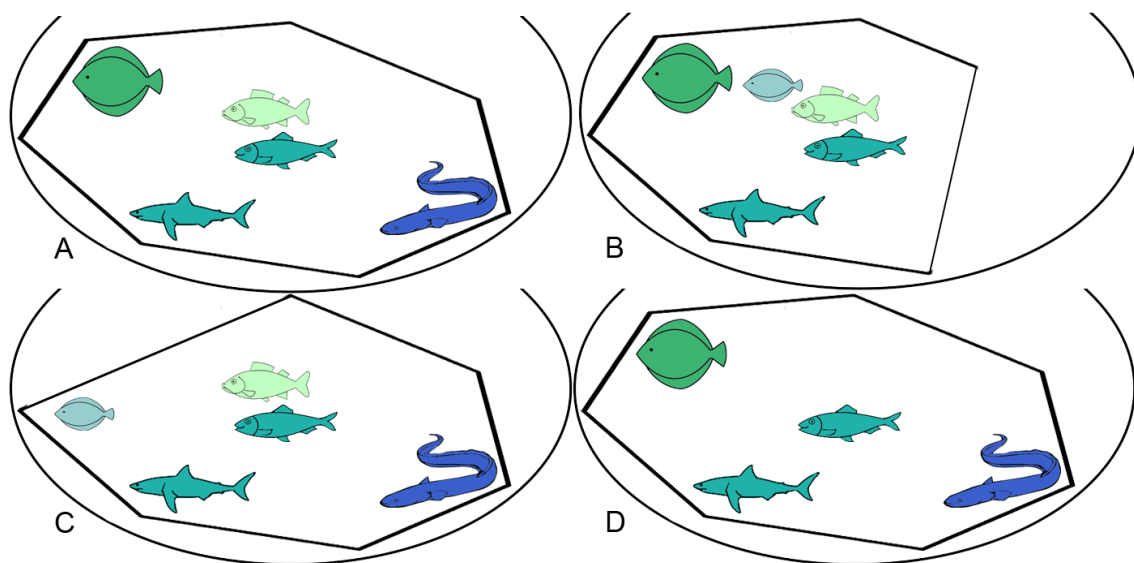
where  $FR_{tc}$  represents the functional richness of trait  $t$  in community  $c$ ,

$SF_{tc}$  the space occupied by species within the community  $c$ , and

$R_t$  the range of trait  $t$

Equation adapted from Mason et al (Mason *et al.*, 2005) and computed using the functions provided by Villéger (Villéger, 2017)

As functional richness is directly related to species richness (see section 2.3.1.1.2) it follows that an increase in species within an assemblage will often correspond to an increase in functional richness. However, this will not necessarily always hold true as, if the new species possess similar traits to those already found in the assemblage, they will be positioned close to them in functional space leading to little or no change in functional richness (Schleuter *et al.*, 2010). Alternatively, the introduction of additional species to an assemblage where there are no existing similar species is likely to expand the functional space occupied by the assemblage, thus increasing functional richness.



**Figure 2.12:** Changes in functional richness do not need to happen in tandem with changes in species richness as illustrated in the above figure. In the first assemblage (A) there are five different species (S=5) that are distributed throughout the functional space, both on the outer edges and towards the centre. In (B and C) there are still five distinct species but since the more functionally distinct conger eel (B) or plaice (C) have been replaced by a sole (which is related to the plaice), the actual space being occupied has contracted significantly in (B) and slightly in (C). Finally, in (D) the functional space occupied is unchanged from (A) despite the decrease in S to four (S=4).

### 2.3.3.1.2 Functional evenness

Functional evenness takes account of species abundances and describes the regularity of distribution of species throughout the functional space with reference to both the uniformity of species position as well as consistency of abundance weighting. More regularly distributed species (and abundances) indicate higher functional evenness whilst irregular distributions point to lower evenness. High and low functional evenness scores are often used to indicate the utilisation of available resources, with a low score suggesting under-utilisation which can in turn lead to lowered productivity (Mason *et al.*, 2005). A benefit of this approach is the fact that it is independent of species richness (see section 2.3.1.1.2), functional richness (see section 2.3.3.1.1) and functional divergence (see section 2.3.3.1.3) (Villéger *et al.*, 2008). This metric was first developed as the functional regularity index (Mouillot *et al.*, 2005) for a single trait and later work (Mouillot *et al.*, 2005) extended this process to include multiple traits using ordination techniques, however, this method of extension can lead to loss of information if there are weak correlations between the traits used (Villéger *et al.*, 2008). For this reason, Villéger *et al.* further developed the metric using minimum spanning trees to link species positions within the multi-dimensional functional space (Villéger *et al.*, 2008).

$$FE = \frac{\sum_{l=1}^{S-1} \min\left(PW_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$$

$$PW_l = \frac{EW_l}{\sum_{l=1}^{S-1} EW_l}$$

$$EW_l = \frac{dist(i,j)}{w_i + w_j}$$

where  $l$  is the length of the branch of the minimum spanning tree,  $w_i$  and  $w_j$  are the proportional abundances of species  $i$  and  $j$ ,  $dist(i,j)$  represents the Euclidean distance between  $i$  and  $j$ , and  $S$  represents the assemblage of species concerned

Equations adapted from Villéger *et al.* (Villéger *et al.*, 2008) and computed using the functions provided by Villéger (Villéger, 2017)

### 2.3.3.1.3 Functional divergence

Functional divergence indicates the variance of species traits and their position in the functional space occupied. When using a single trait functional divergence illustrates the pattern of abundance across a trait axis relative to the total range of trait values in a system (Mason *et al.*, 2005). Low divergence therefore occurs when the most abundant species are located at the centre of the trait axis, divergence then rises as the abundances of species with trait values towards the ends of the axis increase. As this metric takes account of the abundance of species rather than just their identity, changes in divergence reflect variation in the proportion of abundance supported by species with more extreme traits. Higher levels of divergence suggest greater niche differentiation leading to less competition for resources (Mason *et al.*, 2005; Villéger *et al.*, 2008).

$$FD = \frac{\Delta d + \overline{dG}}{\Delta|d| + \overline{dG}}$$

$$\Delta d = \sum_{s \in S_c} \frac{A_s}{A} (dG_s - \overline{dG})$$

$$\Delta|d| = \sum_{s \in S_c} \left( \frac{A_s}{A} \right) |dG_s - \overline{dG}|$$

$$G_t = \left( 1/|V| \right) \sum_{s \in V} X_{ts}$$

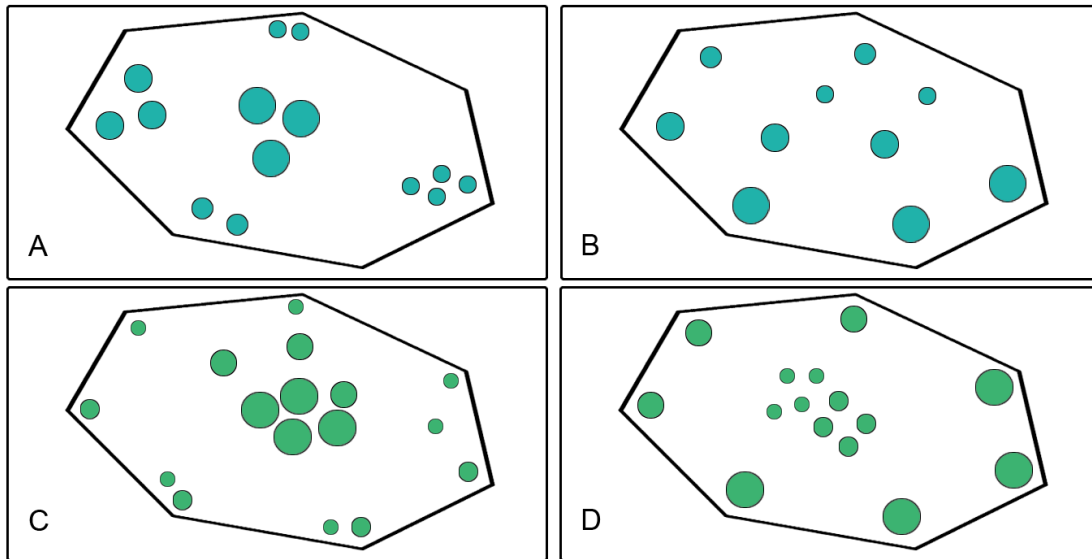
where  $dG_s$  is the distance between species  $s$  and  $G$  which is the gravity center of the convex hull,

$G_t$  is the gravity centre of trait  $t$ ,  $V$  is the set of species from the vertices of the convex hull,

$A$  is total abundance of individuals in assemblage,  $A_s$  is the abundance of species  $s$ ,

$X_{ts}$  is the mean trait value of trait  $t$  in species  $s$  and  $\overline{dG}$  is the mean value of  $dG_s$  over all species present

Equations adapted from Schleuter *et al.* (Schleuter *et al.*, 2010) and Villéger *et al.* (Villéger *et al.*, 2008) and computed using the functions provided by Villéger (Villéger, 2017)



**Figure 2.13:** Each plot represents an assemblage with either high or low divergence or evenness, the position of the circles represents a species' place in functional space whilst the size is representative of the abundance amount (larger points show higher abundance). (A) shows an assemblage with low functional evenness – species are clustered together in groups of both trait combinations and abundances. However, (B) illustrates high functional evenness where both abundance and trait combinations are regularly distributed throughout the space. (C) shows an assemblage with low functional divergence, species with distinct combinations of traits are located on the edges of the functional space and the small circles show that they contain the lowest abundances of the species, the larger circles representing the more dominant species are all towards the centre of the space suggesting similar combinations of traits (example species could be herring and mackerel). Finally, (D) illustrates an example of high functional divergence, here the more distinct species on the edges have the highest abundances whilst those in the centre of the space are less abundant.

**Table 2.5:** Table listing the main diversity indices used throughout this thesis, fuller descriptions of the methodology and equations found in the relevant sections.

<b>Metric symbol</b>	<b>Method</b>	<b>Diversity Type</b>	<b>Section</b>
$N$	Numerical species abundance (number of individuals)	Taxonomic $\alpha$	2.3.1.1.1, page 42
$q_0$	Number of species (species richness)	Taxonomic $\alpha$	2.3.1.1.2, page 43
$q_1$	Exponential Shannon index	Taxonomic $\alpha$	2.3.1.1.3, page 43
$q_2$	Reciprocal of Simpson index	Taxonomic $\alpha$	2.3.1.1.4, page 44
$q_\infty$	Reciprocal of the relative abundance of the most dominant species (Berger-Parker index)	Taxonomic $\alpha$	2.3.1.1.5, page 44
$MH_{Diss}$	Morisita-Horn dissimilarity	Taxonomic $\beta$	2.3.1.2.1, page 46
$Jacc_{Diss}$	Jaccard dissimilarity	Taxonomic $\beta$	2.3.1.2.2, page 46
$FR$	Functional richness	Functional $\alpha$	2.3.3.1.1, page 49
$FE$	Functional evenness	Functional $\alpha$	2.3.3.1.2, page 50
$FD$	Functional divergence	Functional $\alpha$	2.3.3.1.3, page 51

## 2.4 Data analysis methods

Analyses use R statistical software (RCoreTeam, 2021). The `vegdist` function in the R package `vegan` (Oksanen *et al.*, 2015) is used to compute dissimilarities. The functional metrics were calculated using the `mFD` package in R (Magneville *et al.*, 2021). All mapping functions were carried out using the ESRI GIS software ArcGIS (ESRI, 2015). Specific packages in R used for other purposes are described and cited in the relevant chapters.

In the trait analyses I use principal component analyses to calculate the extent of the convex hull relating to the functional space of an assemblage. This is done using Gower's distance (Gower, 1971) as the traits are a combination of categorical and continuous.

### 2.4.1 Methods used in R

Where comparisons between systems are done the thesis study site comprises 35 ICES statistical regions for each coastal system (North Sea (NS-IBTS) and West Coast (SWC-IBTS)) as illustrated in Figure 2.1. Most of these comparative analyses were carried out on the latitudinal bands derived from these rectangles (see Figure 2.4). This results in a set of nine bands on the west coast and eleven on the east. Community time series were compiled for each assemblage (latitudinal band or coastal ecosystem) following sample based rarefaction (Dornelas *et al.*, 2014b) techniques. Because species richness and other diversity metrics are sensitive to sample size, raw (unrarefied) data can lead to bias. Rarefaction (Gotelli & Colwell, 2011) (see section 2.3.2 for more detail) is a statistical resampling methodology that reduces this bias. Here the minimum number of samples per year, per appropriate assemblage, was resampled to generate a constant number of samples to be used in the analyses. Where appropriate, this resampling procedure was used throughout this thesis, as – in contrast to



individual based rarefaction- it retains species identity. The code used for this resampling (see Appendix 2.1), along with other general functions can be found as R markdown code in the relevant chapter Appendices.

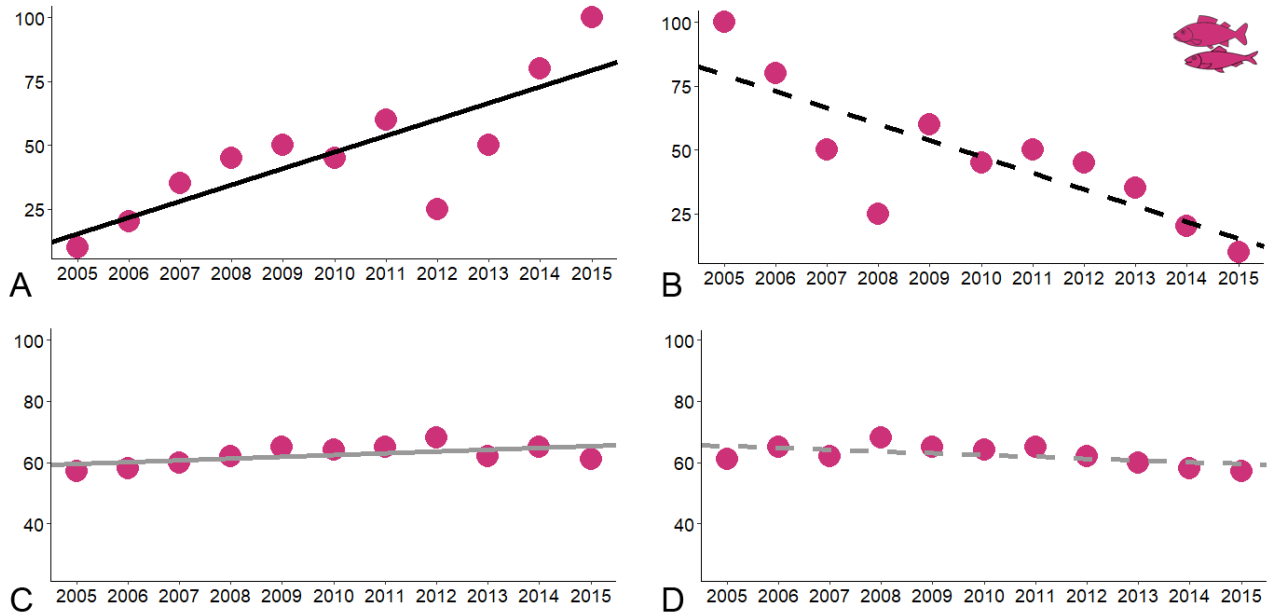
#### 2.4.2 Calculating trends, slopes and correlations

I quantify temporal change in the different metrics by examining the value found in each year of the time series. Similarly, I quantify spatial change between assemblages or systems by looking at the differences in values between them. For the detection of trends, I first fit a linear regression model to each of the metrics using a simple Ordinary Least Squares regression model as illustrated below:

$$y = X\beta + \varepsilon$$

where  $x$  is the time step (or latitude) and  $y$  is the metric

I then calculate slopes of change for the appropriate metrics over the time periods or between assemblages and/or systems. I next extract a set of results from the summary statistics, namely Adjusted  $R^2$ , p-value, estimate (or slope) and intercept. A table of the summary statistics for all analyses carried out can be found in the relevant chapter Appendix of this thesis. Although this work does not include any formal hypothesis testing I consider slopes to be trends of ecological interest (either increasing or decreasing) if the p-value is less than 0.05; slopes that do not meet this criterion are seen as non-significant increases or decreases. Figures detailing temporal or spatial change indicate the significance or otherwise of the slopes they represent by highlighting positive significance with a black solid line, negative significance with a black dashed line and the same line types in grey for non-significant cases.



**Figure 2.14:** Mock version of typical plots showing temporal change as (A) significant positive, (B) significant negative, (C) non-significant positive and (D) non-significant negative. The x-axes are years whilst the y-axes are generic values used for illustration purposes only.

In some parts of this thesis, I also investigate the relationships between various metrics. Generally, the method used for this was either Pearson’s Product Moment Correlation (Pearson, 1909) or Spearman’s rank correlation coefficient (Rho) but where different metrics were used the methodology is expanded on in the relevant chapters.

#### Pearson’s Product Moment Correlation

$$Pearson = \frac{\sum(x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum(x_i - \bar{x})^2 \sum(y_i - \bar{y})^2}}$$

where  $x_i$  represents values of  $x$  in sample,  $\bar{x}$  the mean of these  $x$  values,

$y_i$  represents values of  $y$  in the sample and  $\bar{y}$  the mean of these  $y$  values

Equation for Pearson’s correlation coefficient (Pearson, 1909)

### **Spearman's rank correlation coefficient**

$$\rho = 1 - \frac{6 \sum d_i^2}{n(n^2 - 1)}$$

*where n represents the number of ranks and d is the difference between ranks*

Equation for Spearman's rank correlation coefficient taken from (Spearman, 1904; 2008)

### **2.4.3 Tools used in ArcGIS**

I used ArcGIS extensively throughout the course of this thesis. The main tools used include spatial joins where I load shape files for ICES data, namely ICES statistical rectangles and ICES ecoregions, then plot trawl survey data before performing a spatial join to associate each species record with the selected polygon area (rectangle or ecoregion) that it falls within. This process allows analysis of smaller community areas, either by carrying out temporal analyses on each or through spatial analyses between sites. To create the latitudinal bands, I use the merge function in the ArcGIS toolbox to combine the chosen ICES rectangles into single latitudinal bands. Tabular joins and unions are used for various different combinations of point shape files, for example, linking slope data (calculated in R) with central points of ICES rectangles. I use the calculate geometry function to generate the central points of grid cells or polygons and to calculate the extent or area contained within a polygon shape. For calculations of areas or distances within or between point shape files I use the convex hull function within the Minimum Bounding Geometry tool, this ensures that the resultant area or extent will be of the least possible size, and it also produces a useful polygon shape which can then be used as part of future analyses. Finally, I use the create fishnet tool to build enclosed grid cells to a chosen specification and size.

My work aims to provide a better understanding of how fish communities change through time, what the causal factors in these changes are and how best to act to protect and maintain not only our fish communities which are in danger but also to keep our economically valuable fishing industry as sustainable as possible and perhaps create better relationships and links between science and industry.

This chapter outlines the materials used throughout the thesis and the main methods and metrics that feature in the research chapters that follow, other, more specialised methods are detailed in the relevant sections of this work.

### Chapter Three – Taxonomic diversity – changes in alpha diversity over three decades\*



*Trawler off the North East coast of Scotland, 1997*

\*A version of this chapter has been published in the *Journal of Fish Biology* (see Appendix A and Moyes, F. and A. E. Magurran (2019). "Change in the dominance structure of two marine-fish assemblages over three decades." *Journal of Fish Biology* **94**(1): 96-102.)

## Chapter 3 – Taxonomic diversity – changes in alpha diversity over three decades

### 3.1 Introduction

In this first research chapter, I ask how the diversity of Scottish fish assemblages has changed over time and space. Specifically, I compare the temporal trends and latitudinal gradients of change in the taxonomic diversity of the two marine fish assemblages over three decades.

The ongoing biodiversity crisis is the consequence of a combination of anthropogenic impacts including over exploitation and climate change (Jackson, 2008; García Molinos *et al.*, 2016; Cheung, 2018). To date, most of the evaluations of marine fish assemblages, particularly in the context of stock assessment, have focused on trends in individual species (Pershing *et al.*, 2015; Boyd *et al.*, 2018), with marked changes in recent years widely reported (Baudron *et al.*, 2011; Engelhard *et al.*, 2014; Dutz *et al.*, 2016). As a consequence, there is limited understanding of the extent and direction of change in the structure of marine fish assemblages in which these populations of interest are embedded, although investigators, e.g. (Jung & Houde, 2003; Magurran *et al.*, 2015b; Morley *et al.*, 2017; Iacarella *et al.*, 2018), increasingly recognise the need to quantify spatial and temporal shifts in biodiversity.

Anthropogenic climate change is increasingly being recognised as an important driver of community reorganisation and recent research (Magurran *et al.*, 2015b) highlights the fact that this can be rapid, taking place over decades rather than centuries. There are documented physical differences between the two coastal systems to the east and west coast of Scotland (see Chapter 2 sections 2.1 and 2.2 for more details). Additionally, there are contrasting temporal changes in temperature (ICES, 2018c, 2019) and fishing pressure (Pauly & Zeller, 2015a; ICES, 2018b, 2020) which can affect the performance of species. These physical differences in the coastal ecosystems (Heessen *et al.*, 2015) could favour different temporal trends in the taxonomic diversity of the fish assemblages .

There are a variety of methods available to quantify change in taxonomic diversity (Magurran, 2013b). For this work I focus on simple numerical abundance, relative dominance and selected metrics from the Hill number framework (Hill, 1973) - see Chapter 2.3 for further details. This choice allows me to illustrate my findings in a unified statistical framework and makes meaningful ecological comparisons between systems possible. In addition, the use of multiple diversity metrics can help illuminate the changes and underlying structural events taking place (Chao *et al.*, 2014; Dornelas *et al.*, 2014a; Morris *et al.*, 2014).

Marine biodiversity is a field in itself with its own challenges (Gray, 1997; Borja *et al.*, 2020). There have been many studies quantifying recent changes in fish temporal and spatial patterns of taxonomic diversity (Rijnsdorp *et al.*, 1996; Rogers & Ellis, 2000; Genner *et al.*, 2004; Elahi *et al.*, 2015; Frelat *et al.*, 2018). The responses of marine communities to both natural and anthropogenic drivers (Genner *et al.*, 2010; Henderson *et al.*, 2011; Kowalewski *et al.*, 2015; Brown *et al.*, 2016; Cheung, 2018; Beukhof *et al.*, 2019a) illustrate that these

responses are hugely variable and can be linked to a variety of factors including habitat, climate and scale (Cusson *et al.*, 2015; Chase *et al.*, 2019).

In this chapter I first examine the changes in the assemblage as a whole using numerical abundance and the Hill numbers framework, before focusing on taxa, where I ask which species contribute most to temporal change in dominance. One frequently used measure of biodiversity is relative species abundance; this quantifies the commonness or rarity of species in comparison to the overall abundance of the assemblage. Species abundance distributions (SADs), which describe the pattern of relative abundance within an assemblage, generally follow the shape of a ‘hollow curve’ with a few abundant species and many rare ones (McGill *et al.*, 2007). The most dominant species typically account for a large fraction of the overall abundance, and play an important role in ecosystem function (Davies *et al.*, 2011; Ellingsen *et al.*, 2015a; Wohlgemuth *et al.*, 2016; Jones & Magurran, 2018). For this reason, the relative dominance of the most numerically abundant species in an assemblage is an informative measure of community structure and can potentially reveal changes that would otherwise be unseen using metrics such as species richness or total abundance.

Here I draw on time series data of fish assemblages to the east and west of Scotland (see Figure 2.1 for illustration) to ask how the taxonomic diversity of these commercially important regions has changed over three decades. This time scale represents the period over which high quality assemblage data are available (ICES, 2014) (see Chapter 2, sections 2.1 and 2.2 for further details). The study areas being compared in the analysis are geographically close yet are exposed to different climatic conditions and exploitation practices; as such they provide an insight into the extent of recent change in taxonomic diversity, including assemblage dominance structure, in heavily fished regions of the Northeast Atlantic.

The physical contrasts between the two ecosystems suggest that I will be able to reject the null hypothesis of no difference in diversity trends between the systems. Moreover, I expect this to be the case for the suite of metrics that I apply. As the North Sea system has experienced more intensive fishing practices (Stamoulis & Torreale, 2016; ICES, 2018a) in the past (see Chapter 5.3, Figure 5.15 for details) and has undergone greater sea surface temperature warming (Baudron *et al.*, 2013; ICES, 2018c, 2019) (see Chapter 2.2 for further details) my expectation is that there will be greater change in the northerly latitudes for the east coast system as climate change can lead to greater range shifts among fishes (Perry *et al.*, 2005; Dulvy *et al.*, 2008; Fredston-Hermann *et al.*, 2020).

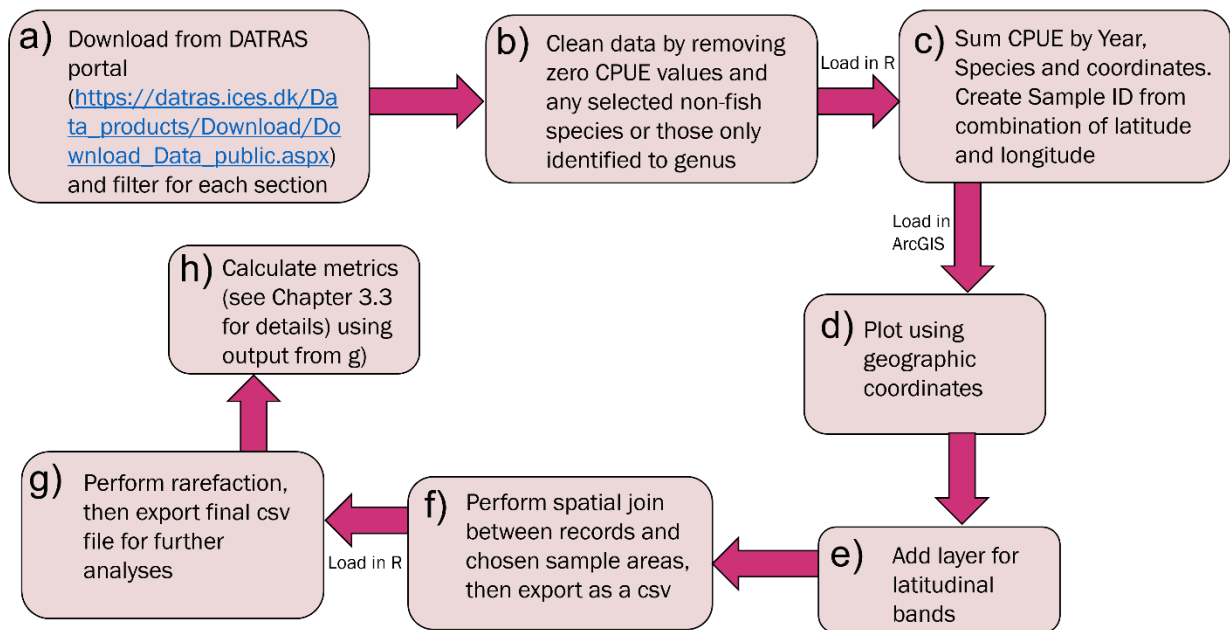
This first part of my analyses does not focus on individual fish or their contribution to the changes I find, but the latter part of my analysis quantifies temporal change in relative dominance, including the identities of the most dominant species. Relative dominance, as calculated here, is the numerical abundance of the most abundant species as a proportion of total numerical abundance during a defined time period. However, it is known that fish assemblages to the west of Scotland are undergoing rapid biotic homogenization (Magurran *et al.*, 2015b), and that biotic homogenization and homogenization of water temperatures are correlated in the west coast assemblages. In contrast, the North Sea to the east of Scotland has exhibited a smaller overall increase in water

temperature during the same period (ter Hofstede *et al.*, 2010). Thus, I expect to be able to reject the null hypothesis that the two coastal systems will exhibit similar patterns of change.

### 3.2 Methods

This section gives an overview of the methods used in this chapter. The main taxonomic alpha diversity measures are also described in more detail in Chapter 2.3 (see individual sections for further information). The data used were sourced from the International Council for the Exploration of the Sea (ICES) and have been taken from two standardised scientific trawl surveys incorporating the ICES areas VIa (West Coast), IVa and IVb (North Sea) (DATRAS, 2015, 2019). Species records contain a precise geographical location and numerical species abundance represented by the CPUE (catch per unit effort) which, for these analyses, refers to the number of individuals of any given species caught per hour (tow duration is generally half hour periods).

Throughout this thesis I focus only on records collected using the Grande Overture Verticale (GOV) gear, a type of bottom trawl net with a small mesh. As detailed in Chapter 2.2 I use the ICES rectangles to form the boundaries of assemblages before combining longitudinally (5 x 1) to create latitudinal bands. These ICES rectangles are freely available for download on the ICES website (ICES, 2014) and represent 30' latitude by 1° longitude in a grid cell. To ensure there is no bias in sampling effort between latitudinal bands I perform a single resampling prior to analyses (see Chapter 2.3.2 for further information on this process).



**Figure 3.1:** Simple workflow detailing the steps performed in this chapter. In a) the data is downloaded from the public website (link included) and filtered for the ICES regions studied, in b) the data are cleaned by removing non species level individuals. In c) I sum the species abundance data to year and location before d) plotting by location in ArcGIS (ESRI, 2015), the layer file for latitudinal bands is then added to the map in e). The final steps are to f) carry out a spatial join between the latitudinal bands and the species abundance records and perform rarefaction (or resampling) in g) before exporting the csv ready for analyses – h) calculating the metrics outlined in the next sections.

### 3.2.1 Species numerical abundance

Here I use the number of individuals per species recorded each year in a geographical location based on the CPUE given in the trawl survey data. This is then aggregated by latitudinal band to give a total abundance count per species, per year, see Chapter 2.3.1.1.1 for further details. I then use the total numerical abundance (N) within a latitude at each time step before performing any further analyses.

### 3.2.2 Hill number $q_0$ – equivalent to species richness

This measure refers to the number of distinct species found at a particular time and location. Here I use the count of different species found each year within each latitudinal band (see Chapter 2.3.1.1.2 for further details). This metric takes no account of species abundance, only identity.



### **3.2.3 Hill number $q_1$ – exponential Shannon**

This metric, which is based on the exponential of the Shannon index (Hill, 1973), includes both the abundance and identity of a species. For further information and associated equation see Chapter 2.3.1.1.3. As with the previous metrics discussed in this chapter, I calculate  $q_1$  for each year within each assemblage (latitudinal band).

### **3.2.4 Hill number $q_2$ – reciprocal Simpson**

This measure, which is based on the reciprocal of the Simpson index (Magurran, 2013b) relates to the evenness of an assemblage. For further information and equation see Chapter 2.3.1.1.4. I calculate  $q_2$  for each year within each latitudinal band. This measure includes both identity and abundance and a higher value indicates a more evenly balanced assemblage.

### **3.2.5 Hill number $q_\infty$ – reciprocal Berger-Parker**

$q_\infty$  is related to the Berger-Parker index (Hill, 1973), a simple index representing the relative dominance of an assemblage. Because the reciprocal form of the index is used,  $q_\infty$  increases as a system becomes more even. For further information and the equation see Chapter 2.3.1.1.5. As with the previous metrics discussed in this chapter, I calculate  $q_\infty$  for each year within each latitudinal band. The dominant species section in Chapter 3.2.6 is based on the relative dominance (Berger-Parker) of the assemblage rather than its reciprocal ( $q_\infty$ ).

### **3.2.6 Dominant species**

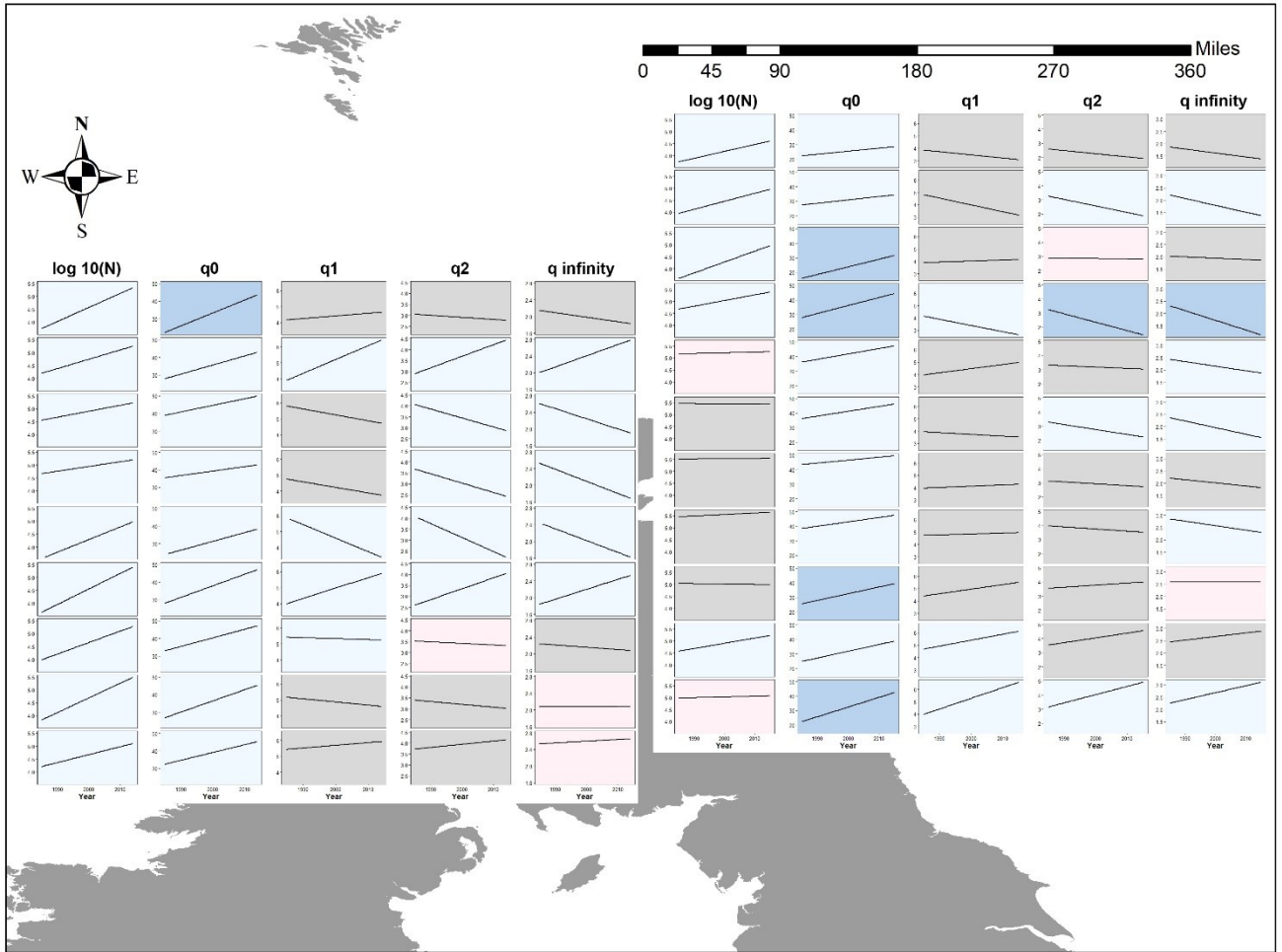
Here I focus on the opposite side of the coin to the  $q_\infty$  metric outlined in section 3.2.5 and explicitly consider dominance rather than evenness. To do this I calculate the numerical abundance of each species per year in an assemblage before dividing this by the total numerical abundance of the latitudinal band at that time step. The species are then ordered from highest to lowest by this measure. The top species (the most abundant) for each assemblage and year is extracted, and in the event of ties the species coming alphabetically first is taken. This species is then noted as the most dominant for the time step and assemblage. I also note the relative dominance of the most dominant species at each time step within an assemblage and calculate the mean values for each year across all latitudinal bands within the two ecosystems. Next, I perform a linear regression (Ordinary Least Squares (see Chapter 2.4.2 for details)) of mean relative dominance through time for each coastal system. Additionally, I calculate the six most dominant species for each latitude by decade. This is done to examine the identities of the most dominant species, not only through time and by system but also within latitude. To provide an overview of change in the identity of the six most dominant species I focus on decadal shifts in this part of the analysis.

I use simple linear regressions to calculate the slopes of change for each metric. This gives a single value for each latitudinal band which can then be used in correlation plots. I quantify the strength and direction of the pairwise correlations between each of the yearly assemblage level measures ( $q_0$ ,  $q_1$ ,  $q_2$ ,  $q_\infty$  and numerical

abundance). Unless otherwise stated, the correlations throughout this thesis are calculated based on Pearson's correlation coefficient (Pearson, 1909). See Chapter 2.4.2 for further details on this method. When examining the changes in relative dominance as described in Chapter 3.2.6, I also use the mean of all latitudinal bands for each coastal system, to make a direct comparison between the two ecosystems. Throughout this chapter any reference to significance in slopes or trends refers to a p-value of  $<0.05$  as reported in the OLS summary statistics provided in base R (lm() function).

### **3.3 Results**

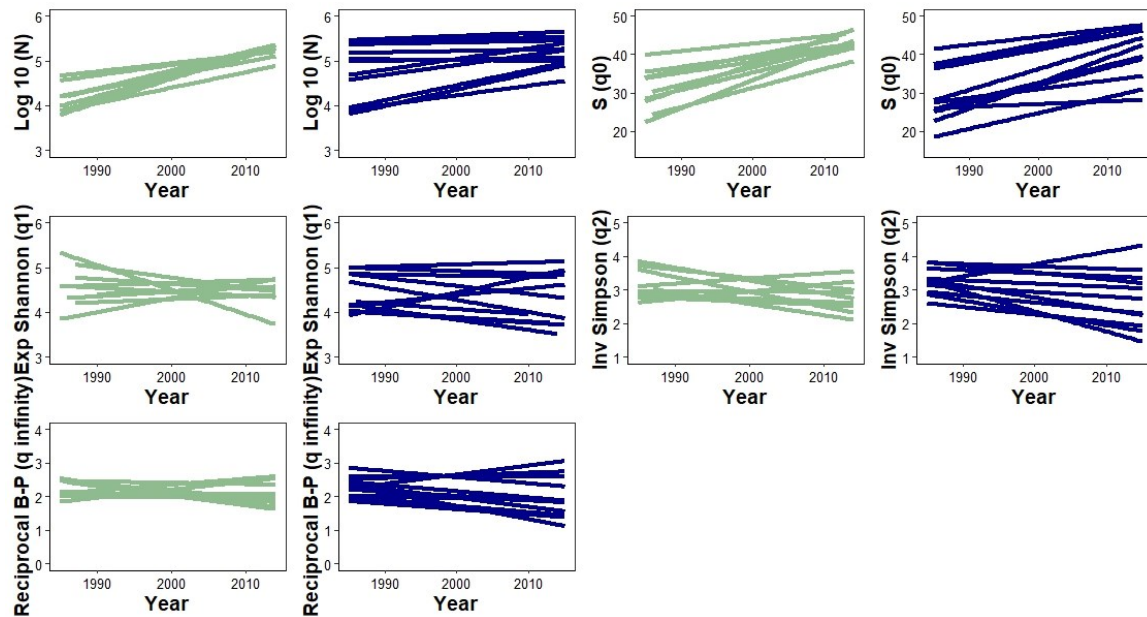
Here, my key findings include the clear distinctions between the coastal systems for most metrics and a change in the dominance structure (Moyes & Magurran, 2019) both latitudinally and by ecoregion. These trends are mirrored by changes in sea surface temperatures over the same time and location (see Chapter 2.2 for details and Figure 2.3 for illustration).



**Figure 3.2:** The map details the five main metrics calculated by latitudinal band and shows these in the geographic position they fall in, the numbers on the plot strips represent the mid-point of the band in decimal degrees latitude. Each metric is plotted at each time step (year) (yearly points are not illustrated here) before a simple OLS regression trend line is added, the plot panels are coloured by z score (based on the qnorm of their p-value (calculated using R)) with the following key applied. Scores -  $z \leq -4$  in darker blue,  $-4 > z \geq -1$  in light blue,  $-1 > z < 1$  in grey,  $1 \geq z < 4$  in light pink and (although none apply here)  $z > 4$  in dark pink.

### 3.3.1 Species numerical abundance

Numerical abundance (N) is increasing in most places for both systems (see Figures 3.2 and 3.3). There are three latitudinal bands on the east coast where I find a decrease in N (27%) but none of these exhibit significant trends. The west coast system is significantly increasing in N for all but one of the latitudinal bands (89%) whilst the North Sea system is non-significant in most (72%). There is no clear pattern evident for the west coast system, but the east coast system shows that the more southerly latitudinal bands are shallower slopes whilst moving northwards they appear to become steeper with more variation between yearly N (see Figures 3.2 and 3.3 for illustration).



**Figure 3.3:** This figure shows the same slopes as shown in Figures 3.2 and 3.4 but allows for a quick visual comparison both between and within the systems. Here the slopes for each metric are plotted side by side and coloured by coastal system (as with previous figures this is exemplified by green for the west coast and blue for the east). It is evident that the differences between systems are clearly visible and that the only similarity in pattern is in the case of  $q_0$  (see Figure 3.4 and legend for the results of the median absolute deviation).

### 3.3.2 Hill number $q_0$ – equivalent to species richness

This measure indicates that all assemblages (latitudinal bands) are gaining species, with only two of the east coast bands being non-significant in trend. As with numerical abundance, there is no pattern evident although the slopes in the east coast system tend to be shallower than those on the west (see Figure 3.5 for density patterns and Figures 3.2 and 3.3 for pictorial representation).

### 3.3.3 Hill number $q_1$ – exponential Shannon

My results show a varied pattern of increases and decreases in  $q_1$  across both ecosystems although only three of these trends exhibit significance (18% of the North Sea system assemblages and 11% of the west coast assemblages). Additionally, all slopes are close to zero, but the east coast is more ordered as the trends begin in the southern bands as slight increases and then gradually flatten before decreasing towards the northern latitudes whilst the west coast direction is more varied with no real pattern evident (see Figure 3.3 for slope illustration and Figure 3.4 for latitudinal signal).

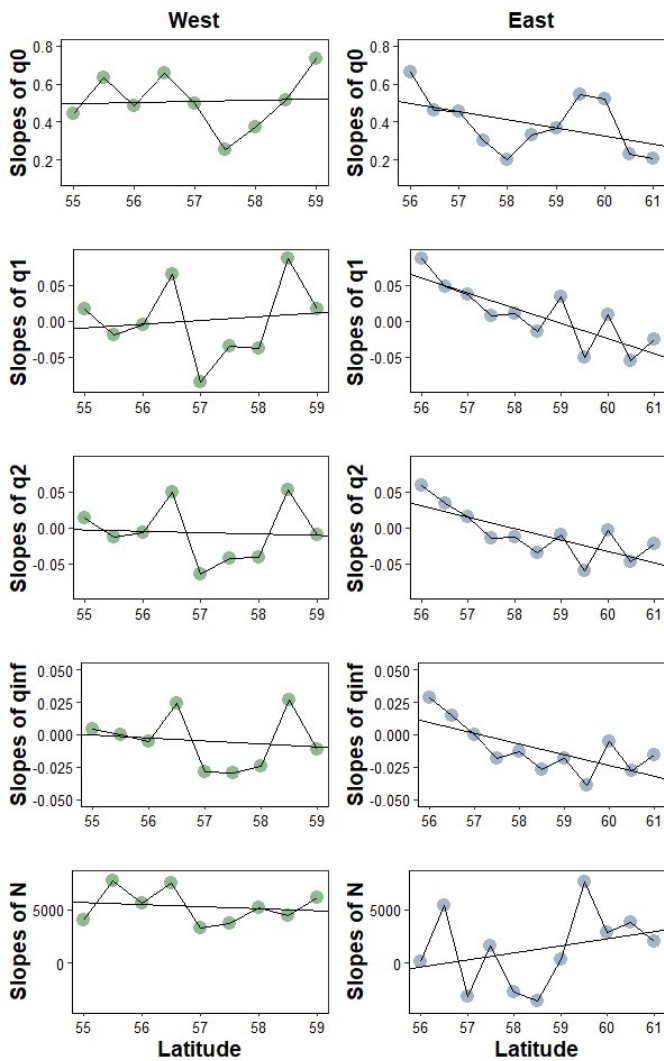
### 3.3.4 Hill number $q_2$ – reciprocal Simpson

This measure is decreasing for almost all latitudinal bands in both systems. As with  $q_1$ ,  $q_2$  tends to show stronger trends towards the northern latitudes on the east coast but no real pattern is evident on the west. There are only

three significant slopes, all from the east coast system (27%), of these, one, which is also the most southerly latitudinal band, is also positive. Additionally, as with the  $q_1$  slopes, there is more disparity between years for the east coast system in the southern and northern bands whilst those in the centre tend to exhibit less variation between years (see Figures 3.3 and 3.4 for details).

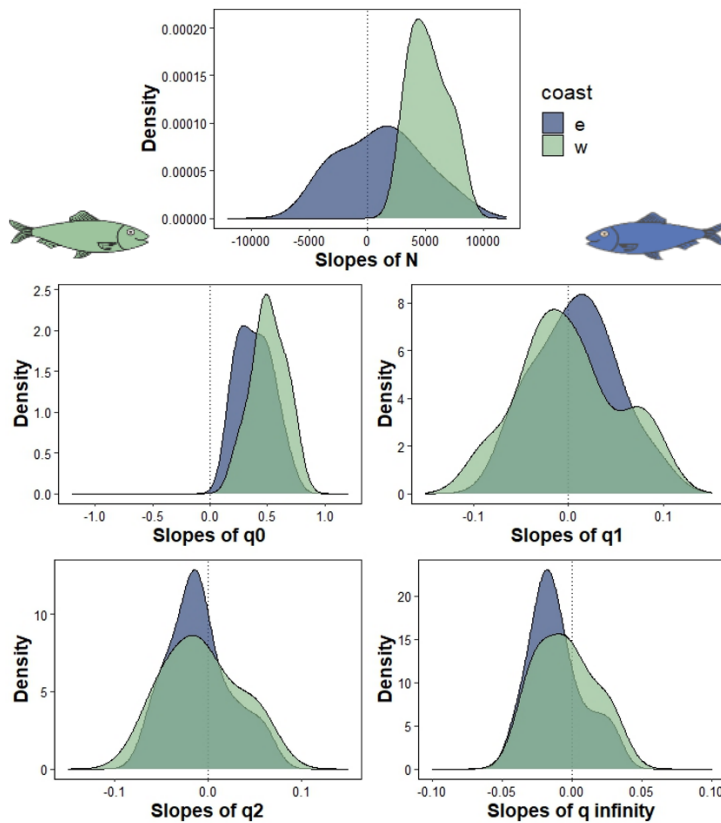
### **3.3.5 Hill number $q_\infty$ – reciprocal Berger-Parker**

Using the  $q_\infty$  metric, I find that although they are balanced, on the west coast there are slightly more decreasing slopes (56%), albeit non-significantly (only one negative latitudinal band shows significance and none of the 44% positive slopes are significant). As this is the reciprocal of the Berger-Parker measure, these results suggest that the assemblages are decreasing in evenness but increasing in dominance. However, the pattern on the east is towards decreasing as 72% of the bands are negative (three of which are significant) with only 28% of bands increasing, there are no significantly positive slopes.



**Figure 3.4:** Here the slopes of change as shown in Figures 3.2, 3.3 and 3.5 are plotted against latitude. This suggests a clear latitudinal signal on the east coast for all metrics, but no pattern is evident for the west coast system. The east coast exhibits a decreasing trend in the strength of slopes towards the higher latitudes in all measures except N (numerical abundance) which appears to be increasing towards the north.

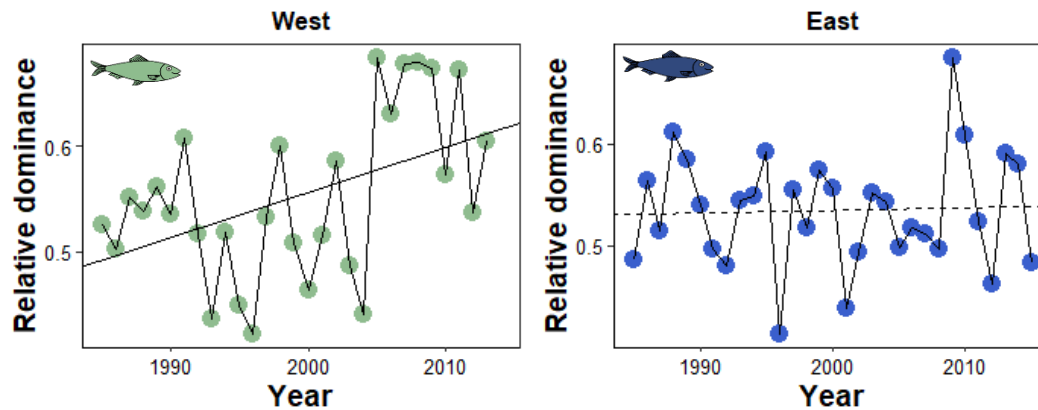
On the east coast I find a stronger latitudinal signal in almost all the metrics (see Figure 3.4), and, except for N, this signal shows a decline in all metrics in a northward direction, for  $q_1$ ,  $q_2$  and  $q_\infty$  this is significant (p-values as follows:  $q_1=0.002$ ,  $q_2=0.01$ , and  $q_\infty=0.02$ ). In contrast, on the west coast, although I find variation between latitudes, this does not follow any clear latitudinal pattern for any metric. The general pattern of increasing and decreasing slopes in assemblages for both systems is variable with no clear arrangement evident (see Figure 3.3 and Figure 3.5 for illustration).



**Figure 3.5:** Slopes of change (OLS regression) as density plots coloured by coastal system. Each plot is centred around zero, represented here by a dotted line. The distinction in variation is clear with particular emphasis on the differences for  $N$ ,  $q_2$  and  $q_\infty$ . I also computed the Median absolute deviation for each system using the `mad` function in base R (RCoreTeam, 2021). These results are as follows: east coast –  $N=3375$ ,  $q_0=0.2$ ,  $q_1=0.04$ ,  $q_2=0.03$ ,  $q_\infty=0.02$ . West coast -  $N=1863$ ,  $q_0=0.18$ ,  $q_1=0.04$ ,  $q_2=0.05$ ,  $q_\infty=0.03$ .

### 3.3.6 Dominant species

As described in section 3.2.6 I use the mean of all latitudinal bands to calculate an overall slope of change for each ecosystem. The dominance structure of both systems changed over the thirty-year duration of the study (see Figure 3.6). However, although dominance is increasing in both cases, this increase is only significant for the west coast system ( $p$ -value=0.01). In addition, the identity of the most dominant species not only varies through time (see Figure 3.7 for latitudinal, decadal changes) but is also different for each coast. The east coast exhibits less temporal variation in identity of the most dominant species. Here the Norway pout *Trisopterus esmarkii*, (Nilsson, 1855) is the overall dominant for around two thirds of the time series, whereas on the west coast the identities change from Atlantic herring *Clupea harengus* (Linnaeus, 1758) in the first decade, to *Trisopterus esmarkii*, (Nilsson, 1855) in the second and finally Atlantic mackerel *Scomber scombrus* (Linnaeus, 1758).

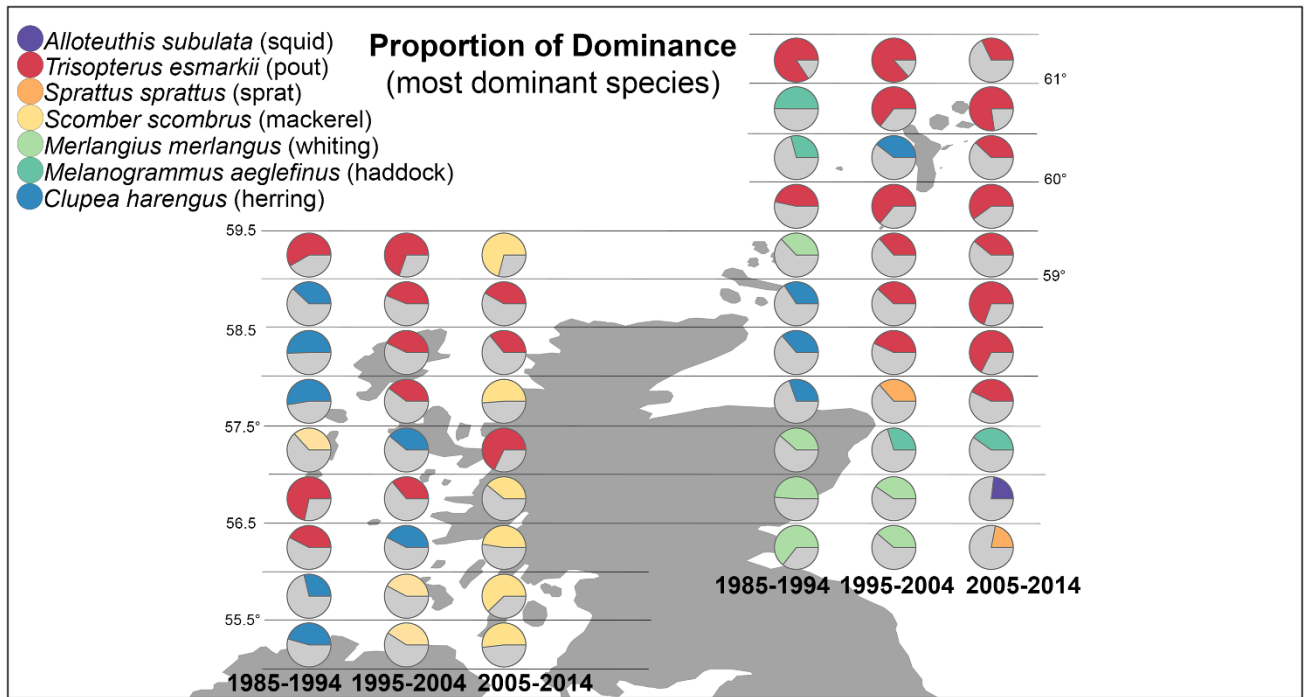


**Figure 3.6:** This plot shows the trend in relative dominance by year. The relative dominance of the most dominant species is calculated across all latitudes with an OLS regression trend line added, represented as a solid line for a significant slope and dashed for non-significant. The trend is increasing in both systems but only significantly on the west coast.

Considering the relative dominance across all latitudes and all years, the two systems show different species as the ‘winners’ with mackerel, *Scomber scombrus*, (Linnaeus, 1758) being overall dominant on the west coast whilst pout, *Trisopterus esmarkii*, (Nilsson, 1855) are most dominant on the east. A two-way analysis of variance test (ANOVA) using the proportion of dominance as the dependent alongside year and coast as independent variables was carried out. This revealed that although there was a statistically significant main effect for both year ( $p\text{-value}=0.005$ ) and coast ( $p\text{-value}=0.03$ ) there was no significant interaction of coastal system and year on the proportion of dominance seen [ $F(1, 56)=0.63, p=0.43$ ].

As well as the overall differences in dominance between the two ecosystems as detailed in the previous section there are also differences in the degree of heterogeneity in latitudinal bands (see Figure 3.7) between the systems. Additional two-way ANOVAs were performed for each ecosystem using proportion of dominance as the dependent and year and latitudinal band as the independent variables. West coast: no statistically significant main effect for latitude, but the main effect for year is significant ( $p\text{-value}=0.001$ ) and no significant interaction of these on relative dominance [ $F(1, 256)=0.59, p=0.44$ ]. East coast: no statistically significant main effect for year, significant main effect for latitude ( $p\text{-value}<0.001$ ) and significant interaction of the two on relative dominance [ $F(1, 306)=4.8, p=0.03$ ].





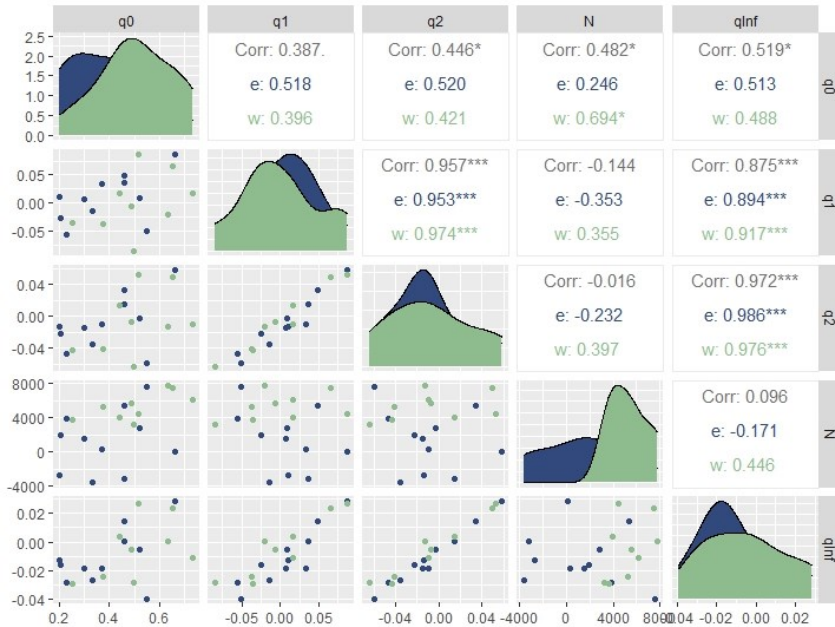
**Figure 3.7:** Figure showing the spatio-temporal changes in dominants (by both identity and amount). The map illustrates changes in the dominance of the most dominant species by latitudinal band. Each pie summarises a ten-year period and is colour coded to show the relative dominance of the most dominant species, the key to species identity is included at the top left corner. The three columns on each coast are not situated longitudinally but only according to decade (decade 1 – 3 left to right on each coast).

My findings show that not only does the pattern of dominance between the coastal systems differ, but the patterns found within exhibit considerable variation in both time and space. As implied with the results of the analysis of variance the bands on the east coast are more diverse and are also more significant in most cases. However, a Mann-Whitney-Wilcoxon test (Wilcoxon rank sum test) performed between the systems was non-significant ( $p$ -value=0.23 and  $W=66$ ). In addition, a Spearman's correlation (see Chapter 2.4.2 for details and equation) was carried out which showed only a weak (non-significant), negative monotonic correlation ( $r_s=-0.14$ ,  $S=64$ ,  $p=0.78$ ).

For clarity of visualisation the latitudinal analysis divides the temporal aspect of dominance into three decades with relative dominance pertaining to decades rather than years (see Figure 3.7). This partitioning of time further emphasises the changes to dominance identity and amount and presents distinctive patterns across the coastal systems. Figure 3.7 illustrates that the west coast alternates between three main species; *Clupea harengus*, (Linnaeus, 1758), *Trisopterus esmarkii*, (Nilsson, 1855) and *Scomber scombrus*, (Linnaeus, 1758), whilst the east is largely dominated by *Trisopterus esmarkii*, (Nilsson, 1855) except in the initial years where haddock *Melanogrammus aeglefinus* (Linnaeus, 1758) feature more prominently.

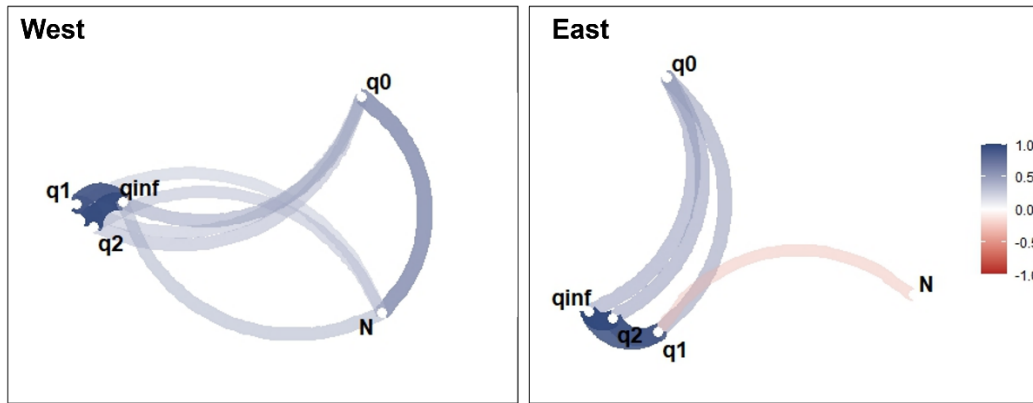
In order to discover more about the relationships between the slopes of the various metrics I carried out a pairs analysis with the GGally (Schloerke *et al.*, 2018) package in R and using the Pearson correlation coefficient

(Pearson, 1909). The results suggest that although there are strong positive correlations between  $q_1$  and  $q_2$ , the only real differences between the systems are found when looking at the relationships between change in  $N$  and the other diversity metrics but these are mostly weakly correlated (see Figure 3.8).



**Figure 3.8:** The pairs plot shows the scatter plot and densities of the slopes (as in Figure 3.3) alongside the correlations between each of the pairs of metrics. Here the overall correlation is shown in grey whilst the green and blue are representative of the coastal systems as previously (west = green and east = blue). The asterisks indicate strength of correlation from . to \*\*\* where \*\*\* is the strongest. Asterisks represent p-values ( $<0.1$ ,  $*<0.05$ ,  $**<0.01$ ,  $***<0.001$ ).

It is possible to examine the relationships in a slightly different way, and the network plot in Figure 3.9 shows the clear distinction between the overall relationship amongst metrics for each system. The network plot also highlights the greater strength of correlation between  $q_\infty$  and  $q_1$  and  $q_2$  on the west coast and illustrates the negative relationship between  $N$  and  $q_1$  and  $q_2$  for the east coast system which is not found on the west.



**Figure 3.9:** Each metric (slope of change) is connected to the others within their coastal system, the strength of correlation is based on Pearson's correlation coefficient and ranges from -1 to +1 where -1 is strongly negative related and +1 is strongly positively related. A white or near invisible link indicates no correlation or only very weakly correlated.

### 3.4 Discussion

As outlined in the introduction (Chapter 3.1) the contrasting conditions in the two ecosystems suggested that despite their close proximity and similarity in fish populations (ICES, 2018b, 2020) there would be clear differences in their response to environmental change (Rijnsdorp *et al.*, 2009; Wright *et al.*, 2018). My analyses confirm this view as I find variation between systems for all metrics although the extent and direction of the variation differs according to location, either by latitude or coast or both.

It is well documented that the world's biodiversity is undergoing significant change due to environmental factors such as climate change (Dornelas *et al.*, 2014a; Primack *et al.*, 2018; Blowes *et al.*, 2019a; Antão *et al.*, 2020) and the marine realm is no exception (Pörtner & Peck, 2010; Beaugrand *et al.*, 2015; García Molinos *et al.*, 2016; Bruno *et al.*, 2018; Burrows *et al.*, 2019; Moullec *et al.*, 2022). Additionally, warming waters are not the only environmental issue affecting marine fish, there is also the effect, and the after effects of overfishing (Jackson *et al.*, 2001; Scheffer *et al.*, 2005; Pinsky & Byler, 2015; Gordon *et al.*, 2018; Dulvy *et al.*, 2021; Yan *et al.*, 2021). Despite the problems facing the fishes in these systems, my work has shown that, for these regions at least, assemblages are increasing in both numbers of species and individuals (see Results sections 3.3.1 and 3.3.2). This highlights the need to move towards an assemblage based assessment of biodiversity change rather than focusing only on population losses (Kupschus *et al.*, 2016). It also points to the fact that even in a relatively short time span (thirty years in this case) and small geographic area it is possible to see marked temporal and spatial change. Although metrics of diversity in both systems are generally increasing with time, the North Sea system shows more variation between latitudinal bands in both species increases ( $q_0$ ) and individual increases (N) and in the case of N, the increases are more subtle with some assemblages decreasing in number. The disparity between the systems regarding N suggests that the differences in numerical abundance are contributing to the discrepancies found between the metrics which include species abundances, namely,  $q_1$ ,  $q_2$  and  $q_\infty$ .

The use of the Hill numbers statistical framework (Hill, 1973; Magurran, 2013b; Chao *et al.*, 2014) allows me to ‘turn the dial’ on the emphasis placed on abundance as I move through the metrics,  $q_0$  (equivalent to species richness), as discussed in section 3.2.2, takes no account of species abundance, only presence (or absence) but the remainder of the measures I chose do incorporate the number of individuals. As seen previously there are differences in the change in numerical abundance between the systems, suggesting that the metrics including abundance will also exhibit similar inconsistencies. Indeed, it is clear from the map (see Figure 3.2) that the North Sea system includes not only more variation in many assemblages than the West but also appears to follow a latitudinal gradient to some extent (see Figure 3.4), which is not as evident in the West coast system. This difference could be due in part to the disparity between the sea surface temperatures between the systems (ICES, 2018c, 2019) (see Chapter 2, Figure 2.3 for details). Combining the results from a suite of metrics creates a clearer picture of the changes taking place (Dornelas *et al.*, 2013; McGill *et al.*, 2015) and can help to inform fisheries management in maintaining these systems at a sustainable level with regard to fishing practices (Hammer *et al.*, 1993; Gordon *et al.*, 2018; Engelhard *et al.*, 2019).

The focus here on marine fish assemblages, rather than fish populations, reveals community wide changes that can be obscured in single species studies. A spatio-temporal approach (Henderson, 2017) in combination with examination of key attributes of community structure, such as the changes in dominance, is an important starting point for understanding the consequences of the melting pot of pressures these systems are currently under (Majewski *et al.*, 2017).

The two coastal systems show distinct differences not only in the proportion of dominance but also in the identity of the most dominant species. Interestingly, it was in the west coast assemblages that the greatest change was detected. Previous work (Magurran *et al.*, 2015c) highlighted an increase in biotic homogenization over the same period and hypothesised that changes in water temperature may have contributed to this pattern. The observed differences in dominance found between the east and west coasts are therefore potentially linked to the different patterns of change in sea surface temperatures (Simpson *et al.*, 2011; Stuart-Smith *et al.*, 2017; Townhill *et al.*, 2017) since water temperature is a key driver of distribution patterns in marine fishes (Perry *et al.*, 2005). Indeed, the impact of climate change on North Sea circulation and its fish stocks has been discussed elsewhere (Turrell, 1992; Baudron *et al.*, 2013; Hiddink *et al.*, 2014). However, temporal variation in sea surface temperatures (Genner *et al.*, 2004; Henderson *et al.*, 2011; Miller *et al.*, 2011) is unlikely to be the only driver influencing the trends since fishing pressure also leads to marked changes in the structure of marine assemblages (Jackson *et al.*, 2001).

The contrasting outcomes in these two geographic localities illustrate why it is difficult to predict how different systems will respond to environmental and anthropogenic drivers (Poloczanska *et al.*, 2016). Such spatial heterogeneity may be a widespread phenomenon. For example, contrasting patterns of biodiversity change were also evident in two zones of a bay in Brazil, monitored over three decades, (Araújo *et al.*, 2016).

On the east coast - which exhibits less temporal variation in identity of the most dominant species - the Norway pout *Trisopterus esmarkii*, (Nilsson, 1855) is the overall dominant for around two thirds of the time series with

the exception of the initial decade where haddock *Melanogrammus aeglefinus*, (Linnaeus, 1758) features more prominently. In contrast, on the west coast the identities change from Atlantic herring *Clupea harengus*, (Linnaeus, 1758) in the first decade, to *Trisopterus esmarkii*, (Nilsson, 1855) in the second and finally Atlantic mackerel *Scomber scombrus*, (Linnaeus, 1758) in the third. These species make different contributions to ecosystem function and have different economic values. For example, *Scomber scombrus*, (Linnaeus, 1758) is thought to be a predator of juvenile *Trisopterus esmarkii*, (Nilsson, 1855) (ICES, 2005), and while *Scomber scombrus*, (Linnaeus, 1758) catches have high commercial value, *Trisopterus esmarkii*, (Nilsson, 1855) is considered useful mainly as food in the aquaculture industry (ICES, 2005).

A better understanding of fish communities can lead to more efficient management strategies (Cheung *et al.*, 2018; Moriarty *et al.*, 2018). Currently there are new opportunities for the development of broader, constructive approaches to fisheries management (Jacobs *et al.*, 2018) where fish biology plays an important role in informing wild fisheries and their continued sustainability.

Science has a vital part to play in the conservation and management of fish resources (Obregón *et al.*, 2018) if it is used correctly (Smith & Link, 2005; Galland *et al.*, 2018; Syed *et al.*, 2018), but, as this study has demonstrated, greater understanding of how fish assemblages respond to change can be gained if fisheries managers take advantage of the rich toolkit of biodiversity metrics available (Hill, 1973; Magurran, 2013b). Even simple measures, such as the dominance index used here, reveal patterns that have hitherto been masked in population based analyses (Perry *et al.*, 2010). As such they have the potential to shed new light on the causes and consequences of ecosystem restructuring.

Dominance is an important indicator of how biodiversity is changing; it can reveal subtleties in community diversity that might otherwise be overlooked. This chapter reveals how the dominance structure of commercially important fish assemblages in the North East Atlantic has changed over the last three decades, and highlights the need to understand how the drivers of change, including fishing and climate change (Perry *et al.*, 2010) contribute to the restructuring of these assemblages.

The two coastal systems show distinct differences not only in the proportion of dominance but also in the most dominant species. A recent study (Hansen *et al.*, 2017) found that there were shifts in species dominance expected in freshwater lake systems as a result of warming waters. Therefore, the differences in dominance found between the study areas could potentially be linked to the disparity of their sea surface temperatures (Hiddink *et al.*, 2014).

There are likely to be numerous contrasting factors which will, either singly or in combination, affect marine fish assemblages (Peltonen & Weigel, 2022). These elements may trigger different reactions depending on several other features, for example, tolerance to water depth, salinity, warmth; introduction of prey or predator; fishing activity; capacity within the system. My results show that the ‘winners’ in the dominance patterns have different roles in the ecosystems as *Scomber scombrus*, (Linnaeus, 1758) is of high commercial value in comparison to *Trisopterus esmarkii*, (Nilsson, 1855) which is generally only commercially viable as food in the

aquaculture industry (Froese & Pauly, 2019). In addition, as one of the smaller species it is vulnerable to predators, including some of those that have themselves been the most dominant. These contrasting outcomes illustrate the fact that success is contingent on several factors and that to properly protect and sustain our fisheries, these all need to be taken into account. Fish do not exist in isolation (Traugott *et al.*, 2021), and interactions between species contribute to changes in their assemblages. For example, the increased abundance and dominance of the mackerel, *Scomber scombrus*, (Linnaeus, 1758), within the west coast system has implications for small prey species, particularly the juveniles and larvae (Dahl & Kirkegaard, 1986; Runge *et al.*, 1987) of other commercial fish such as herring, *Clupea harengus*, (Linnaeus, 1758) (Skaret *et al.*, 2015) leading in turn to a possible depletion in the future strength of herring stocks. Adopting an approach which includes these types of potential interactions within an assemblage can assist with innovative methods of sustainable fisheries based on herring spawning grounds (Frost & Diele, 2022).

The findings in this study could potentially have implications for fisheries management and marine planning as it is evident that even small geographic distances can display marked differences in temporal and spatial diversity responses. An approach such as this study, which takes into account whole assemblage change, rather than simply population change can assist effective fisheries management strategies (Branch *et al.*, 2011; Hilborn, 2011; Trochta *et al.*, 2018; Hilborn *et al.*, 2020). The changes seen in dominance, both in amount and identity, can be an important indicator of how marine fish assemblages are changing both spatially and temporally. The distinct patterns found to the east and west alongside those of the sea surface temperatures (see Chapter 2, Figure 2.3) implicate climate change as one of the possible drivers of change.

### 3.5 Conclusion

This chapter suggests that temporal trends in taxonomic diversity are spatially heterogeneous, and that although general patterns may be consistent across geographically close systems, the strength and direction of these patterns can differ considerably. Additionally, this work indicates, for the first time, that there have been marked temporal changes in the dominance structure of Scottish marine assemblages over the last three decades (Moyes & Magurran, 2019). Contrasting patterns in both the identity of the dominant, and shifts in the relative abundance of the dominant, on the east and west coasts implicate climate change as one of the drivers of this change. This result highlights the importance of multi-species analyses of harvested stocks and has implications not only for fisheries management but also for consumer choices (Godfray *et al.*, 2010; Engelhard *et al.*, 2019).

Historically, Scotland's economy has enjoyed a significant contribution from the fishing sector, and it is important that this tradition be maintained, but only if it can be done in a sustainable manner. Here, I have highlighted the importance of tracking changes in metrics such as the Hill number framework and the identities of dominant species. By adopting a practical approach such as this I have shown that there is much to be learnt about the changes occurring within these fish assemblages and reinforced the view that science has a vital part to play in the conservation and management of fish resources (Obregón *et al.*, 2018). The approach adopted in this chapter has the potential to reveal hitherto unseen responses to environmental change.

My next chapter follows on from this work by examining the assemblage level change in these systems through the lens of functional diversity. It will add to the information already presented and help to better understand the traits that contribute to the changes found. It also considers the connections between two of the facets of diversity, namely taxonomic and functional, and assesses the strength and direction of these relationships within and between systems.

## Chapter Four – Functional diversity – patterns of change over thirty years



*Lower Largo Harbour, 2015*



## Chapter Four – Functional diversity – patterns of change over thirty years

### 4.1 Introduction

It is becoming increasingly evident that to successfully monitor biodiversity change it is necessary to adopt a multi-faceted approach (Villéger *et al.*, 2008; Crandall, 2009; Naeem *et al.*, 2016; Dencker *et al.*, 2017; Ottaviani *et al.*, 2019; Nakamura *et al.*, 2020). Until recently, most studies focused on a taxonomic approach which suggests that all species are equally contributing to the systems they live in. In fact, many species differ markedly in the way they respond to environmental change and anthropogenic pressures (Kraft *et al.*, 2015b; Kraft *et al.*, 2015a). This is particularly true in the marine realm as fishes have some of the most diverse life history traits in the animal kingdom and possess the highest functional diversity of all vertebrate species (Helfman *et al.*, 2009). Marine fish have a range of diverse functional traits reflecting the variation in their roles within their systems (Tilman *et al.*, 1997; Tilman, 2001). Additionally, a shared trait does not signify similar roles. For example, smaller pelagic species such as herring, *Clupea harengus*, (Linnaeus, 1758) and mackerel, *Scomber scombrus*, (Linnaeus, 1758) may occupy the same part of the water column as larger species such the picked dogfish, *Squalus acanthias*, (Linnaeus, 1758) but their roles within their assemblages will be very different. The dogfish consumes a wide diversity of prey (Froese & Pauly, 2019), including smaller herring and/or mackerel. Additionally, these three species occupy very different positions on the fast-slow continuum (pace of life) (Beukhof *et al.*, 2019b). The wide range of trait values possessed by fish suggest that complementing taxonomic diversity measures with those including traits will assist in biodiversity monitoring (Swenson, 2011; Díaz *et al.*, 2016; Cadotte & Tucker, 2018). Furthermore, a broader understanding of changes in functional diversity can play a key role in management strategies to support the maintenance of important functions in assemblages (Laureto *et al.*, 2015).

Many methods of quantifying biodiversity change (Magurran & Dornelas, 2010; Dornelas *et al.*, 2013; Magurran, 2013a, b; Morris *et al.*, 2014; McGill *et al.*, 2015) are based on taxonomic measures such as species richness and evenness. However, recent advances in trait-based approaches (Kjørboe *et al.*, 2018; Boyé *et al.*, 2019; Dawson *et al.*, 2021; Green *et al.*, 2022) coupled with the advent of comprehensive databases of traits such as FishBase (Froese & Pauly, 2019), the Tundra Trait Team (Bjorkman *et al.*, 2018), TRY (Kattge *et al.*, 2011), FISHMORPH (Brosse *et al.*, 2021) and AVONET (Tobias *et al.*, 2022) has led to increased use of functional diversity measures. The idea of functional diversity is not a new one and has not been solely limited to ecological studies (Laureto *et al.*, 2015) but the 21<sup>st</sup> century has seen a rise in the popularity and effectiveness of this type of approach (Petchey & Gaston, 2002; Petchey *et al.*, 2004; Petchey & Gaston, 2006; Mason *et al.*, 2013). However, until relatively recently, these trait-based approaches were more commonly used for terrestrial systems such as plants and less frequently in the marine realm but are now becoming more widely used (Villéger *et al.*, 2017). Fish are often seen as ecosystem engineers (Helfman *et al.*, 2009) whereby their contribution to their system is dependent on the combination of traits they possess (Nelson *et al.*, 2016). Using functional diversity metrics in conjunction with taxonomic measures, both independently and together, can help to provide a fuller picture of how assemblages are changing (Cilleros *et al.*, 2016; Baker *et al.*, 2021).

In this chapter I focus on three aspects of functional diversity (see section 4.2 for more detail), namely functional richness, which quantifies the amount of functional space occupied by the species within an assemblage (Mason *et al.*, 2005; Schleuter *et al.*, 2010); functional evenness, which measures how even, in terms of both trait combination and abundance, an assemblage is and functional divergence which examines how abundant species with more unusual combinations of traits are (those found at the borders of the functional space). These measures were chosen primarily as they are well established indices (Petchey *et al.*, 2004; Mason & De Bello, 2013; Mason *et al.*, 2013; Jarzyna & Jetz, 2016; Gross *et al.*, 2017; Villéger *et al.*, 2017; Pimienta *et al.*, 2020) which can be broadly linked to similar counterparts in the taxonomic suite of indices. I quantify temporal change in each of these measures for assemblages in both coastal systems. As in the previous chapter (Chapter Three) and, indeed, throughout this thesis, the assemblages consist of twenty latitudinal bands, separated by coastal system, and the data are sourced from the ICES (ICES, 2014) data portal (see Chapter 2.2 for full details).

This chapter also examines the correlations between the focal functional diversity measures and the taxonomic metrics discussed in Chapter Three, with the goal of understanding how related these facets of biodiversity are to each other, as this can be beneficial in the overall understanding of these systems (Cilleros *et al.*, 2016; Morelli *et al.*, 2017; Morelli *et al.*, 2018; Lamothe *et al.*, 2020; Baker *et al.*, 2021; Mattos *et al.*, 2022). I also focus on the linear relationships between three pairings of functional and taxonomic diversity metrics and investigate how these change between decades. This is done primarily using a single assemblage (latitudinal band) from each coastal system.

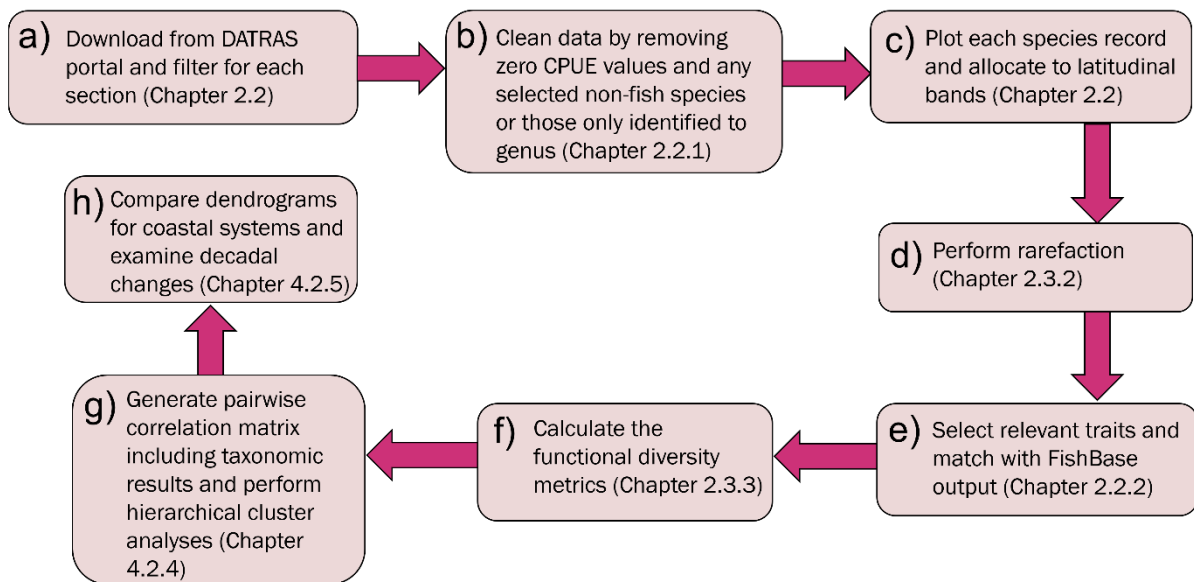
Finally, I examine the hierarchical clustering for each system and quantify how related the coasts are, this is done by decade to give an overall view of the changes found. Past changes in the relationships between and within the systems can help to inform possible future challenges (Gordon *et al.*, 2018; Peltonen & Weigel, 2022).

In this chapter I additionally ask if trends in functional diversity are consistent with those in taxonomic diversity. To do this, and using well studied metrics (Villéger *et al.*, 2008; Magneville *et al.*, 2021) I examine how functional diversity has changed over three decades and compare the coastal systems before further investigating how these metrics are related to the taxonomic measures studied in Chapter Three.

To calculate the functional diversity metrics, I chose eleven complementary traits, both continuous and categorical (see Chapter 2.2 for details). These were selected as they were relatively independent of each other and represent the main functional groups, namely, life history, morphological, environmental, and reproductive. I use a suite of functional diversity metrics (Magneville *et al.*, 2021) based on the concept of functional space calculated using Gower distance (Gower, 1971), these are functional richness, functional evenness, and functional divergence.

## 4.2 Methods

The data used in this work were sourced from the International Council for the Exploration of the Sea (ICES) and are taken from two standardised scientific trawl surveys incorporating the ICES areas VIa (West Coast), IVa and IVb (North Sea). Each species record contains a precise geographical location and numerical species abundance represented by CPUE (catch per unit effort) which in this instance refers to the number of individuals of a given species caught per hour using a tow duration of half an hour. Trawl speed is measured as 4 knots and this work focuses only on those records collected using the Grande Overture Verticale (GOV) gear, a type of bottom trawl net with a small mesh which is now the recommended gear for all bottom trawl surveys carried out by ICES. Here I use ICES rectangles to form the boundaries of assemblages before combining longitudinally (5 x 1) to create latitudinal bands. These ICES rectangles are freely available for download on the ICES website (ICES, 2014) and represent 30° latitude by 1° longitude in a grid cell (for further details on the data, systems and preliminary methods see Chapter Two, sections 2.2 and 2.3).



**Figure 4.1:** Workflow diagram illustrating the steps carried out within this chapter and where to find further details on each. In a) the data is downloaded after filtering for the ICES regions and trawl methods, in b) the data is cleaned by removing any zero abundances or any non-fish/unidentified species. In c) the individual species records are plotted in ArcGIS (ESRI, 2015) and allocated to the latitudinal band layer before d) resampling is carried out. In e) the selected traits are extracted from FishBase and matched to the species identities before calculating the chosen functional diversity metrics in f). In g) a pairwise matrix is created by combining with taxonomic results from Chapter 3 before finally h) comparative pairs plots and dendrograms are built.

The traits selected for the question in this chapter are the same as those used throughout this thesis (for further details on these traits and their complementarity nature see Chapter 2.2.2). After resampling and the selection and merging of traits with species I calculated three functional diversity metrics, using the mFD package

available in R (Magneville *et al.*, 2021). These metrics result in functional diversity values, namely richness, evenness and divergence, for each assemblage at a given time (year or decade).

#### **4.2.1 Functional richness**

Functional richness is calculated based on the amount of functional space occupied by an assemblage and takes no account of species' abundances. Species' positions in functional space (Maire *et al.*, 2015) are calculated using Gower distance (for full details see Chapter 2.3.3.1.1). Species with similar trait combinations will be clustered more closely together, whilst those with unusual trait combinations will tend towards the outer edges of the assemblage functional space. Functional richness is strongly correlated with species richness as the introduction of new species to the assemblage (an increase in species richness) is likely to correspond to an expansion in the functional space occupied by the assemblage. However, the species being introduced may possess similar trait combinations to others already present which would result in little or no change in functional richness (see Chapter 2.3.3.1.1 for further information, equation and pictorial representation, Figure 2.12).

#### **4.2.2 Functional evenness**

Functional evenness is also based on species position in the assemblage functional space but includes individual abundances. How even or otherwise an assemblage is can therefore be calculated based on the regularity of distribution of species, and their abundances, throughout the assemblage (Mason *et al.*, 2005). This metric has some correlation with taxonomic evenness measures but, unlike functional richness, is independent of species richness and can therefore add an extra dimension to the understanding of assemblage diversity change. For full details on this measure along with equation see Chapter 2.3.3.1.2 (see Figure 2.13, A and B for exemplification).

#### **4.2.3 Functional divergence**

As with functional evenness, this metric uses a species position in functional space and its abundance to calculate the assemblage value. Essentially, divergence will be lower if the most abundant species are also the most common in terms of trait combinations whilst it will increase as the more unusual species gain in abundance (see Chapter 2.3.3.1.3 for more details, equation, and illustrative figure, Figure 2.13, C and D).

#### **4.2.4 Correlations with taxonomic diversity metrics**

In this section I examine the relationships between the three functional diversity metrics and selected taxonomic measures. The comparisons were chosen according to my expectation that there would be a connection between them. For example, it is easy to anticipate that there will be a positive link between species richness as measured using  $q_0$  (see Chapter 3.2.2) and functional richness (see section 4.2.1 in this chapter). The second combination of functional and taxonomic metrics chosen was functional evenness (see section 4.2.2) and  $q_\infty$ , which was selected as a measure related with taxonomic evenness as it represents the reciprocal of the Berger-Parker

(Berger & Parker, 1970) index (see Chapter 3.2.5 for details). Finally, I investigated how functional divergence (see section 4.2.3) and numerical abundance (N) (see Chapter 3.2.1) are linked. Functional divergence takes account of numerical abundance in its calculation and therefore a positive relationship between it and N could suggest that the more divergent species (with more unusual combinations of traits) are becoming increasingly abundant. The chosen measures help to reinforce the importance of abundance as they tend to ‘turn the dial up’ on abundance in a similar way to the Hill numbers (Hill, 1973; Magurran, 2013b) (see Chapters 2 and 3 for details).

In this section I also consider the overall correlations between the three functional metrics and the two of the functional taxonomic diversity metrics discussed in Chapter Three, namely  $q_0$  and  $q_2$ . This was done using the slopes (simple linear regression using OLS) of change for each of these measures. I used Pearson’s correlation coefficient (Pearson, 1909) (see Chapter 2.4.2 for the equation) to generate the results and these are grouped by coastal system.

#### **4.2.5 Decadal change**

To further examine how the functional and taxonomic measures are related and how these relationships change over time I focused on a single assemblage from each coast split into three decades (Decade 1 – 1985 to 1994, Decade 2 – 1995 to 2004 and Decade 3 – 2005 to 2014, where each are inclusive of those years). I chose a central latitudinal band that was common to both systems (latitude = 58 degrees) and calculated the linear regressions of the pairs of metrics (as covered in section 4.2.4 – functional richness and  $q_0$ , functional evenness and  $q_\infty$  and functional divergence and numerical abundance).

#### **4.2.6 Decadal change in correlations between systems**

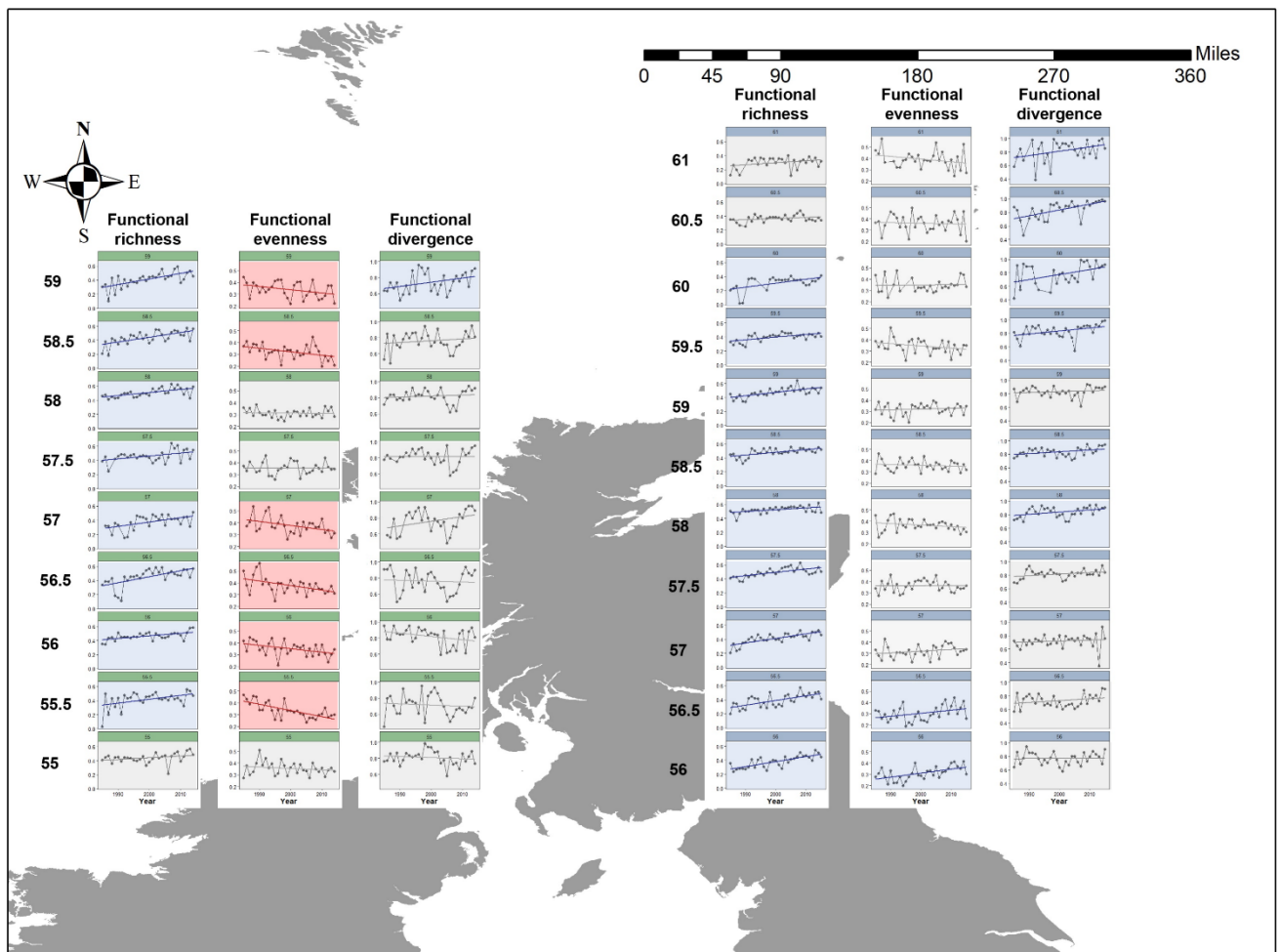
This section introduces the overall comparison of dendrograms for the coastal systems using cluster analyses. I built dendrograms for each system and examined the relatedness of these trees for each decade. This was done using the `cor_cophenetic` function from the `dendextend` package (Galili, 2015) in R to calculate the correlation between the cophenetic distance matrices of the two systems (Sokal & Rohlf, 1962). I did this for each decade separately to investigate whether there had been a temporal change in relatedness, where relatedness equates to the congruence of the trees. To complement this analysis I also computed the Baker’s Gamma Index (Baker, 1974) between the systems and the entanglement function (both available in the `dendextend` package). For both the cophenetic correlation and the Baker’s Gamma, the resulting values range between -1 and 1 with values close to zero indicating that the trees being compared are not statistically similar. The entanglement measure ranges between 0 and 1 with 1 representing full entanglement and 0 no entanglement. These analyses were performed only for those central latitudes common to both systems.

### 4.3 Results

In line with my findings for taxonomic diversity in the previous chapter (see Chapter 3.3 for details) I uncovered differences between the coastal systems in the temporal functional change of assemblages. This is most marked for the functional evenness (see Figure 4.2) metric which ties in with previous findings regarding dominance (Moyes & Magurran, 2019) - see also Chapter Three.

#### 4.3.1 Functional richness

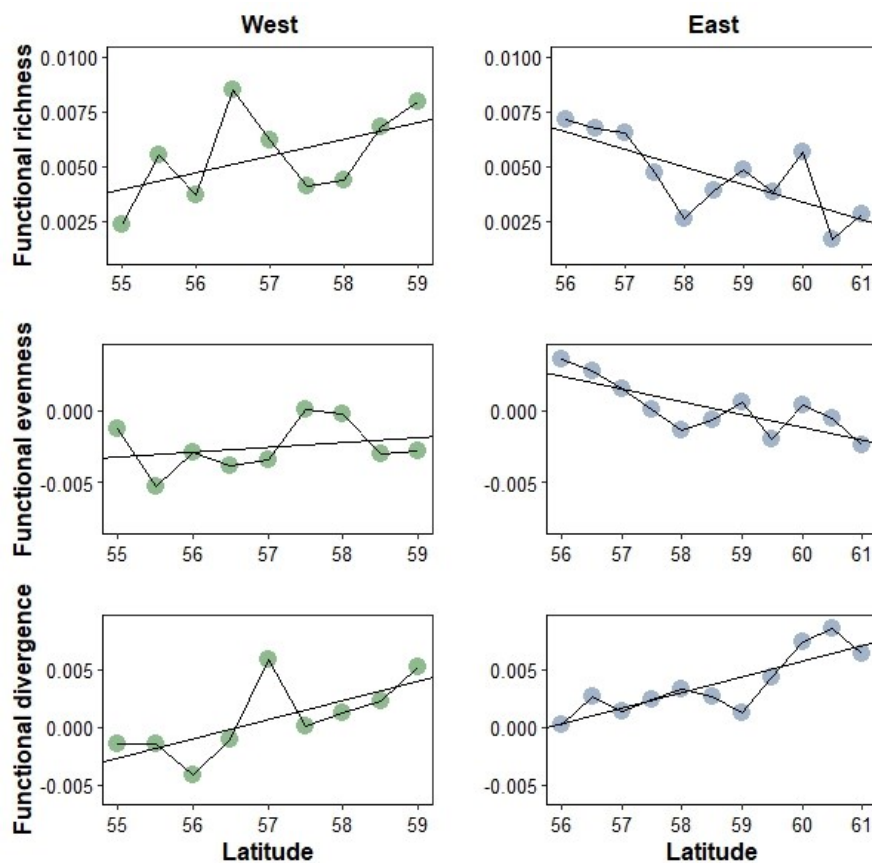
As with taxonomic species richness (Hill number  $q_0$ , see Chapter 3.3.2, Figure 3.2) all assemblages in both systems are increasing in functional richness. Additionally, most of these trends are significant (89% on the west coast and 81% on the east). This suggests that not only are these latitudinal bands gaining species over time but also that the species being added to the assemblages are generally different in terms of trait combinations to those already present.



**Figure 4.2:** The map shows the changes in the three functional diversity metrics plotted through time. The plots are overlaid on the map at approximately the latitude and coastal system they are located in, with the exact central latitude of each plot row labelled on the left. From left to right on each coast the panels show functional richness, functional evenness and functional divergence. Lines connect the yearly points, and a linear regression is added, coloured and shaded red for significantly negative, blue for significantly positive and grey for non-significant.

#### 4.3.2 Functional evenness

There are clear differences between the two systems in functional evenness. On the west coast, most (89%) of assemblages are decreasing in evenness and six of these (75%) are doing so significantly. However, the east coast shows a mixed picture with 55% of assemblages increasing in evenness but only two of the 45% decreasing bands being significant. This suggests that the west coast assemblages are recruiting species that are different in terms of trait combination to those already present but that there is little difference in the distribution of abundance amongst them. As functional evenness takes account of numerical abundance in addition to trait combinations (i.e., how evenly or unevenly the species are distributed in functional space), a decrease can be caused by either or both factors. However, the relatively flat  $q_\infty$  trend in Chapter 3.3.5 combined with the increasing trend for functional richness shown in section 4.3.1 suggest that difference in trait combination is the strongest contributor to the trends found here. The east coast, however, shows no clear pattern suggesting that species introductions and/or replacements are likely to be those with similar trait combinations and abundances.

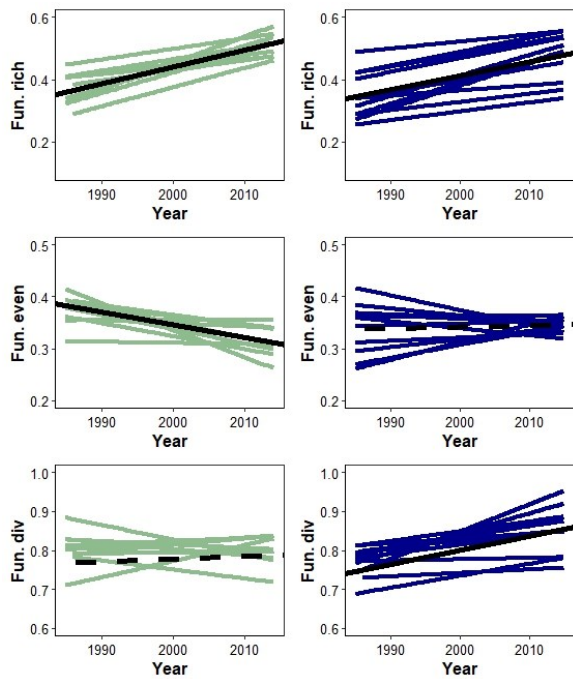


**Figure 4.3:** This figure shows the latitudinal trend of the slopes for each of the three metrics. The y-axes represent the slopes of the named metric. On the west all three metrics show steeper increasing slopes northwards (although only significantly so for functional divergence (p-value=0.04)). In contrast, the east coast slopes tend to become shallower towards the northern latitudes for functional richness and functional evenness whilst functional divergence is increasing as the bands move north. All trends on the east coast are significant (FR p-value=0.01, FE p-value=0.004. FD p-value=0.001).

### 4.3.3 Functional divergence

In contrast to functional evenness, here I find that the west coast presents a varied pattern in comparison to the east. In the west coast system 44% of the assemblages are decreasing (none significantly) and of the 66% increasing slopes there is only one significant one. However, the east coast assemblages are all increasing and 55% show significant trends. As functional divergence increases it is likely that the most functionally diverse species found in the assemblages are also becoming the most abundant suggesting that on the east coast the more unusual trait combinations are also those with greater numbers of individuals.

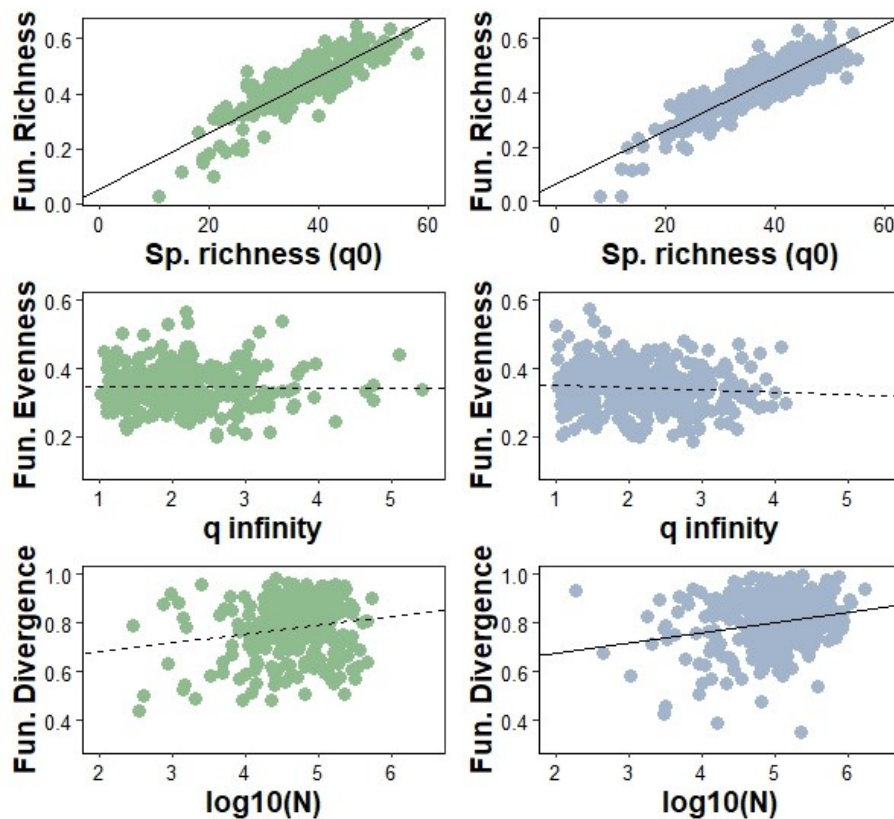




**Figure 4.4:** This figure shows the slopes of temporal change for each metric by coastal system (these are the same slopes as represented in Figure 4.2). The black lines denote the overall trend, significant as solid and non-significant as dashed. This figure helps to clarify the distinctions in slope variability between the systems for each metric.

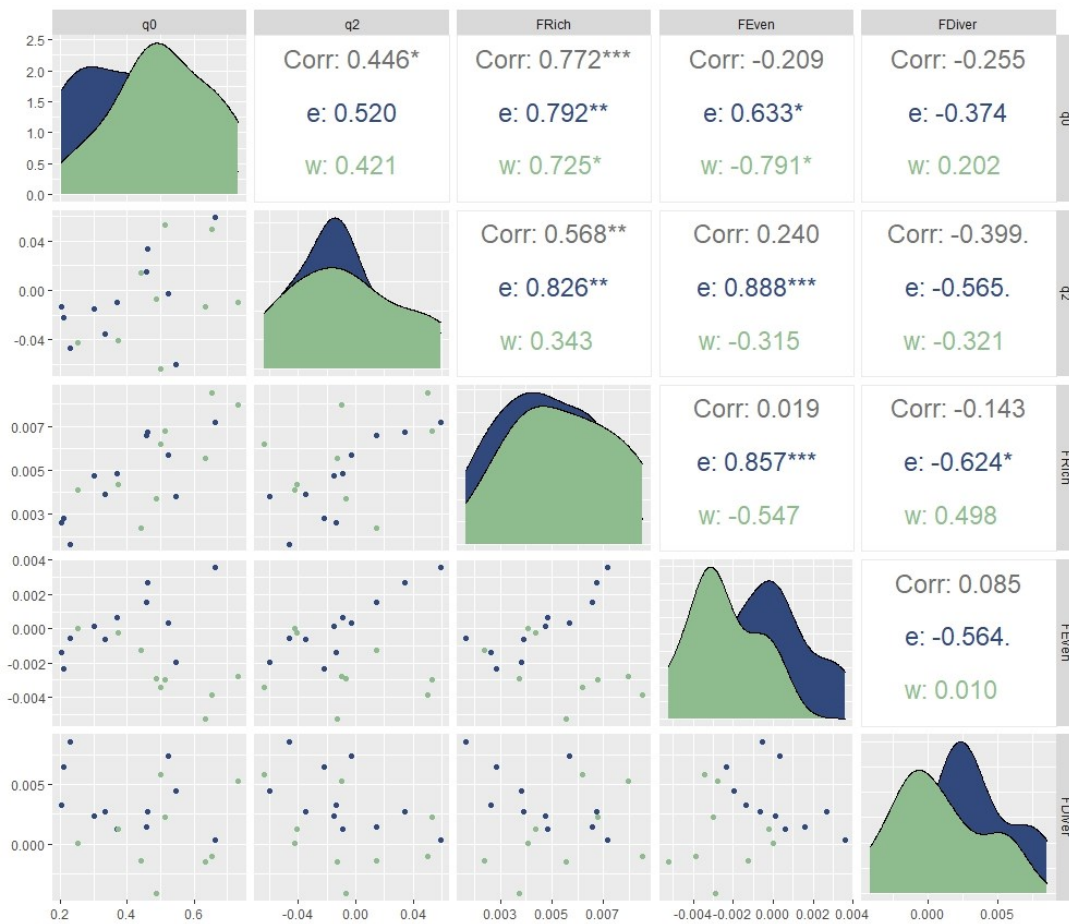
#### 4.3.4 Correlations with taxonomic diversity metrics

The expectation that functional richness and  $q_0$  would be highly correlated was met, as exemplified in Figure 4.5 (upper panel), for both systems with a strong linear trend shown. The fact that there is a strong correlation between functional richness and  $q_0$  suggests, however, that the species entering the assemblage are likely to have different combinations of traits than those already present, indicating low functional redundancy (da Silva Camilo *et al.*, 2018). When examining the relationship between functional evenness and  $q_\infty$  however, I find that the results as illustrated in Figure 4.5 (middle panel) show no evidence of any relationship between the two suggesting that the species with more unusual combinations of traits remain at similar abundance levels or are being replaced by others with comparable trait combinations. For these first two combinations, there is little difference between the two systems (see Figure 4.5 legend for an overview of p-values and adjusted  $R^2$ ) but when examining the relationship between functional divergence and numerical abundance I do find discrepancies between the coasts. As numerical abundance increases there is a corresponding increase in functional divergence suggesting that the species with more unusual trait combinations, those on the borders of the functional space, are becoming more abundant. Although this is true of both systems, only the east coast shows a significant trend.



**Figure 4.5:** This figure illustrates the relationship between functional and selected taxonomic metrics. The west coast system is shown in green, whilst the east coast is blue. The plots represent the yearly values for a functional metric plotted against a taxonomic metric, a simple linear regression (OLS) is then added, solid lines indicate a significant trend whilst dashed lines are non-significant. For all three functional metrics the two systems behave in a similar manner, functional richness is increasing in line with  $q_0$  (species richness) and both coasts show strong significant trends (West -  $p$ -value $<0.0001$ ,  $Adj.R^2=0.72$ ; East -  $p$ -value $<0.0001$ ,  $Adj.R^2=0.79$ ). Although both coasts show a very weak negative slope for functional evenness when  $q_\infty$  increases this is non-significant and the adjusted  $R^2$  very close to zero suggesting no linear relationship between the two variables exists. Functional divergence is increasing as  $N$  increases for both systems, but this relationship is a weakly significant one on the east coast ( $p$ -value $<0.0001$ ,  $Adj.R^2=0.05$ ).

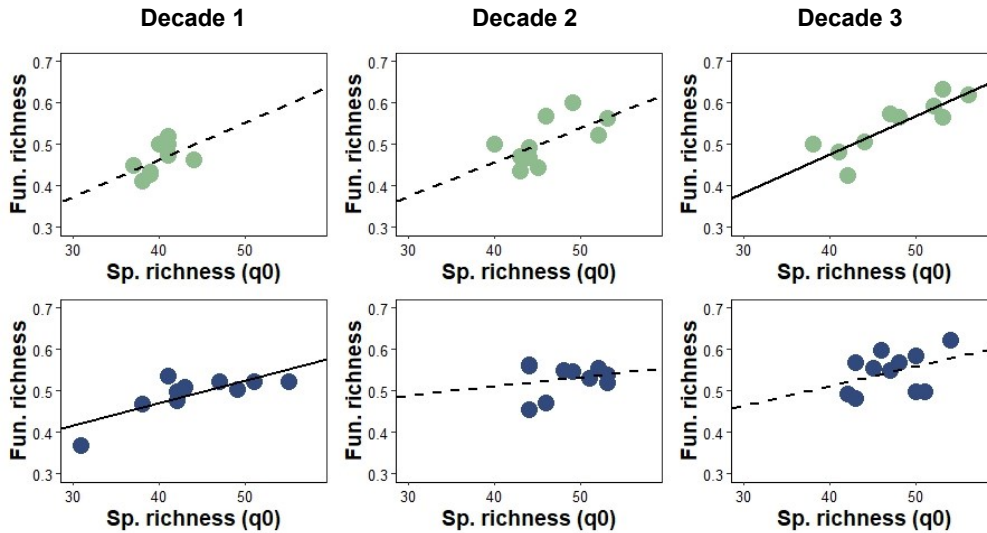
When examining the relationship between the regression slopes for the combined taxonomic and functional metrics I find differences between both the strength and direction of the correlations between the systems in many cases. The most interesting of these are the pairings between functional evenness and  $q_0$ ,  $q_2$ , functional richness and functional divergence and between functional divergence and  $q_0$ , functional evenness and functional richness. In these cases, both the direction and strength of the correlations differs between systems. It should be remembered that these correlations are between the slopes of change rather than the yearly values shown in Figure 4.5 and as such present a slightly different pattern.



**Figure 4.6:** This plot shows the correlations between the slopes of change of the pairs of metrics grouped by coastal system. The west coast plots and correlations are shaded in green with the east coast in blue. The overall correlation for both systems is shown in dark grey. The strength of the correlation is indicated by the ., \*, \*\*, or \*\*\* shown alongside (no symbol = weak or no correlation). Asterisks represent p-values (. <0.1, \* <0.05, \*\* <0.01, \*\*\* <0.001).

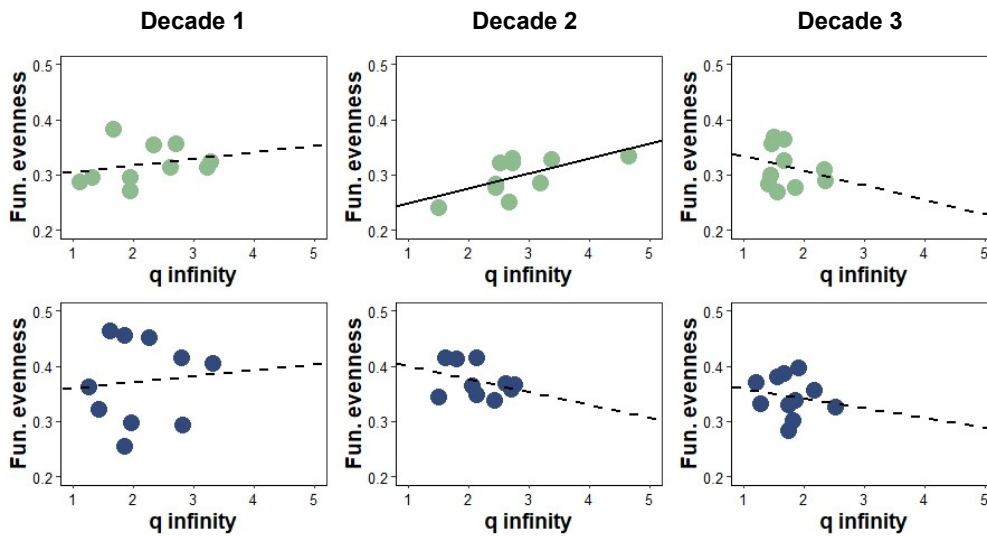
#### 4.3.5 Decadal change

The investigation of temporal, between decade, change in the relationship between functional richness and  $q_0$  shows that it is increasing in both systems for the three decades. However, there are clear differences in both time and space as in the west coast assemblage the increasing trend becomes progressively stronger over time, with a greater distinction between the first and second decades being evident (see Figure 4.7 legend for p-values and adjusted  $R^2$  values). The east coast, however, begins with the strongest trend and flattens out in the second decade before increasing again in the third, this ties in with previous findings suggesting a greater variability in temporal trends on the east.



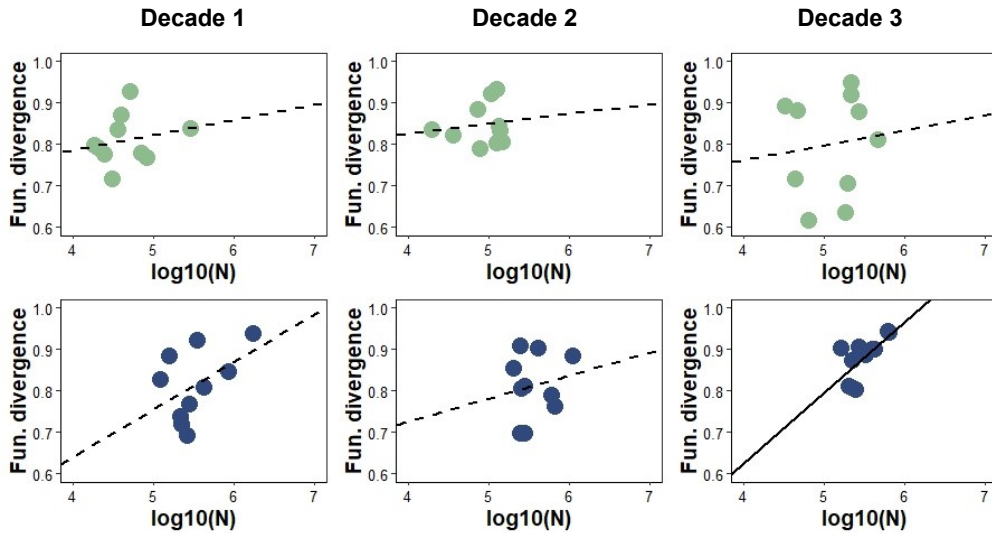
**Figure 4.7:** This shows the linear relationship between functional and taxonomic richness ( $q_0$ ) and how this relationship changes for a single assemblage by decade. Here I take the assemblages at the latitudinal band centred around 58 degrees from each coastal system (with the west represented by green and the east by blue). The points represent the yearly values of each metric and the lines the linear trend (simple OLS regression), these are solid for significant trends and dashed for non-significant (West latitude 58: Decade 1 – p-value=0.14, Adj.  $R^2$ =0.16, Decade 2 – p-value=0.05, Adj.  $R^2$ =0.31, Decade 3 – p-value=0.001, Adj.  $R^2$ =0.7; East latitude 58: Decade 1 – p-value=0.01, Adj.  $R^2$ =0.54, Decade 2 – p-value=0.05, Adj.  $R^2$ =-0.07, Decade 3 – p-value=0.24, Adj.  $R^2$ =0.05).

When I examine the decadal changes in the relationship between functional evenness and  $q_\infty$  I find marked differences both over time and between systems. The west coast shows that functional evenness rises slightly when  $q_\infty$  increases, followed by a steeper (significant) incline in the second decade and ending with a final decrease. In contrast, the east coast has no significant trends (see Figure 4.8 legend for p-values and adjusted  $R^2$ ) and begins to decrease immediately after a slight incline in the first decade.



**Figure 4.8:** This shows the linear relationship between functional evenness and q infinity and how this relationship changes for a single assemblage by decade. Here I take the assemblages at the latitudinal band centred around 58 degrees from each coastal system (with the west represented by green and the east by blue). The points represent the yearly values of each metric and the lines the linear trend (simple OLS regression), these are solid for significant trends and dashed for non-significant (West latitude 58: Decade 1 – p-value=0.47, Adj. R<sup>2</sup>=-0.05, Decade 2 – p-value=0.04, Adj. R<sup>2</sup>=0.34, Decade 3 – p-value=0.5, Adj. R<sup>2</sup>=-0.06; East latitude 58: Decade 1 – p-value=0.79, Adj. R<sup>2</sup>=-0.12, Decade 2 – p-value=0.32, Adj. R<sup>2</sup>=0.01, Decade 3 – p-value=0.6, Adj. R<sup>2</sup>=-0.07).

Perhaps the most interesting result is the spatial and temporal change in the relationship between functional divergence and numerical abundance. Here I find that although all slopes are increasing there is substantial variation between the decades and coasts. On the west, the increasing numerical abundance does not have a significant effect on functional divergence in any decade whilst on the east, I find that it does appear to be correlated, particularly in the third decade where the trend is significant (see Figure 4.9 legend for reported p-values and adjusted R<sup>2</sup>).



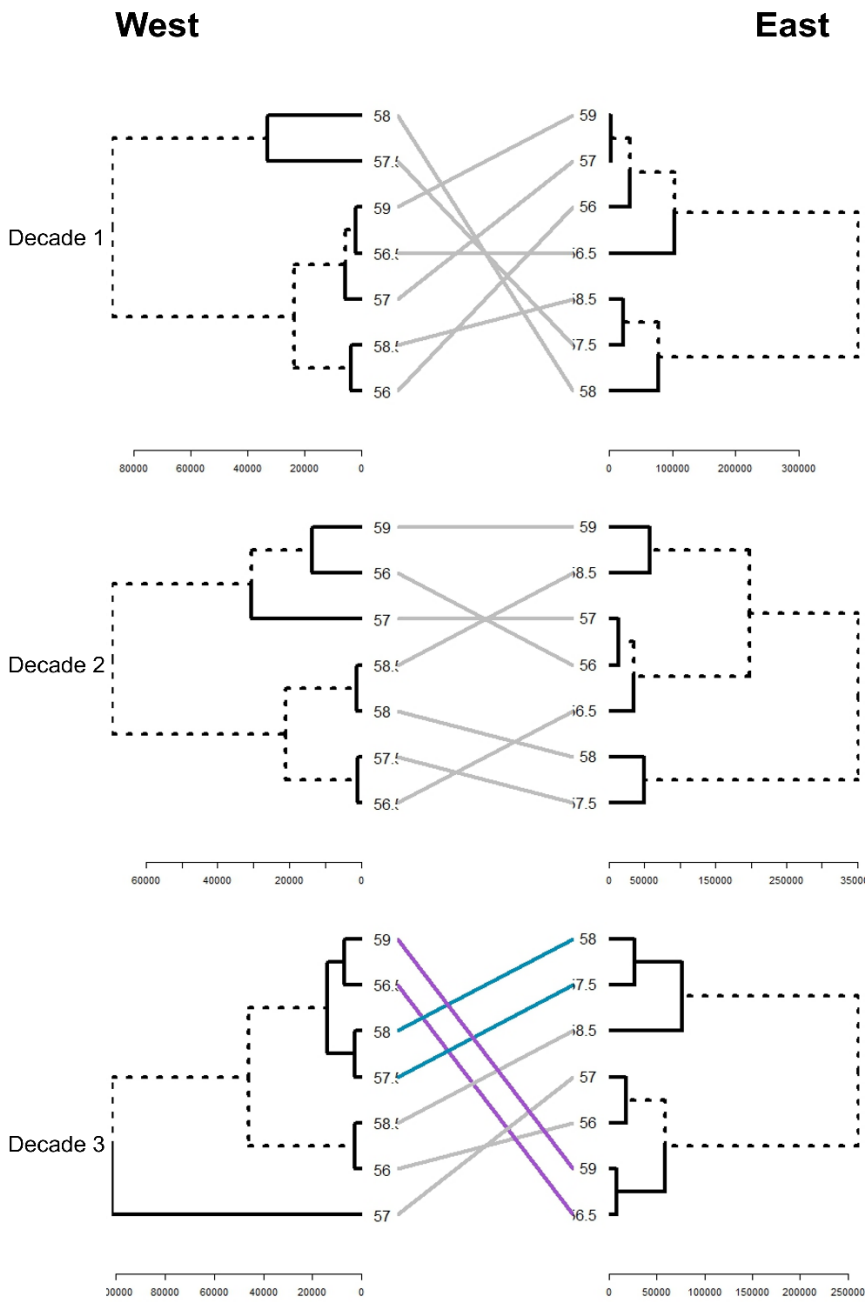
**Figure 4.9:** This shows the linear relationship between functional divergence and N (shown as  $\log_{10} N$  for ease of visualisation and comparison) and how this relationship changes for a single assemblage by decade. As with previous examples I take the assemblages at the latitudinal band centred around 58 degrees from each coastal system (with the west represented by green and the east by blue). The points represent the yearly values of each metric and the lines the linear trend (simple OLS regression), these are solid for significant trends and dashed for non-significant (West latitude 58: Decade 1 – p-value=0.54, Adj.  $R^2$ =-0.07, Decade 2 – p-value=0.7, Adj.  $R^2$ =-0.1, Decade 3 – p-value=0.75, Adj.  $R^2$ =-0.11; East latitude 58: Decade 1 – p-value=0.18, Adj.  $R^2$ =0.12, Decade 2 – p-value=0.63, Adj.  $R^2$ =-0.09, Decade 3 – p-value=0.03, Adj.  $R^2$ =0.37).

#### 4.3.6 Decadal change in correlations between systems

It is evident from the tanglegrams shown in Figure 4.10 that there are differences in the congruence of the systems by decade. A closer examination of the results (see Table 4.1) shows that initially there is some correlation between the systems in the first decade, whilst in the second decade they are becoming less similar and then slightly more similar again in the third decade.

**Table 4.1:** Results of correlation measures of similarity between systems through the decades. The cophenetic correlation and Baker’s Gamma metrics are scaled between -1 and 1 with values close to zero indicating little or no statistical similarity between trees whilst the entanglement measure ranges from 0 to 1 with values close to zero representing no entanglement (or similarity).

Metric	Decade 1 (1985 – 1994)	Decade 2 (1995 – 2004)	Decade 3 (2005 – 2014)
cor_cophenetic	0.42	-0.07	-0.11
cor_bakers_gamma	0.78	0.21	0.73
entanglement	0.34	-0.08	-0.06



**Figure 4.10:** Tanglegram showing the difference between the three decades. The dashed lines indicate distinct edges in those trees whilst the coloured lines connecting the two represent subtrees that are common to both systems.

#### 4.4 Discussion

Key findings in this chapter include the differences between the strength and direction found for some correlations when analysing functional metrics alongside the taxonomic measures and weaker correlations between functional and selected taxonomic diversity measures on the west coast. This point of difference suggests that changes in functional diversity in the systems are due, at least in part, to those species containing more diverse combinations of traits being either more or less abundant depending on location.

Based on my findings from the previous chapter (Chapter Three), my expectation was that I would find differences between the coastal systems when examining temporal change in the functional diversity metrics. In addition, I expected to find strong correlations between the functional and taxonomic diversity measures as well as evidence of change when investigating by decade. Heterogeneity of habitat can often promote higher biodiversity of assemblages (Tews *et al.*, 2004; Kissling *et al.*, 2008; Hortal *et al.*, 2009). Fish are an extremely diverse taxonomic group and there are often marked differences in the trait combinations found in species with varying habitat structures (Aguilar-Medrano & Arias-González, 2018; Carrington *et al.*, 2021). It is already well documented that there is evidence of temporal change in many marine fish systems (Gifford *et al.*, 2009; Henderson, 2017; Araújo *et al.*, 2019; Beukhof *et al.*, 2019a; McLean *et al.*, 2019a), with sometimes rapid reorganisation of community structure taking place (Magurran *et al.*, 2015b). The temporal changes I find within these latitudinal bands suggest that assemblages are generally increasing in both size and diversity with little variation being evident in how evenly distributed the trait combinations are. I do find strong latitudinal signals for all three measures (see Figure 4.3 for illustration), particularly on the east coast; this could in part be due to how the species respond to the environmental factors affecting them (Beukhof *et al.*, 2019a; Baptista *et al.*, 2021; Chaikin *et al.*, 2021; Peltonen & Weigel, 2022). For example, a recent study (Fujiwara *et al.*, 2022) suggested that the variation in species response could be attributed to life history traits (Winemiller & Rose, 1992). Work by Dahlke *et al.* (Dahlke *et al.*, 2020) also suggested that a species ability to cope with the pressures of environmental changes such as warming waters could be dependent upon their life stage (Sunday *et al.*, 2012). Based on these results, it seems likely my findings point to life history traits such as generation time being important contributors to the coastal distinctions for latitudinal signal. This differentiation is not only in the strength of the signal but also in the direction, with all metrics trending northwards on the west coast whilst on the east this is only true of functional divergence. Since most species are shared between the two systems, these findings suggest that heterogeneity of environments could be responsible for the differences I find, either due to the variation in response (Fujiwara *et al.*, 2019; Fujiwara *et al.*, 2022) or the adaptation of traits (Beukhof *et al.*, 2019b).

It is sometimes assumed that increases in the number of species found within an assemblage, species richness, should directly correspond to a similar increase in the functional richness (Biggs *et al.*, 2020), the extent of functional space occupied by the species. This is not always true as the species being recruited to these assemblages may share similar trait combinations to those already present, thus creating little or no change in the functional space being occupied, known as functional redundancy (Aune *et al.*, 2018). Redundancy is quantified by the number of species playing similar roles within an assemblage, an assemblage with very diverse



species all performing similar functions will be low in redundancy. High functional redundancy in a system can be important in creating resilience and stability (McLean *et al.*, 2019b; Biggs *et al.*, 2020), thus leading to better adaptability to environmental change (Dee *et al.*, 2016) and fishing practices (Rincón-Díaz *et al.*, 2021). My findings overall suggest that as there is a strong positive relationship between taxonomic and functional richness (see Figure 4.5 upper panel), the species being introduced to assemblages possess different trait combinations to the existing species, or alternatively that species are being replaced with fish with distinct combinations of traits in comparison to those they are replacing. These results indicate low functional redundancy in these systems suggesting vulnerability to anthropogenic stressors (Auber *et al.*, 2022).

There is no linear relationship between functional evenness and  $q_\infty$  evident overall (see Figure 4.5 middle panel) but I do find a correlation between functional divergence and numerical abundance (Figure 4.5 lower panel), particularly on the east coast where the trend is significant. This suggests that the species towards the borders of the functional space, that is those with more unusual trait combinations, are becoming more abundant than their neighbours. Often the more functional divergent species are larger, predatory fish, for example, Atlantic halibut, *Hippoglossus hippoglossus* (Linnaeus, 1758), tope shark, *Galeorhinus galeus* (Linnaeus, 1758) and monkfish, *Lophius piscatorius* (Linnaeus, 1758), and any increases in the abundance of fish such as these will have implications for smaller prey types such as Atlantic cod, *Gadus morhua* (Linnaeus, 1758). Consequently, the knock down effect caused by a potential increase in the abundance of predators in turn influences abundances of smaller prey species, including those who are of commercial value.

I used the slopes of change to quantify the strength and direction of the correlations between the pairs of metrics, using some of those described in this and the previous (Chapter Three) chapter. The main point of interest here was the difference, often in both strength and direction, between the two systems. This reinforces my expectation of a distinction between the coasts and suggests that structural differences between the assemblages could be driving these differences (Bell *et al.*, 2018).

Gaining an understanding what has happened in the past can help to shape future plans (Beaugrand *et al.*, 2015) and expectations. When working with longer term marine systems (Miller *et al.*, 2011; Araújo *et al.*, 2016; Troast *et al.*, 2019; Baker *et al.*, 2021; Durante *et al.*, 2021) it can be useful to compare between decades to visualise temporal change more clearly. Accordingly, here I focused on a single assemblage from each system and investigated the relationships between taxonomic and functional metrics by decade. This provided interesting insights hitherto unseen in the earlier overall analyses (see Figure 4.5). The linear relationships between functional and taxonomic richness are positive but with nuance between systems and decades evident particularly on the east coast (see Figure 4.7) suggesting that the factors influencing the temporal changes found are affecting the systems at different rates (Dencker *et al.*, 2017; Buyse *et al.*, 2021). This is reinforced by the patterns I find when examining the decadal change in the relationship between functional evenness and  $q_\infty$  (see Figure 4.8). When studying the systems at this level there is a weak linear relationship found and this presents differently according to system and decade. However, the most interesting result here was the relationship between functional divergence and numerical abundance (see Figure 4.9) on the east coast. The third decade shows a significant increasing trend in functional divergence when abundance rises, suggesting that the latter

part of the time series has not only experienced increased abundance levels but also that these abundances are likely to belong to species with more diverse trait combinations. This could be due, in part, to the responses of specific traits to the twin pressures of overfishing and climate change (Zhao *et al.*, 2022).

I also wished to quantify how ‘related’ the coastal systems were when including all taxonomic and functional diversity measures already studied, namely the suite of Hill numbers,  $q_0$ ,  $q_1$ ,  $q_2$ ,  $q_\infty$ , numerical abundance and functional richness, evenness and divergence. The cluster analysis was performed only using those latitudes common to both systems and was done separately for each decade. The tanglegrams in Figure 4.10 illustrate the differences in the relatedness of these systems by decade. It is clear that there is temporal change in how similar the trees are (see Table 4.1 for details of metrics) with the second decade being the most similar, this suggests that there could be a cyclical effect at play (Blonder *et al.*, 2017; Ryo *et al.*, 2019) which could potentially also help to explain the distinctions between systems, particularly with regard to differing rates of sea surface warming (ICES, 2018c, 2019).

#### 4.5 Conclusion

In conclusion, this chapter shows that despite the close geographic proximity of the Celtic Sea (west) and North Sea (east) systems, their contrasting environmental and structural features lead to differences in the way that functional diversity responds at the assemblage level. It also examines the correlations between selected taxonomic diversity measures and the functional diversity metrics, revealing interesting relationships which help explain the differences I find. There are many challenges facing fish species including overfishing (Frank *et al.*, 2016; Trindade-Santos *et al.*, 2020) and climate change (Jacobs *et al.*, 2018) but gaining a better understanding of the basic biology and trait combinations of these species can help to improve their ability to adapt and thrive thus leading to better sustainability (Hammer *et al.*, 1993; Winemiller, 2005; Karp *et al.*, 2019).

Taking an ecosystem approach such as discussed in this chapter can have important implications for fisheries management and conservation planning. For example, modelling techniques can be developed using assemblage level data on occupancy and abundance, this would give a fuller picture of potential scenarios based on current and expected fisheries targets and total allowable catches (TACs), which could then be adjusted accordingly. The next chapter (Chapter Five - Temporal and spatial rarity – geographical patterns and changes through time) further explores these ideas by investigating the relationships between taxonomic and functional rarity and the underlying structural changes within assemblages.

## Chapter Five - Temporal and spatial rarity – geographical patterns and changes through time\*\*



*Lower Largo Beach, 2021*

\*\*A version of this chapter has been published in Proceedings for the Royal Society B (see Appendix A and Moyes, F., I. Trindade-Santos and A. E. Magurran (2023). "Temporal change in functional rarity in marine fish assemblages." Proceedings of the Royal Society B: Biological Sciences **290**(1993): 20222273.)

## Chapter Five – Temporal and spatial rarity – geographical patterns and changes through time

### 5.1 Introduction

Contemporary ecological communities are experiencing biodiversity change that has little precedence in the historical record, with marine systems amongst those in which this change is particularly marked (Beaugrand *et al.*, 2015; Blowes *et al.*, 2019b; Antão *et al.*, 2020). This biodiversity crisis underlines the importance of measuring biodiversity in robust and ecologically meaningful ways. But because biodiversity is a multifaceted concept (Chao *et al.*, 2014; Naeem *et al.*, 2016), it also raises questions about the extent to which information on change in one dimension of diversity, such as taxonomic diversity, sheds light on change in other dimensions, such as functional diversity. Growing evidence that ecosystems are being restructured along multiple dimensions of biodiversity (Su *et al.*, 2021) underlines the need for improved understanding of the linkages between these dimensions.

Ecological assemblages typically consist of a few common and many rare species, a pattern that is described by a species abundance distribution. Species that are considered to be taxonomically rare occupy the lowest ranks in this distribution (Gaston, 1994; Magurran, 2013b), with other categorisations of rarity drawing on species occurrence data, and/or features such as habitat specificity (e.g., (Rabinowitz, 1981)). A recent macroecological analysis (Jones *et al.*, 2020) showed that increases in taxonomic rarity are widespread. Such shifts have been attributed to immigration and warming (Perry *et al.*, 2005; Hansen *et al.*, 2017; Burrows *et al.*, 2019; Erauskin-Extramiana *et al.*, 2019; Friedland *et al.*, 2019; Stuart-Smith, 2021) and may occur alongside an increase in assemblage size due to greater number of species and/or individuals. Taxonomically rare species could contribute unusual trait combinations to a system (Mouillot *et al.*, 2013c; Chapman *et al.*, 2018) and play an important role in supporting ecosystem functioning (Leitão *et al.*, 2016b; Le Bagousse-Pinguet *et al.*, 2021). Temporal change in taxonomic rarity thus has the potential to shed light on underpinning changes in functional rarity. However, the biodiversity literature contains many examples of cases where change in one attribute of diversity is uncorrelated or only weakly correlated with another (e.g., (Ritter *et al.*, 2019; Vereecken *et al.*, 2021)). Moreover, a taxonomically rare species can have a dominant trait value and vice versa. Therefore, even though metrics of functional rarity can be weighted by taxonomic abundance (Violle *et al.*, 2017) it does not necessarily follow that trends in taxonomic rarity, and trends in trait (functional) rarity will coincide. To predict whether change in taxonomic rarity and change in functional rarity are correlated, it is first necessary to understand how metric responses are shaped by shifts in the underlying species abundance distribution.

If an assemblage gains more biomass, or larger numbers of individuals, the number of species in the assemblage is expected to rise, but in a non-linear way. This is the principle that underlies rarefaction analyses used to make fair comparisons between assemblages (Gotelli & Colwell, 2001; Colwell *et al.*, 2012; Chao *et al.*, 2014). Due to the constraints imposed by the uneven distribution of species that characterise species abundance distributions (SADs) (May, 1975) other assemblage properties will also change as an assemblage grows (or shrinks). For example, larger assemblages are generally less (taxonomically) even than smaller ones (Magurran, 2004). I

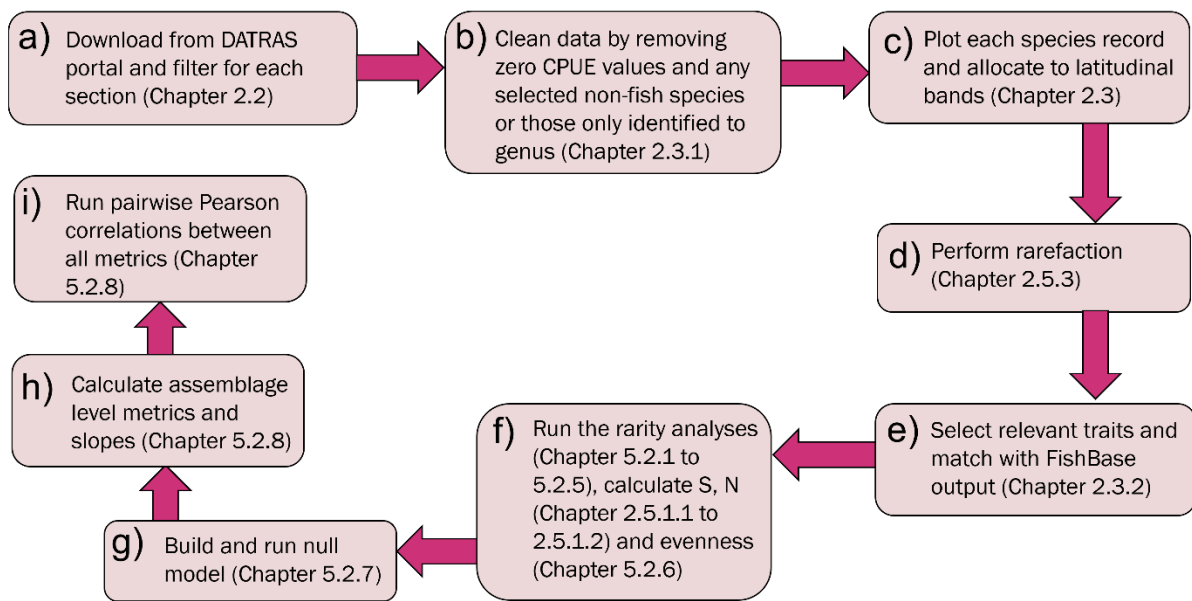
therefore expect larger assemblages to exhibit increases in taxonomic rarity. However, trait abundance distributions (TADs) tend to be more even than species abundance distributions (SADs) (e.g., (Gross *et al.*, 2017)). This higher evenness in TADs (Gross *et al.*, 2021) suggests that functional rarity may be less responsive to a change in assemblage size than taxonomic rarity. To explore these questions I construct a null model taking account of both observed species and trait abundance distributions and in which individuals are progressively drawn at random from a gamma (Whittaker, 1972) assemblage to construct local assemblages of different size. Departures from this null will shed light on how rare trait combinations are conserved or lost, as assemblages change in size.

Here I focus on two Scottish marine fish assemblages (see Figure 5.6 for map of area), each sampled by scientific trawling over a period of three decades. Although matched by latitude, these assemblages belong to different marine ecosystems: the seas to the west of Scotland are part of the Celtic-Biscay ecosystem (DATRAS, 2015) while those to the east of Scotland are placed in the North Sea ecosystem (DATRAS, 2019). These systems share many, but not all, fish species, but have different dominant species, and differ in how species dominance changes over time (Moyes & Magurran, 2019). They thus provide an interesting test case in which to ask whether shifts in taxonomic rarity are a proxy for change in functional rarity as well as whether these biodiversity changes are consistent across different geographic regions.

The main purpose of this chapter is to investigate how rarity is changing over the thirty-year time period. My expectation is that despite the differences between the ecoregions based on habitat, climate and productivity, the similarity of the species pool in each system suggests that there will be little coastal distinction in the patterns of rarity found. A key secondary aspect to this work is to link any changes in rarity found with the structural changes in the underlying assemblages. Again, my expectation is that these relationships would largely be consistent between the systems.

## 5.2 Methods

The data used in this work were sourced from the International Council for the Exploration of the Sea (ICES) and are taken from two standardised scientific trawl surveys incorporating the ICES areas VIa (West Coast), IVa and IVb (North Sea). Each species record contains a precise geographical location and numerical species abundance represented by CPUE (catch per unit effort) which, as used here, refers to the number of individuals of a given species caught per hour using a tow duration of half an hour. Trawl speed is measured as 4 knots and this work focuses only on those records collected using the Grande Overture Verticale (GOV) gear, a type of bottom trawl net with a small mesh which is now the recommended gear for all bottom trawl surveys carried out by ICES. I use ICES rectangles to form the boundaries of assemblages before combining longitudinally (5 x 1) to create latitudinal bands. These ICES rectangles are freely available for download on the ICES website (ICES, 2014) and represent 30' latitude by 1° longitude in a grid cell (for further details on the data, systems and preliminary methods see Chapter 2).



**Figure 5.1:** Workflow diagram illustrating the steps carried out within this chapter and where to find further details on each. In a) I download the data from DATRAS as described in Chapter 2.2 before cleaning in b) and plotting in ArcGIS (ESRI, 2015) to c) allocate latitudinal bands. In d) I resample the data as previously before e) matching fish to FishBase (Froese & Pauly, 2019) and assigning trait values. In f) I perform the rarity analyses as described in section 5.2 before g) running the null models and h) calculating assemblage level metrics and slopes. Finally in i) I examine the correlations between measures.

The traits selected for the question in this chapter are the same as those used throughout this thesis (for further details on these traits and their complementarity nature see Chapter 2.2.2). After rarefaction and the selection and merging of traits with species I calculated both taxonomic and functional rarity; this was done using the ‘funrar’ package available in R (Grenié *et al.*, 2017). These metrics result in rarity values for each species within an assemblage at a particular time. To produce assemblage level measures I use the mean rarity value of all species present within an assemblage at any given time point.

### 5.2.1 Taxonomic rarity

Taxonomic rarity (here measured as scarcity) within an assemblage can be measured simply by using the inverse of relative abundance. However, it should be standardised between 0 and 1 with a pivotal value of 0.5 for a species with a relative abundance corresponding to  $1/N$ , where  $N$  is the number of species in the assemblage. Very rare or scarce species will have a value very close to 1 whilst common/abundant species will be close to 0.

$$\text{Taxonomic rarity}_i = \exp[-N * \ln(2) * \text{RelAb}_i]$$

where  $N$  is the total number of species in the assemblage,  $i$  represents species  $i$  and  $\text{RelAb}_i$  is the relative abundance of species  $i$

Equation adapted from (Violle *et al.*, 2017)

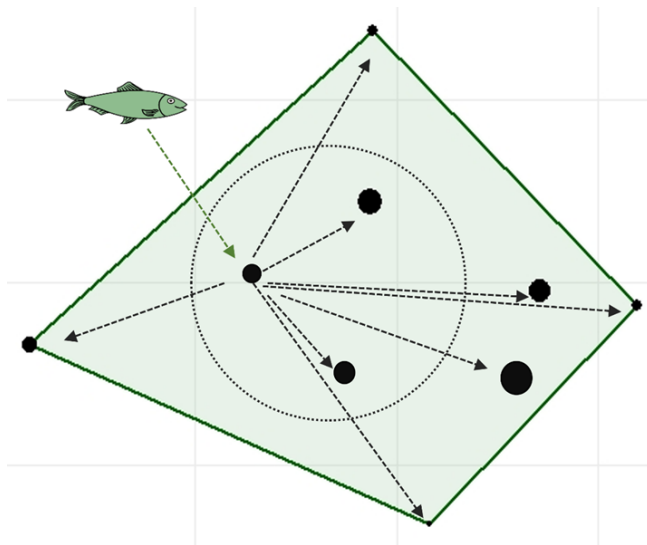
### 5.2.2 Functional rarity

Functional rarity (measured as distinctiveness) as used here is weighted by abundance and corresponds to the mean pairwise distance between species within the assemblage. It takes all species into account to measure whether a given species is functionally close to its neighbours, i.e., whether it contains a similar or distinct combination of traits (see Figure 5.2 for a pictorial representation). Functional rarity can therefore be identified as the mean distance in functional space between a species and the others within the assemblage. However, because this is weighted by numerical abundance, a species can have a higher rarity value if it does not share many traits with the most abundant species in the assemblage. As with taxonomic rarity, functional rarity ranges between 0 and 1, with rarer species tending towards 1 and more common tending towards 0.

$$\text{Functional rarity}_i = \frac{\sum_{j=1, j \neq i}^N d_{ij} * \text{Ab}_j}{\sum_{j=1, j \neq i}^N \text{Ab}_j}$$

where  $N$  is the number of species in the assemblage,  $d_{ij}$  is the distance in functional space between species  $i$  and  $j$  and  $\text{Ab}_j$  is the relative abundance of species  $j$  from the remaining  $N - 1$  species

Equation adapted from (Violle *et al.*, 2017)



**Figure 5.2:** Simplified 2-D example of species position in functional space and the calculation of functional rarity. This herring like fish is represented by the medium sized point shown by the green arrow, whilst the black arrows indicate the distances between this fish and all others within the assemblage. Each point is weighted by abundance with the larger dots indicating a higher number of individuals. Functional rarity is calculated based on the mean pairwise distance between species, so in the example above it would be the mean of the distances of each dashed arrow.

### 5.2.3 Functional rarity (no abundance weighting)

This metric is identical to Section 5.2.3 but without any weighting of numerical abundance.

$$\text{Functional rarity NoAb}_i = \frac{\sum_{j=1, j \neq i}^N d_{ij}}{N - 1}$$

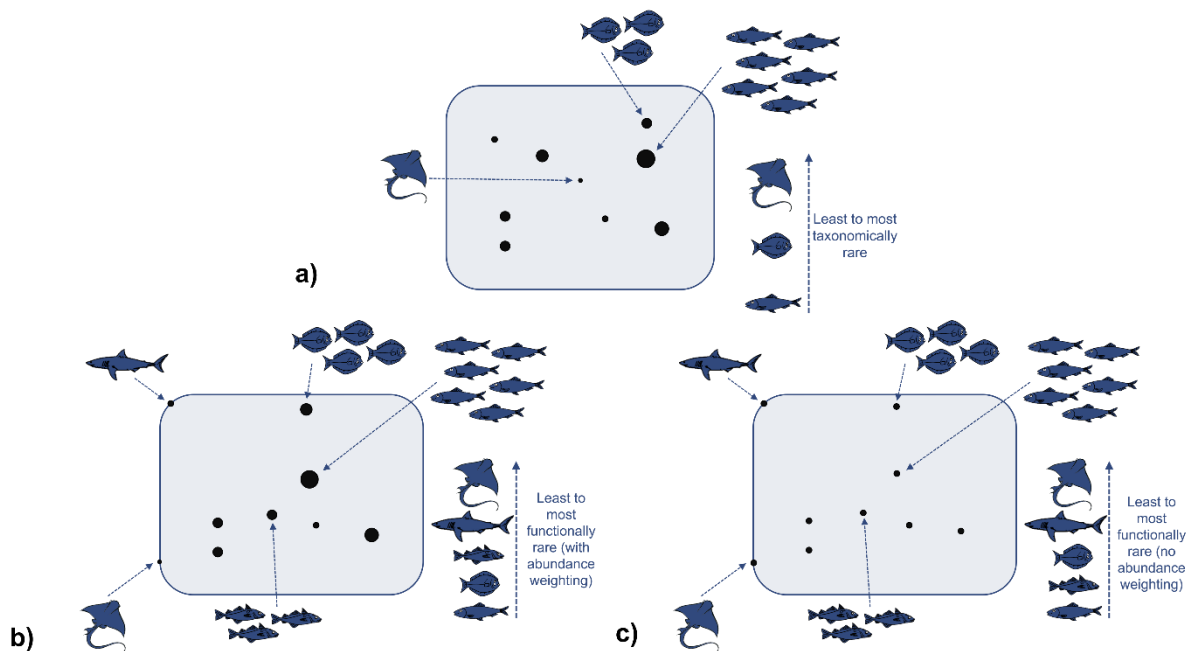
*N* is the number of species in the community,  $d_{ij}$  is the distance between species *i* and *j*

Equation adapted from (Violle *et al.*, 2017)

This metric is most useful where there are no abundances available but in this instance I chose to add it in order to help disentangle the contributions of trait combinations and abundance to the overall rarity value. As before it is possible to calculate the values for a species at a particular time step in an assemblage.

The calculations for each of the rarity metrics result in values for each species, at each time point within an assemblage. In this chapter my focus is on assemblage level change, and I therefore generate the ‘rarity’ values for each assemblage at a given time step by calculating the mean functional or taxonomic rarity across each assemblage for each year.





**Figure 5.3:** Simple pictorial representations of the rarity metrics. Taxonomic rarity is shown in a) as a mock assemblage where level of abundance is the main influence of rarity. Three species are shown here with differing abundances (size of the dot indicates abundance), the skate type, of whom there is only one will be the rarest, the herring type which is the most dominant and has six individuals will be least rare and the flat fish of whom there are three will be central to the other two. In b) functional rarity is illustrated, here the species with more unusual combinations of traits will be located on or close to the border of the functional space, this version of the rarity calculation takes abundance into account, so the size of the dot is increased with the number of individuals per species. The rarity of a species will depend on how different they are in terms of both abundance and trait combinations from the other fish in their assemblage. Here the skate and shark types which are low in abundance and have more unusual trait combinations will be the rarest, whilst the herring type which has a common combination of traits and is very abundant will be least rare. In this example the flat fish is rarer than the haddock type despite the fact that it has a more unusual combination of traits, this is due to the higher number of individuals in this representation. In c) functional rarity with no abundance weighting is shown, this example is identical to b) except there are no abundances counted, this results in a slight shifting of the ordering, namely, the flat fish is now higher (rarer) than the haddock type.

#### 5.2.4 Simpson's Evenness, S and N

I decided to use Simpson's Evenness to measure the evenness of an assemblage. This metric is represented by the inverse Simpson's divided by the number of species within an assemblage. Simpson's index itself is an informative measure that shows how evenly distributed species are within an assemblage. This metric is closely related to Hurlbert's PIE (Hurlbert, 1971)) which measures the probability that two individuals, selected at

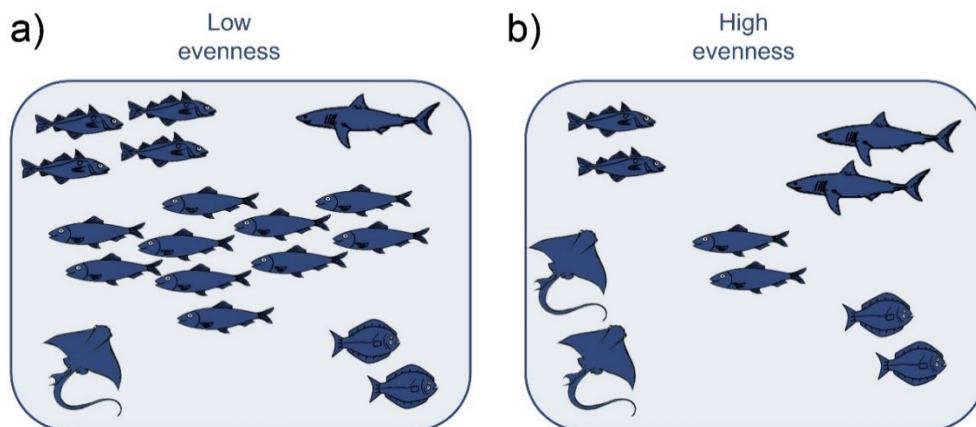
random, will be different species. In order to generate a measure of temporal change within an assemblage I first evaluated Simpson's Evenness within each assemblage at each time step.

$$SimpEven = \frac{\left(\frac{1}{\sum p_i^2}\right)}{S}$$

where  $p$  represents the proportion of individuals in the  $i^{th}$  species and  $S$  is the total number of species in the assemblage

Equation adapted from Hill (Hill, 1973) and Magurran (Magurran, 2013b)

I also examined two other relatively simple alpha diversity metrics, these were numerical abundance or  $N$ , which in simple terms is the number of individuals recorded in any given location at a given time, and species richness ( $S$ ), or the number of distinct species found within a location at a given time (see Chapters 2.3.1.1.1 and 2.3.1.1.2 for more details).

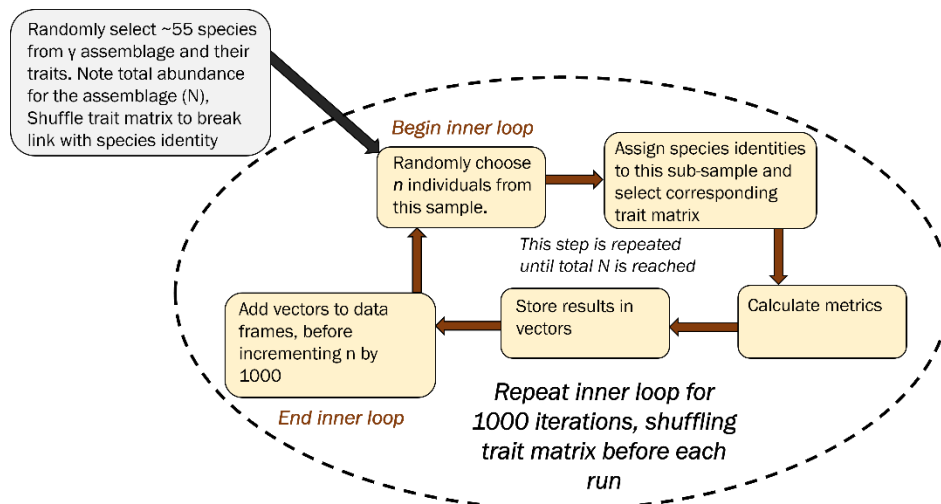


**Figure 5.4:** Simple pictorial illustration of assemblages exhibiting high and low evenness. In a) the herring type fish found towards the centre of the rectangle is the most dominant and all other species have relatively low abundances leading to an uneven pattern of distribution of individuals among species suggesting low evenness. In b) the distribution of individuals among species is very even consisting of two per fish, this suggests a high level of evenness in the assemblage.

Given the potential importance of the distribution of trait values in shaping the response of functional rarity to shifts in assemblage size (Gross *et al.*, 2017; Gross *et al.*, 2021) I decided to also calculate the functional evenness of the trait distribution (see Chapter 4.2.2 for details), and the skewness and kurtosis (calculated using the moments package in R (Komsta & Novomestky, 2015)) of the species-level functional rarity values within each latitudinal band at each time step.

### 5.2.5 Null model

Separate null models (see Figure 5.5) were constructed for the two coastal assemblages. First, a subset of species (58 for the west coast and 55 for the east – these are the typical maximum numbers observed in a latitudinal band) was selected at random from the overall species pool of a given coastal system. A data frame of trait values for these species was created. Next, trait values were re-assigned to each species in this null gamma assemblage by independently randomising the vector of each trait in the data frame. This shuffling broke any inherent correlation between traits and produced a null gamma assemblage in which each of the species had a randomly allocated set of trait values. Species retained their relative numerical abundance, as expressed in the original data set. Following this,  $n=100$  individuals were sampled, at random, from the null gamma assemblage. The same assemblage properties, as before, namely total number of species ( $S$ ), mean functional rarity, skewness and kurtosis of functional rarity, functional evenness, mean taxonomic rarity and Simpson's evenness (Evenness), were computed after each draw. Next, the value of  $n$  was increased in progressive steps (this step was a proportion of the total  $n$  in the chosen assemblage and ranged between 50 and 2000), with assemblage properties again computed at each step, until maximum  $n$  in the subset is reached. The trait array was then re-shuffled before the whole model was re-run. This was repeated 1000 times, with the mean and standard error (95%) of each assemblage property computed on each run. In all cases I constructed a  $S(N)$  rarefaction plot as a check that the null model was behaving as expected (see Figure 5.8 for example). The whole procedure was then repeated five times, starting with a new draw of either 55 or 58 species from the regional assemblage. The final output of the model produced a data frame of metrics at each value of  $N$ . This was used to visualise the relationship between metrics in the null. The model performed consistently using a range of initial sample pools (see Appendix 5.3 for supplementary figures illustrating this), thus providing evidence of the robustness of the results.



**Figure 5.5:** Simple workflow showing the steps performed in the null model. Models are constructed for each coast separately, but the approach used is the same in both cases. We first create a pool of between 55 and 58 species (chosen as typical maximum species in an assemblage for east and west coast) selected at random from the combined coastal data (i.e. the list of species present, with their total abundances summed over 30 years). Next the array of traits for each of these 50 species are assigned, these are the gamma trait distributions. We then shuffle this trait array to break the link between species and traits, this is done separately for each column so that there is no inter-column correlation. Then, n=100 individuals were sampled, at random, from this subset (50 species with 100 individuals). Assemblage properties, namely total number of species (S), mean functional rarity, mean taxonomic rarity and Simpson’s evenness (Evenness), were computed after each draw. Next, the value of n was increased in progressive steps (this step was a proportion of the total n in the chosen assemblage and ranged between 100 and 1000), with assemblage properties again computed at each step, until maximum n in the subset is reached. The trait array is then re-shuffled before the whole model is re-run (1000 iterations).

### 5.2.6 Slopes and correlations

In order to quantify temporal change in the rarity, evenness, species richness and numerical abundance I fit a simple Ordinary Least Squares (OLS) linear regression model to each metric by time. This gives the slope of change for each metric for each assemblage over the time period (for further details see Chapter 2.7.2).

Using the slopes of change generated from the linear regression models I then perform a simple correlation analysis using Pearson’s correlation coefficient which measures the linear relatedness between the slopes of each metric. This value ranges from -1 to 1 with scores closer to 1 indicating a stronger relationship in either direction, e.g., -0.8 represents a strong negative relationship whilst 0.8 a strong positive relationship. This analysis is performed separately for each coastal system.

$$Pearson = \frac{\sum(x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum(x_i - \bar{x})^2 \sum(y_i - \bar{y})^2}}$$

*where  $x_i$  and  $y_i$  are the values of x or y in a sample and  $\bar{x}$  and  $\bar{y}$  represent the means of x and y*

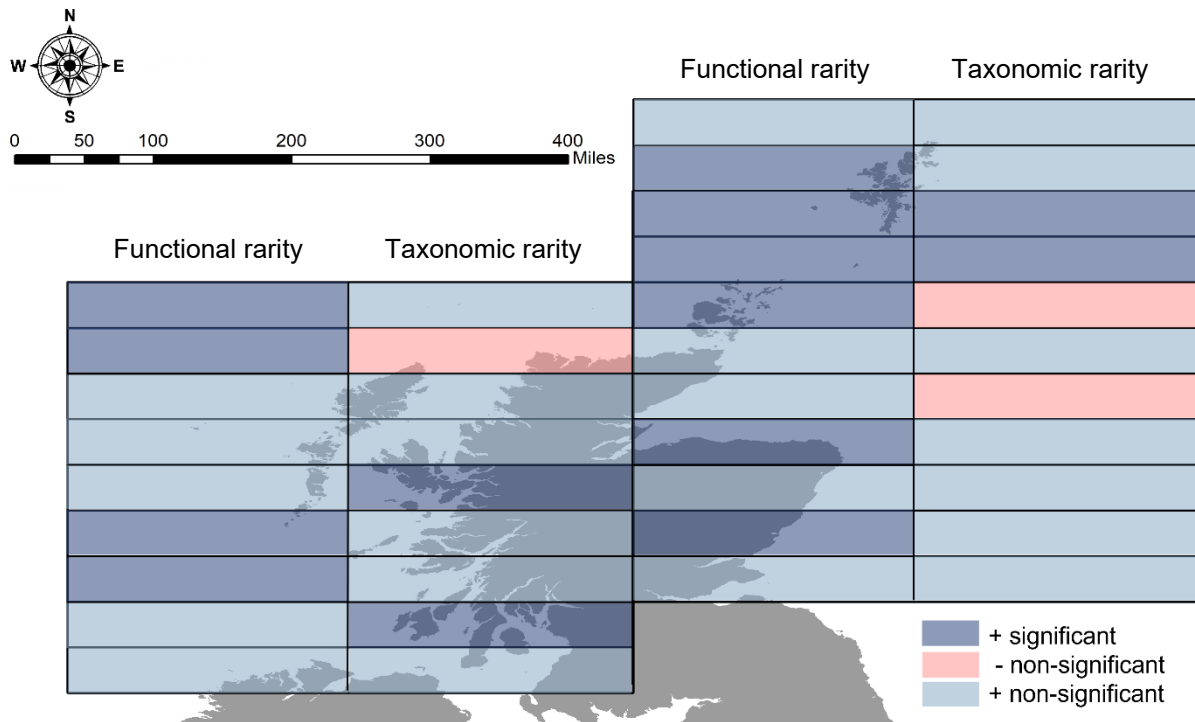
Equation based on (Pearson, 1909)

## 5.3 Results

Results for each of the metrics are detailed in the following sections with a stronger emphasis on the temporal abundance weighted measures, functional rarity and taxonomic rarity. Full results for the observed functional evenness are not shown here but can be found in Chapter 4.3.2.

### 5.3.1 Taxonomic rarity

Taxonomic rarity is increasing in most of the latitudinal bands, including 88% on the west coast and 81% on the east. Most of these, however, are non-significant, excepting 22% on the west and 18% on the east (see Figures 5.6 and 5.7 for visual representation). Additionally, in most cases the slopes of change are very close to zero. The relatively small numbers of fish that present as being persistently low in abundance across bands and years mean that generally there is little change in mean taxonomic rarity at the assemblage level.



**Figure 5.6:** Figure showing the direction and significance of slopes of change in the latitudinal bands for each rarity type. The shaded bands represent the latitudes of each coast with the darker blue shades indicating a significantly positive slope (all slopes were calculated with a simple linear regression (OLS)), pale blue shades a non-significant positive slope and the pale pink shade a non-significant negative slope – there were no significant and negative trends.

### 5.3.2 Functional rarity

The rarity analyses for each assemblage (latitudinal band) show that for functional rarity, all assemblages exhibit increasing trends with 45% of these on the west coast being significant and 55% on the east (see Figure 5.6 for illustrative map). There does not appear to be any pattern to the trends of rarity, either by latitude or by coastal system although generally it does seem as though the slopes on the west are higher than those on the east (see Figure 5.7 for slopes of rarity by year).

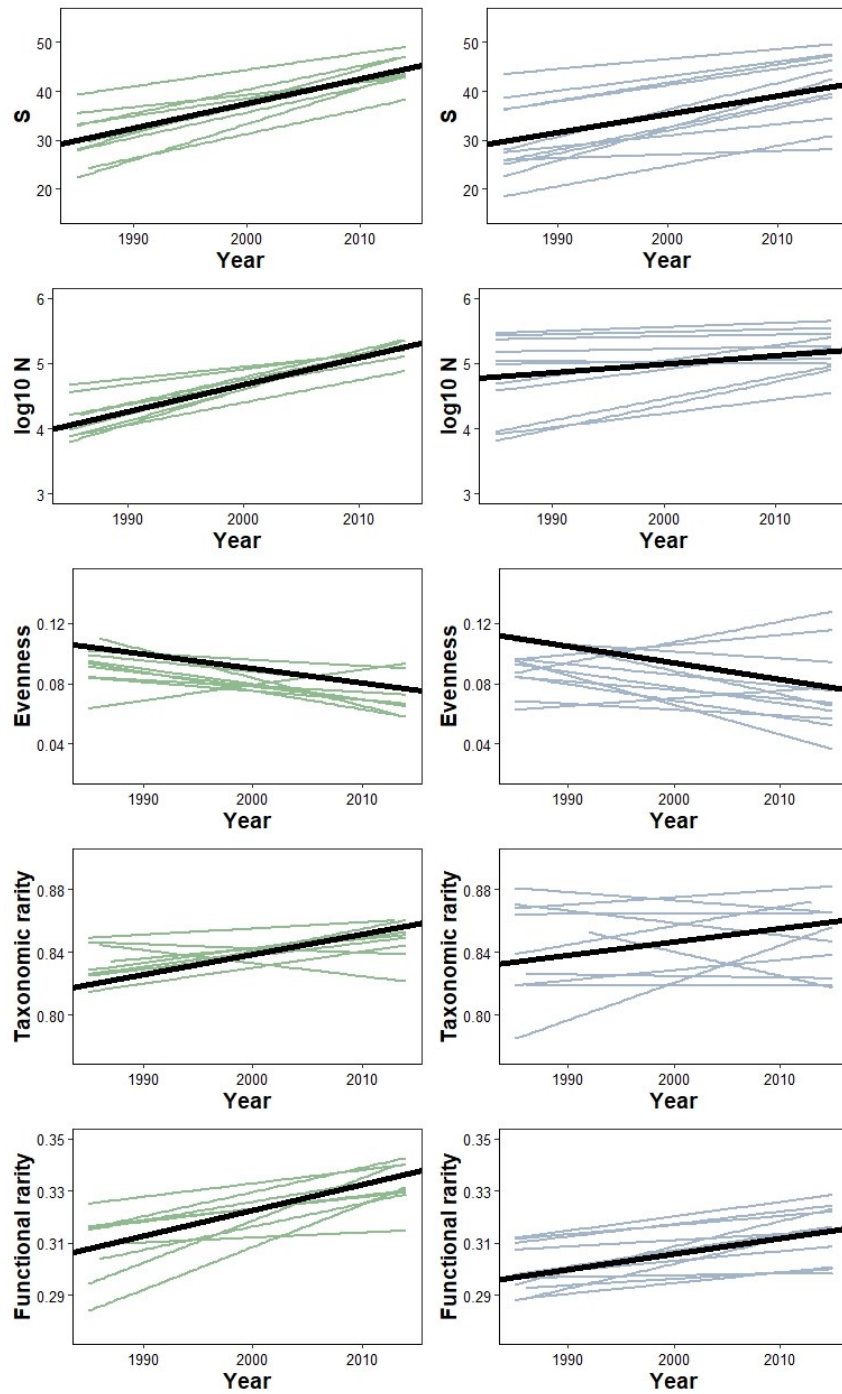
### 5.3.3 Functional rarity (no abundance weighting)

The analyses of the functional rarity without abundance weighting presents very differently to abundance weighted rarity (see section 5.2.3), here only one assemblage (towards the most northerly on the east coast) shows an increasing trend (and this is non-significant). Additionally, of the negative slopes, 70% of those on the east coast are significant along with 55% of those on the west. The considerable variation in the results of the two measures suggest that abundance is an important factor in the rarity or otherwise of these systems.

### 5.3.4 Simpson's evenness, S and N

When examining species richness (S) and numerical abundance (N) I find that although S is increasing everywhere (generally with a significant trend, all bands on the west coast and in 81% of the east coast bands), N is rather more variable. For example, N is decreasing in 27% of the east coast assemblages (non-significantly) with 50% of the positive slopes showing significance, along with 89% of the west coast bands, all of which are increasing. The pattern of slopes as seen in Figure 5.7 also shows clear variation between the systems. Additionally, Simpson's Evenness is decreasing in most assemblages with only 11% on the west coast increasing and 9% on the east coast increasing (none of the increasing slopes are significant). Most decreasing slopes are also non-significant with only 11% of the west coast bands and 18% of the east coast bands showing any significance at all.

In addition, I observed greater variability in trends in the east coast than the west for all metrics apart from evenness. To evaluate this I computed the Median absolute deviation (MAD) using the mad function from the stats package in base R (RCoreTeam, 2021)) of slopes. The results were as follows: west coast – S=0.18, N=1863, Evenness=0.001, Taxonomic rarity=0.0006 and Functional rarity=0.0004. East coast – S =0.21, N=3375, Evenness=0.0009, Taxonomic rarity=0.0014 and Functional rarity=0.0002.



**Figure 5.7:** Slopes of change (using ordinary least squares regression) of latitudinal bands for each metric through time coloured by coastal system. The darker line is the common trend (computed as the OLS regression of all the time series) and the lighter lines the individual latitudinal bands. The figure shows the greater heterogeneity of slopes on the east coast as compared to the west. All slopes are listed in Table 1 and full summary statistics can be found in Appendix 5.2. All overall trends are shown as solid lines, indicating significance. The slopes for functional and taxonomic rarity shown here are identical to those in Figure 5.6.

**Table 5.1:** Regression slopes (OLS) for each metric are shown by latitudinal band, here they are ordered by coast and latitude with the more northerly latitudes being listed first. These slopes are the same as the ones illustrated in Figure 5.7 and the full set of summary statistics for metrics provided in Appendix 5.2.

Coast	Latitude	Functional rarity	Taxonomic rarity	S	N	Evenness	Functional rarity (P/A)
E	61	0.0005	0.002	0.2	1974.54	-0.002	-0.0001
E	60.5	0.0007	0.002	0.23	3833	-0.0016	0.00001
E	60	0.001	0.003	0.52	2844.32	-0.003	-0.0007
E	59.5	0.001	0.002	0.55	7610.44	-0.0026	-0.001
E	59	0.0006	-0.0007	0.37	291.16	-0.0005	-0.0004
E	58.5	0.0002	0.0003	0.33	-3605.4	-0.001	-0.001
E	58	0.0004	-0.0005	0.2	-2683.52	-0.0004	-0.0007
E	57.5	0.0006	0.00003	0.3	1556.54	-0.0007	-0.0001
E	57	0.0005	0.0004	0.46	-3189	-0.0007	-0.0008
E	56.5	0.001	0.001	0.46	5355	-0.0001	-0.0007
E	56	0.0005	0.0003	0.66	74.7	0.0003	-0.001
W	59	0.002	0.001	0.73	6124.1	-0.002	-0.0005
W	58.5	0.001	-0.0002	0.51	4450.22	0.0004	-0.0007
W	58	0.0005	0.0007	0.37	5236.78	-0.0009	-0.0004
W	57.5	0.0007	0.0009	0.25	3681.4	-0.001	-0.00004
W	57	0.0005	0.003	0.5	3245	-0.003	-0.0001
W	56.5	0.002	0.0007	0.7	7519.1	0.00002	-0.0006
W	56	0.001	0.0012	0.5	5606.6	-0.0006	-0.0006
W	55.5	0.0005	0.003	0.63	7748.46	-0.0015	-0.001
W	55	0.0004	0.001	0.44	3979.87	-0.0005	-0.0003

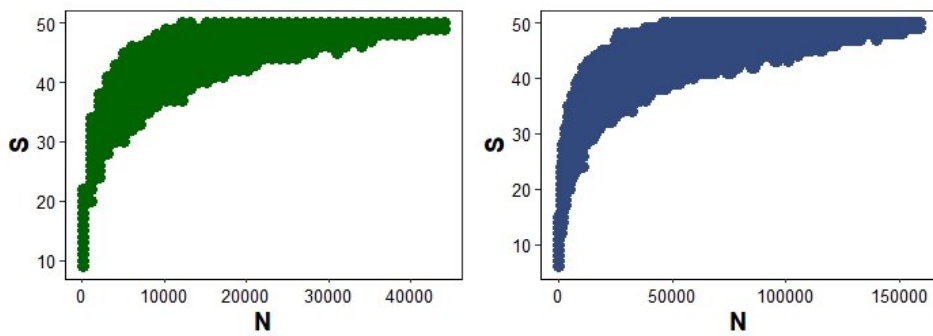
### 5.3.5 Null model

The null model was run several times using various starting samples of 55-58 species (see section 5.2.6 and Figure 5.5 for full details), the results from each run, although naturally showing slight differences, did produce almost identical final results thus ensuring the robustness of the model output (see Appendix 5.3 for examples). The null model showed, as expected, that as the number of individuals in an assemblage increases, so too does the number of species, but in line with expectation on a saturating curve (Figure 5.8). As assemblage size increases, taxonomic rarity is expected to increase, and evenness to decline (see Figure 5.9), and this is what was found (see Figure 5.10 a-d). On the east coast levels of taxonomic rarity and evenness were aligned with the null while west coast assemblages had greater taxonomic rarity and less evenness than expected.

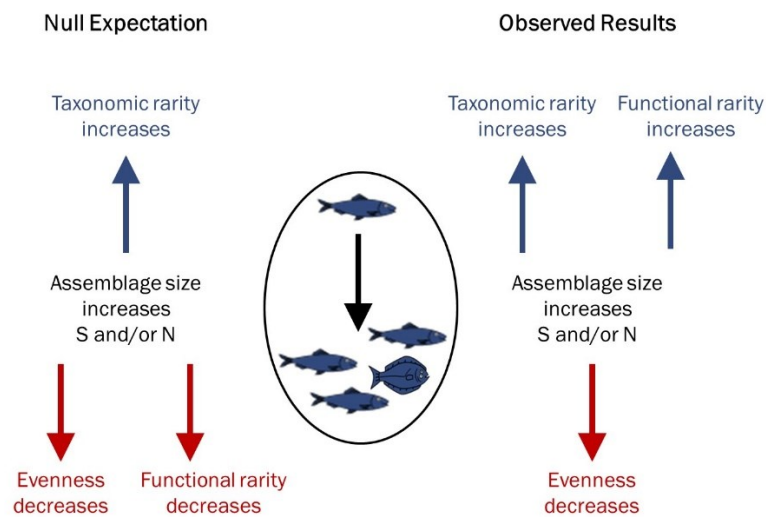
In addition, the null model predicted that functional rarity should decline as assemblages grow in size, and as taxonomic rarity increases (see Figure 5.10 e-h). However, in neither the West Coast system nor the East Coast system (see Figure 5.10) did the observed data show these trends. In both systems functional rarity showed a weak increase in response to both richness and taxonomic rarity and occurred at lower levels than predicted



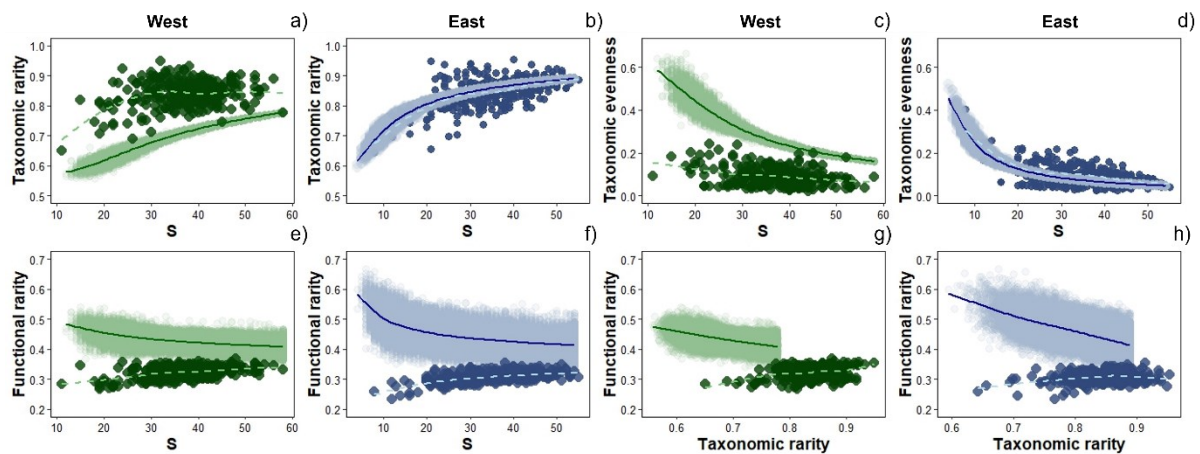
(Figure 5.10 e-h). The same patterns were evident when the null model was re-run with different gamma assemblages indicating that the results are robust against variation in initial composition (see Appendix 5.3).



**Figure 5.8:** Output of the null model showing the relationship between species richness (S) and numerical abundance (N). The flattening curve of S v N is consistent with the pattern typically seen in empirical data sets.

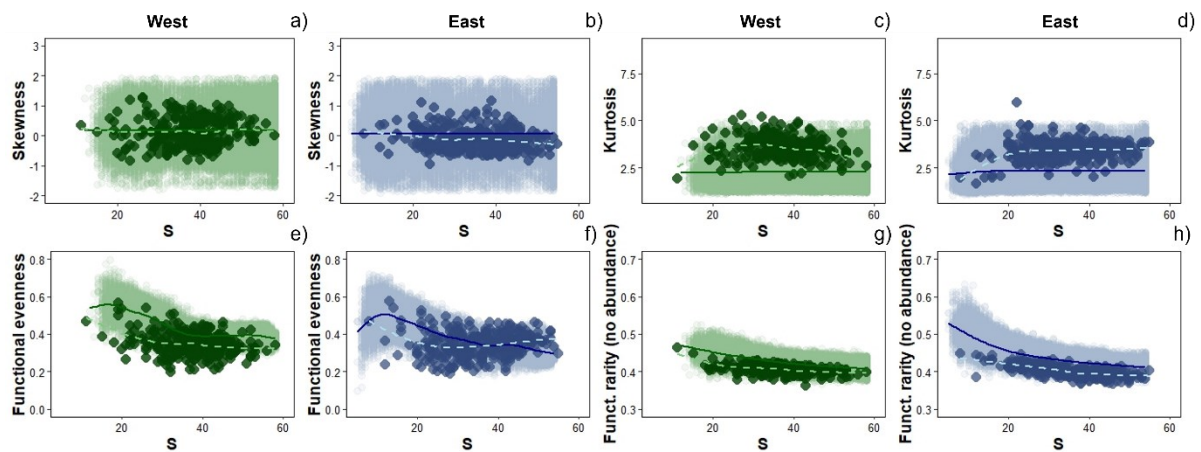


**Figure 5.9:** The null model shows that a positive change in assemblage size is expected to have a direct effect on both evenness and taxonomic rarity (in opposing directions). In turn these structural changes should result in a decrease in the functional rarity of the assemblage. However, in the observed results I find that although evenness and taxonomic rarity behave as expected, functional rarity is increasing, albeit very slightly, in line with assemblage size and taxonomic rarity. This figure compares the expected result with the observed result.

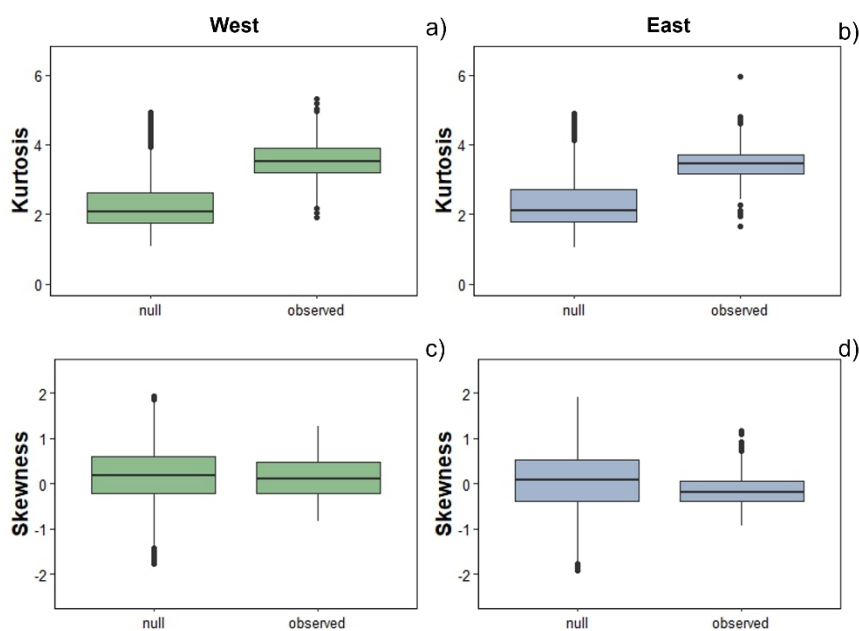


**Figure 5.10:** Relationship between null and observed. Observed values (yearly results by latitudinal band) are shown as solid points, with the distribution of null results indicated by the shaded area. In both cases trends are indicated using a loess fit, computed using the `stat_smooth(method="loess")` option in `ggplot2`. West coast results are shaded green, and east coast blue, with the observed loess as a pale dashed line and the null as a darker solid line.

In both West and East systems values for the skewness of the observed distributions of functional rarity (Figure 11 a and b), plotted in relation to  $S$ , were nested within the null, with average trends close to zero in both cases. There was also overlap between observed and null levels of functional evenness (Figure 11 e and f) and in the kurtosis of functional rarity (Figure 11 c and d). However, in this latter case the distributions of observed functional rarity were moderately leptokurtic (median overall kurtosis: West null=2.08, observed=3.5; East null=2.12, observed=3.45 (see Figure 5.12)). Finally, when functional rarity was recomputed ignoring both the species abundance and trait abundance distributions, the trends in both observed and null were closely matched (see Figure 5.11 g and h).



**Figure 5.11:** Relationship between null and observed. As with Figure 5.10, observed values are shown as solid points, with the distribution of null results indicated by the shaded area and trends shown using a loess fit. The west coast results are shaded green, east coast blue, with the observed loess as a pale dashed line and the null as a darker solid line.



**Figure 5.12:** The boxplots show the distributions of kurtosis and skewness when viewing the null by the observed. Medians are as follows: West kurtosis: null=2.08, observed=3.5. West skewness: null=0.18, observed=0.1. East kurtosis: null=2.12, observed=3.45. East: skewness null=0.07, observed=-0.2.

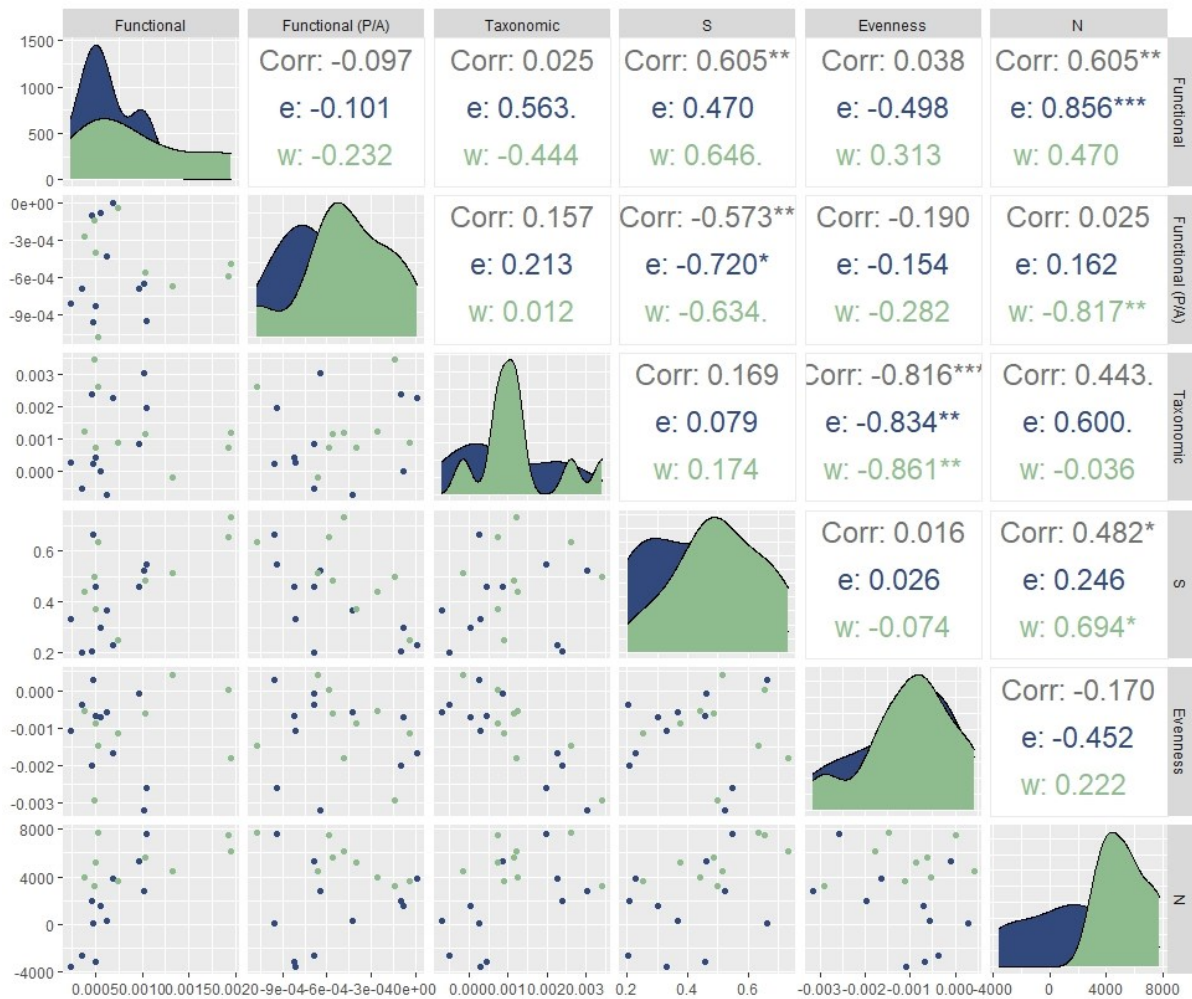
To help clarify how assemblage level metrics can change as a direct consequence of the combinations of fish occupying them, I ran a series of ‘toy’ examples to illustrate the possible outcomes. These are extreme examples designed to show how an assemblage can be affected by the introduction or removal of a single species.

**Table 5.2:** This table shows mock changes to evenness, mean functional and taxonomic rarity and the rarity values for the most and least distinctive fish in the assemblage. This toy example contains the same ten species and always has 100 individuals – the only change is the distribution of these individuals amongst species. These are extreme and unlikely scenarios but illustrate how abundance changes to certain species can affect the collective rarity of the assemblage.

Species	N	N	N	N	N	N	N	N
<i>Clupea harengus</i>	10	14	10	10	1	1	31	1
<i>Gadus morhua</i>	10	12	10	10	1	1	1	1
<i>Scomber scombrus</i>	10	12	10	10	1	1	1	1
<i>Microstomus kitt</i>	10	8	10	10	1	1	1	1
<b><i>Conger conger</i></b>	10	5	1	19	1	91	31	1
<b><i>Melanogrammus aeglefinus</i></b>	10	10	19	1	91	1	1	31
<i>Platichthys flesus</i>	10	10	10	10	1	1	1	31
<i>Trisopterus esmarkii</i>	10	14	10	10	1	1	31	1
<i>Solea solea</i>	10	9	10	10	1	1	1	1
<i>Raja clavata</i>	10	6	10	10	1	1	1	31
Total N	100	100	100	100	100	100	100	100
Total S	10	10	10	10	10	10	10	10
Evenness	1	0.92	0.86	0.86	0.12	0.12	0.35	0.35
Mean taxonomic rarity	0.5	0.51	0.52	0.52	0.84	0.84	0.69	0.69
Mean functional rarity	0.47	0.46	0.44	0.49	0.39	0.64	0.55	0.43
<i>C. conger</i> taxonomic rarity	0.5	0.7	0.93	0.27	0.93	0.002	0.12	0.93
<i>C. conger</i> functional rarity	0.66	0.68	0.65	0.67	0.57	0.66	0.81	0.57
<i>M. aeglefinus</i> taxonomic rarity	0.5	0.5	0.27	0.93	0.002	0.93	0.93	0.12
<i>M. aeglefinus</i> functional rarity	0.39	0.37	0.37	0.4	0.39	0.55	0.43	0.38
<i>C. conger</i> has the most unusual combination of traits whilst <i>M. aeglefinus</i> has the least	All species are evenly distributed	More realistic distribution applied	<i>C. conger</i> is singleton whilst <i>M. aeglefinus</i> has 19	<i>M. aeglefinus</i> is singleton whilst <i>C. conger</i> has 19	All species singletons except <i>M. aeglefinus</i>	All species singletons except <i>C. conger</i>	Three fish with most unusual traits have 31	Three fish with least unusual traits have 31

### 5.3.6 Slopes and correlations

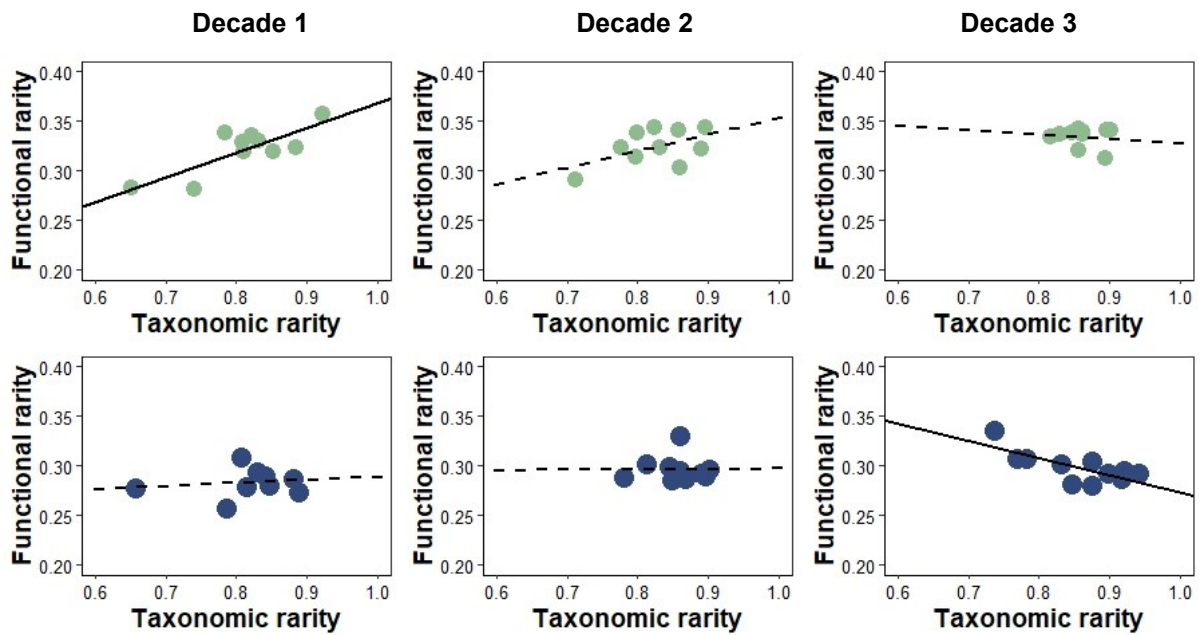
When I examine the relationships between the different slopes of the metrics, I find clear differences between the two coastal systems. In the west coast changes in functional rarity (distinctiveness) track the changes in evenness but on the east coast I find the opposite effect. The addition of the non-abundance weighted metric for rarity also exhibits differences between the systems although these are generally only in strength rather than direction. However, the relationship between the non-abundance weighted rarity metric and N is a very strong negative one on the west compared to a weak positive one on the east (see Figure 5.13).



**Figure 5.13:** Pearson correlations between slopes of change for all metrics. The asterisks indicate strength of correlation from . to \*\*\* where \*\*\* is the strongest. Asterisks represent p-values (. <0.1, \* <0.05, \*\* <0.01, \*\*\* <0.001). The correlations and plot figures are coloured by coastal system, green for west and blue for east as previous figures with the overall correlation results shown in grey. Here Functional P/A refers to the functional rarity measure with no abundance weighting.

To further investigate the relationship between functional and taxonomic rarity I examined the decadal change for a single latitudinal band in each system, here represented as 55.5 degrees latitude on the west coast and 60.5 degrees latitude on the east coast (see Figure 5.14). These were chosen to illustrate the latitudinal variation as well as coastal variation. The west coast system shows a positive (and significant) relationship between taxonomic and functional rarity (i.e., functional rarity increases as taxonomic rarity increases) in the first decade (1985 to 1994 inclusive). The positive relationship is maintained in the second decade (1995 to 2004 inclusive), although with a non-significant trend but in the third decade (2005 to 2014 inclusive) this relationship changes, showing a slight decline in functional rarity as taxonomic rarity increases (non-significant). I find a different pattern on the east coast where the flat but positive relationship between taxonomic and functional rarity in the first two decades becomes a steep and significantly negative relationship in the third decade, i.e., as taxonomic

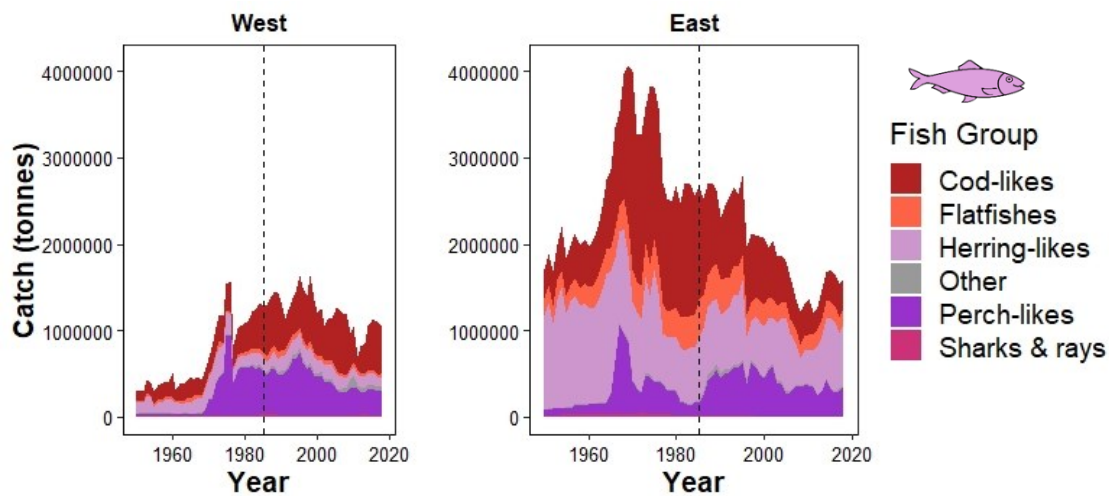
rarity increases, functional rarity decreases. These decadal changes suggest that, for these assemblages at least, the observed results are tending towards the null expectation.



**Figure 5.14:** The plots represent the change in the relationship between functional and taxonomic rarity over the three decades of this study. The west coast band (55.5 degrees latitude) is shown in the upper panel and coloured green whilst the east coast band (60.5 degrees latitude) is coloured blue and shown in the lower panel. Slopes are calculated using OLS and are shown as solid lines if significant and dashed if non-significant. West coast – Decade 1: p-value=0.01, Adj. R<sub>2</sub>=0.61; Decade 2: p-value=0.18, Adj. R<sub>2</sub>=0.12; Decade 3: p-value=0.74, Adj. R<sub>2</sub>=-0.11. East coast – Decade 1: p-value=0.71, Adj. R<sub>2</sub>=-0.12; Decade 2: p-value=0.97, Adj. R<sub>2</sub>=-0.13; Decade 3: p-value=0.01, Adj. R<sub>2</sub>=0.5. For full summary statistics of these and other results see Appendix 5.2.



Changes in fishing pressure over the last sixty years differs between the North Sea and Celtic Sea regions as illustrated in Figure 5.15, see discussion (section 5.4) for details.



**Figure 5.15:** Historic catch data sourced from the Sea Around Us (Pauly & Zeller, 2015a) project. Catch is represented as tonnes and the area is the full Large Marine Ecosystem for each coastal system (West coast – Celtic Biscay Shelf, East coast – North Sea). These catch data are compiled from multiple fisheries sectors (artisanal, industrial, subsistence, recreational) and include discards. The dashed line represents the start point of this study (1985). These data are not partitioned by the latitudinal band system used elsewhere in this analysis but can give some insight into fishing practices in the regions.

## 5.4 Discussion

Assemblages on both coasts are increasing in richness and in numerical abundance. These shifts in assemblage size should lead to increases in taxonomic rarity and decreases in (taxonomic) evenness, and this is what was found. This indicates that the directionality of changes in these taxonomic properties of these species' abundance distributions is consistent with the expectation based on a random draw from the gamma assemblage, albeit with some differences in the magnitude of the response between coasts. All other things being equal, as the null shows, I also expected this observed increase in assemblage size to lead to a decrease in functional rarity (Gross *et al.*, 2021). However, the opposite was found, with both systems exhibiting a weak positive increase in functional rarity, as they gained more species. Moreover, and in further disagreement with the null, observed functional rarity was broadly maintained as taxonomic rarity increased.

A species' functional rarity value is dependent not only on its own trait combination and abundance but also on the trait combinations and abundance of all other fish in the assemblage (Grenié *et al.*, 2017; Violle *et al.*, 2017; Mouillot *et al.*, 2021). The shape of this trait abundance distribution, for example, its degree of skewness and kurtosis, will determine not just the level of functional rarity, but also shed light on the processes involved in community assembly (Gross *et al.*, 2017; Gross *et al.*, 2021). This analysis, which took account of the trait

abundance distribution (TAD) as well as the species abundance distribution (SAD), detected no disagreement between the observed and null for trends in relation to increases in assemblage size for either functional evenness or the skewness of the functional rarity distribution. On the other hand, distributions of observed functional rarity tended towards leptokurtosis which could help explain why my observed values of functional rarity are lower than the null expectation (see Figure 5.10 e and f). This interpretation is supported by the analysis of functional rarity in which both SAD and TAD were ignored (see Figure 5.11 g and h). Here I uncovered a decline in functional rarity in larger assemblages, as predicted by the initial null. I therefore conclude that the functionally rare species that are entering these local assemblages are less abundant than is predicted from a random draw from the gamma assemblage.

A striking feature of these results is that the observed relationships between functional rarity and richness, and between functional rarity and taxonomic rarity were generally weak with relatively little trend in the metric in response to shifts in assemblage properties. Functional evenness also changed little with assemblage size, particularly in the East Coast system (see Figure 5.11 f). Taken together these findings suggest that the functional properties of these marine fish assemblages are conserved as assemblage size changes. Working with within-trait variation (Gross *et al.*, 2017), Gross *et al.* reported more even abundance distributions of trait values within dryland plant assemblages than would be expected by chance. Such patterns help maximise local multifunctionality (Gross *et al.*, 2017; Gross *et al.*, 2021; Le Bagousse-Pinguet *et al.*, 2021). In this case I did not find any marked discrepancy between null and observed functional evenness, but I computed functional evenness across eleven traits rather than within a single trait. It would be interesting to examine the trait abundance distribution at the individual as well as the species level, but I was unable to do this due the unavailability of intraspecific trait information.

This analysis also uncovered interesting differences between the two systems. For example, I observed higher levels of taxonomic rarity relative to the null expectation (see Figure 5.10 a and b), as well as reduced evenness, for given levels of richness, in the West Coast system (see Figure 5.10 c) as opposed to the East Coast system (see Figure 5.10 d). Since increased taxonomic rarity can be associated with habitat complexity (Cardoso *et al.*, 2020; McClain, 2021; Tóth *et al.*, 2022) this result could reflect the increased structural heterogeneity of the west coast, as well as contrasts in warming trends, and/or recovery from historical fishing pressures (Moyes & Magurran, 2019; Murgier *et al.*, 2021b).

Although the coastal systems are geographically close there are substantial differences between them. The west coast system is more structurally heterogeneous and environmentally complex in comparison to the east coast system. A previous study (Moyes & Magurran, 2019) found that the east and west coasts vary in the rate and level of warming waters. The differences I find could be due to warming, and/or recovery from historical fishing pressures (Murgier *et al.*, 2021a). Additionally, although most species are found in both systems, there are differences in how widespread or narrow their distributions are (see Figure 5.7). My results also highlighted the difference in strength and sometimes direction of the relationships between the different metrics, particularly in the case of numerical abundance (see Figure 5.13) which could also be driven in part by the heterogeneity of the systems (Heessen *et al.*, 2015).



Historically, the North Sea system has been more heavily exploited than the Celtic Sea are, but, since the beginning of this time-series in 1985, fishing pressure has been largely similar in both areas (see Figure 5.15). There are, however, differences in industrial fishing practices; the North Sea to the east is more heavily fished for pelagic species such as the Atlantic herring, *Clupea harengus* (Linnaeus, 1758) and Atlantic mackerel, *Scomber scombrus* (Linnaeus, 1758) (ICES, 2020) while the west coast system, which forms part of the Celtic Biscay Shelf, operates mainly smaller fishing fleets primarily targeting demersal species such as the European flounder, *Platichthys flesus* (Linnaeus, 1758), European plaice, *Pleuronectes platessa* (Linnaeus, 1758) and the common sole, *Solea solea* (Linnaeus, 1758) (ICES, 2018b). Recent work suggests that changes to fishing practices can have an effect on some life history traits including an increase in the biomass of slower growing species (Mérillet *et al.*, 2021; Mérillet *et al.*, 2022).

Historic catch data suggest that the east coast system was exploiting demersal cod-like species (including several highly commercial species such as Atlantic cod, *Gadus morhua* (Linnaeus 1758), whiting, *Merlangius merlangus* (Linnaeus 1758), haddock, *Melanogrammus aeglefinus* (Linnaeus 1758) and pollack, *Pollachius pollachius* (Linnaeus 1758)) extensively prior to 1985 but since then recorded catches have declined massively. In parallel it is clear that the west coast system has an increased overall catch with the cod-like and perch-like groups (including mackerel, *S. scombrus*) overtaking in tonnage reported from the east (Froese *et al.*, 2012; Garibaldi, 2012; Kleisner *et al.*, 2013; Pauly & Zeller, 2015a; Pauly & Zeller, 2015b).

The differences in taxonomic diversity could also be linked to the increased variability in trends on the West Coast (see Figure 5.7). Nonetheless, the observed relationship between functional rarity and richness, and the level of functional rarity, were similar in the two coastal systems suggesting that stochastic processes and niche differentiation could be important in shaping the distribution of traits in both cases (Gross *et al.*, 2021).

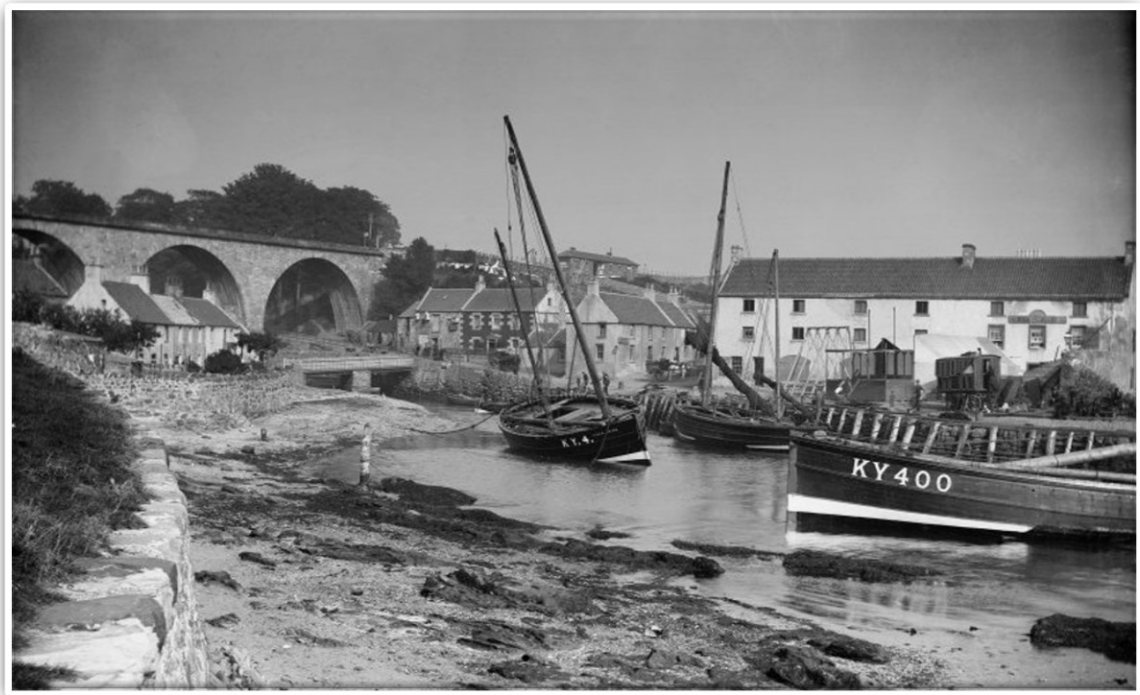
## 5.5 Conclusion

In conclusion, analyses of the two coastal systems revealed that trends in taxonomic rarity are an inadequate proxy for trends in functional rarity, and that the ongoing increases in assemblage size can have complex, and context-dependent, consequences for assemblage biodiversity. A clearer understanding of the potential drivers of change in functional rarity can assist with more targeted conservation plans and fisheries management and it is already clear that shifts in community rarity have implications for ecosystem resilience (Mouillot *et al.*, 2013c; Leitão *et al.*, 2016a; Albuquerque & Astudillo-Scalia, 2020; Loiseau *et al.*, 2020).

This result highlights the importance of taking an integrative approach to protect, maintain and sustain fishes of higher functional rarity (Davies *et al.*, 2022; Trindade-Santos *et al.*, 2022) and the integrity of marine fish assemblages. As rarity can often be a precursor to local extinction an understanding of the processes resulting in this can help maintain sustainable fishing practices and ensure species resilience. The following chapter (6 – Compositional change and rarity) explores rarity from the species level and investigates potential links between the species most influential in driving compositional change and rarity and dominance.

My results underline the importance of measuring both taxonomic and functional dimensions of diversity in biodiversity assessments. They also point to a theoretical deficit in biodiversity science, in relation to predicting the consequences of restructured species abundance distributions for trends in trait diversity and ultimately ecosystem functioning. Finally, my results indicate that there are underlying structural differences between the systems that drive the increases in both taxonomic and functional rarity found.

## Chapter Six – Compositional change and rarity



*Lower Largo Harbour, circa 1870*

## Chapter Six – Compositional change and rarity

### 6.1 Introduction

Temporal change in the composition of assemblages can have important implications for the functioning of fish communities, even when no reductions in species richness are identified (Spaak *et al.*, 2017). It is well documented that changes in assemblage structure can affect the performance of the system (Naeem *et al.*, 1994; Hooper *et al.*, 2005; Thompson *et al.*, 2018; van der Plas, 2019). This type of restructuring can affect fish species in differing ways, for example an increase in the abundance of a predatory fish may have a detrimental effect upon its prey species. Recent decades have seen rapid rates of change in the reorganisation of marine fish assemblages (Magurran *et al.*, 2015b). If these rates of change are to be slowed or halted, a better understanding of the processes that underpin compositional change is needed. In this chapter I examine different aspects of compositional change and investigate the identities of those species that are most influential in this process.

Changes in composition, either temporally or spatially, are often measured using beta diversity indices such as Jaccard (Jaccard, 1908) and Morisita-Horn (Morisita, 1959) and I utilise these methods here. However, compositional change can also be quantified by examining the temporal variation in the structure, or evenness of assemblages. Compositional change is composed of two factors, the number and identities of species within an assemblage and the distribution of their abundances (Magurran, 2013b). Here I investigate the structure of the assemblages by identifying the contributions species make using a selection of methods; firstly, I use two recent approaches that quantify the amount and type of contribution each species makes to compositional change (Chao & Ricotta, 2019; Gotelli *et al.*, 2021). Secondly, I categorise each species according to the role they play within the assemblage (functional rarity), their spatial distribution (taxonomic rarity) and their temporal persistence (core/transient). By identifying species contributions to change, I hope to gain a better understanding of how species' losses, or replacements are influencing the functioning of the overall systems (Basile, 2022).

Beta diversity refers to compositional differences between sites or time periods, in other words, how different the composition of species is at one place or time compared to another (Magurran, 2013b). There are multiple approaches to quantifying change in beta diversity. These methods range from the simple method initially proposed by Whittaker (Whittaker, 1960; Whittaker, 1972) whereby the difference between sites is calculated relative to the overall gamma diversity of the region (all sites together) by dividing total diversity ( $\gamma$ ) by site diversity ( $\alpha$ ) (see Chapter 2.3 for details and example), through the more commonly used metrics comparing the alpha diversity of two or more sites or time periods such as Jaccard (Jaccard, 1908), Bray-Curtis (Bray & Curtis, 1957) and Morisita-Horn (Morisita, 1959) to more complex statistical methods based on the slopes of species area curves (Lennon *et al.*, 2001; Ricotta *et al.*, 2002; Koleff *et al.*, 2003). Although much of the earlier work on beta diversity focused on taxonomic diversity, recent studies have included both functional and phylogenetic dimensions of diversity as well (Chiu *et al.*, 2014; Monnet *et al.*, 2014; Kang *et al.*, 2018; Jia *et al.*, 2020). Beta diversity can be calculated both using only presence-absence data as with Jaccard and by including abundance

as with, for example, Morisita-Horn. In this work I focus on these two approaches and only on the taxonomic dimension.

The approach developed by Chao and Ricotta (Chao & Ricotta, 2019) takes time series of species abundance data and detects the relative change in abundance at the assemblage level. This method also quantifies the contribution that each species makes to the overall diversity change in the system. This novel approach uses the Hill numbers framework (Hill, 1973) to examine the structural changes taking place in assemblages. It provides a valuable tool by allowing the identification of those species most influential in the restructuring of these assemblages. This is done by connecting a Jaccard type compositional change measure to three Hill numbers, namely  $q_0$ ,  $q_1$  and  $q_2$  (see Chapter 2.3 for details on these metrics). Turning the ‘dial’ on these Hill numbers increases the emphasis on species abundance, where  $q_0$  considers all species as equal and subsequent increments of  $q$  ( $q_1$ ,  $q_2$ ) place more weight on abundance.

A recently proposed framework (Gotelli *et al.*, 2021) identified the distinct classes of population change exhibited by species within assemblages, showing that while only a small fraction of the species in marine fish assemblages showed directional turnover, categorised as either increasing or decreasing in temporal prevalence, they disproportionately contributed to compositional change. Most populations were classified into random or recurrent categories, which contribute to ongoing turnover but not to long-term directional change or were continually present (no change). However, the small subset of species classified in one of the directional change groups appeared to contribute disproportionately to assemblage reorganisation. Here I classify assemblages by coastal system, using the methodology described in Gotelli *et al.* (Gotelli *et al.*, 2021) (and see section 6.2.3 for details) and ask which species are most influential in the community reorganisation I find. The Chao-Ricotta and Gotelli methods both identify the species that are main contributors to change, but because they approach the challenge in different ways, the identities of these species will not necessarily be matched across the methods.

Most assemblages are uneven, that is, the distribution of species is irregular with many species being low in abundance and only a few being very high (McGill *et al.*, 2007; Jones & Magurran, 2018). In other words most species are rare whilst a small number are common (Magurran & Henderson, 2011). It is possible to use temporal patterns of occupancy to categorise species into those with high temporal persistence (core) and low temporal persistence (transient) (Magurran & Henderson, 2003). Core species tend to be more abundant and often depend on specific local environmental conditions to enable their continued strength and persistence whilst transient species are usually rare and are more dependent on regional conditions that may allow immigration between habitats and systems (Supp *et al.*, 2015). Rarity in ecological assemblages is often considered to be an important factor in understanding how biodiversity is changing, if species are becoming rarer or less abundant this can be a precursor to species loss (Mace *et al.*, 2008; Wilfahrt *et al.*, 2021). As with other aspects of biodiversity, rarity is multi-faceted (Leitão *et al.*, 2016b; Tóth *et al.*, 2022; Trindade-Santos *et al.*, 2022; White *et al.*, 2022) and species that are taxonomically rare are not necessarily functionally rare and vice versa. This work examines rarity in the form of functional distinctiveness (Violle *et al.*, 2017; Morelli *et al.*, 2018; Pavoine & Ricotta, 2021; Thévenin *et al.*, 2022) (see Chapter 5.2.2 for further information) and taxonomic rarity is defined in terms of how widespread or restricted a species is within a region (see section

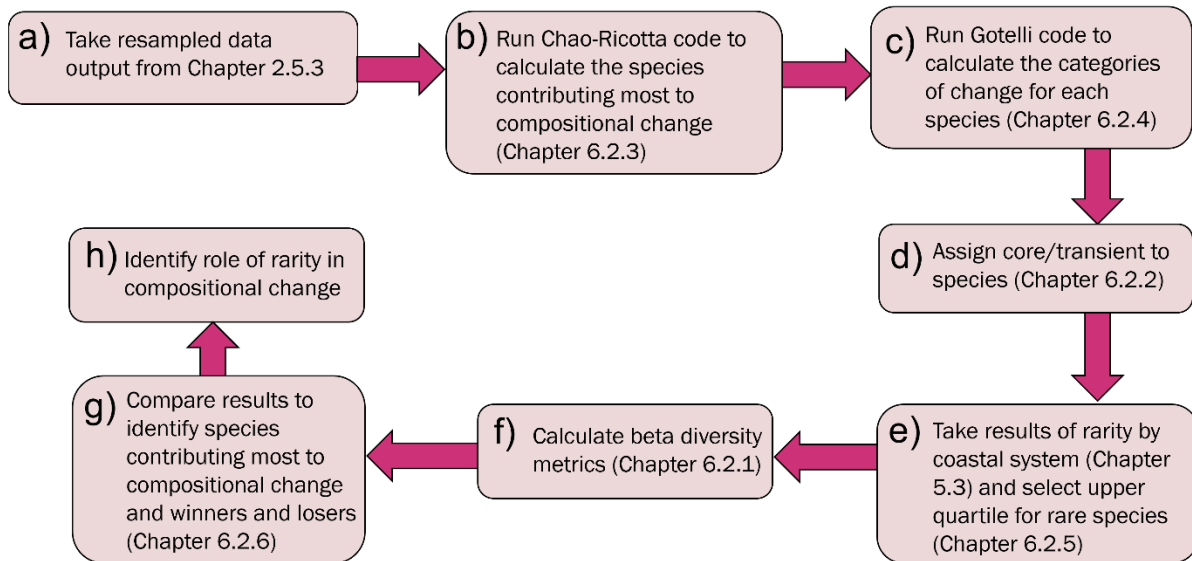
6.2.5 for details). I classify species according to these forms of rarity, before calculating the upper quartiles and choosing those species above that threshold to designate rarity (Gaston, 1994). Here I expand on the previous chapter to identify rare and common species within the assemblages.

Gaining an insight into the roles and functions that these key species play within assemblages can provide valuable insights for managers (Nielsen *et al.*, 2018a). It can be a complex task to balance often opposing needs such as economic stability and sustainable fisheries and an understanding of how biodiversity change can affect fish assemblages and species abundances can assist in the refinement of targeted local plans, particularly those where a co-operative management approach is in place (Ford & Stewart, 2021). Moreover, understanding how the composition and structure of assemblages is changing can help in biodiversity assessments, it can also be beneficial to gain an insight into the species driving the changes found. Here I classify species according to a range of different categories and groupings, building on the previous work in this thesis and examining a range of approaches to help understand how certain species can be ‘winners’ or ‘losers’ and/or be influential in biodiversity change (Pecl *et al.*, 2017; Dornelas *et al.*, 2019; Bowler *et al.*, 2021). I examine the connections between these classifications to try to understand any potential future changes in species contribution and/or classification and investigate any distinction between the systems.

In this chapter my overarching question is to identify the species which are most influential in compositional change. My expectation is that most species within these ecosystems will have little effect on the compositional changes within assemblages. In accordance with previous chapters, I also expect that the proportions of species in different categories of change would be largely similar in the coastal systems but with subtle differences found for certain groups. As the identities of the rarest species differ between systems (see Table 6.2 and Appendix 6.2 for details), I also expect to find that the most influential species in turnover of assemblages to be distinct.

## **6.2 Methods**

As in all previous chapters, the data used in this work were sourced from the International Council for the Exploration of the Sea (ICES) and are taken from two standardised scientific trawl surveys incorporating the ICES areas VIa (West Coast), IVa and IVb (North Sea) (DATRAS, 2015, 2019) (see Chapter 2.2 for full details). Each species record contains a precise geographical location and numerical species abundance represented by CPUE (catch per unit effort) which in this instance refers to the number of individuals of a given species caught per hour using a tow duration of half an hour. Trawl speed is measured as 4 knots and this work focuses only on those records collected using the Grande Overture Verticale (GOV) gear, a type of bottom trawl net with a small mesh which is now the recommended gear for all bottom trawl surveys carried out by ICES. Here I focus mainly on the two coastal systems (DATRAS, 2015, 2019) rather than the latitudinal bands used in earlier chapters.



**Figure 6.1:** Workflow diagram illustrating the steps carried out within this chapter and where to find further details on each. Following on from the steps in earlier chapters I first a) import the resampled data for coastal and latitudinal band level assemblages before b) running code to implement the Chao-Ricotta approach. Using the same input, I c) run code to assign species classifications according to the Gotelli framework and then d) assign the core or transient status to each species according to temporal occupancy of coastal system. The next step is to e) allocate rare/common designations to each species using the output from Chapter 5 before f) calculating the two dissimilarity measures (by coast and latitude). I then g) identify species that are the greatest contributors to change according to the approaches developed by Chao-Ricotta and Gotelli et al. Finally in h) I examine the connections between rarity and these influential species.

### 6.2.1 Beta diversity approaches

Biodiversity is made up of three parts; alpha diversity, beta diversity and gamma diversity (Whittaker, 1972). Alpha diversity refers to the diversity of an assemblage at a point in time and it can be measured using a variety of methods (see Chapter 2.3 and Chapter 3.2 for further details). Gamma diversity is the overall diversity within a region or geographic area. Beta diversity quantifies compositional changes between systems rather than within systems; this can be done either between spatially or temporally (Tuomisto, 2010b, a; Magurran, 2013b). Beta diversity is an important element in quantifying biodiversity change as it can help protect regional diversity and assist with targeted conservation plans at local scales (Socolar *et al.*, 2016). Changes in beta diversity are often used in conjunction with alpha diversity measures (Fontana *et al.*, 2020; Lazzari *et al.*, 2020). Here I focus only on two beta diversity measures, Jaccard (Jaccard, 1908), which takes only presence-absence data and Morisita-Horn (Magurran, 2013b) which includes abundance data (see Chapter 2.3.1.2 for full details on these methods). In this work I calculate change in composition from the baseline (the first year of the time series) so change is measured against this in each consecutive year, and I use the dissimilarity version thus quantifying how different a site is at any time step in comparison to the first year.

The Jaccard index is used to calculate the dissimilarity between assemblages, i.e., how distinct one sample is from another. This was first developed by Paul Jaccard in 1908 (Jaccard, 1908; Jaccard, 1912) to compare regional flora and is simple to understand. The basic premise of this method is that as the number of species shared between two assemblages increases, their similarity in composition will also increase (see Chapter 2.3.1.2.2 for equation and illustration). As I focus on dissimilarity in this work, it is easier to think of it as a reduction in shared species leading to an increase in dissimilarity.

The Morisita-Horn dissimilarity index is based on the premise that the probability of any individual being chosen from a community is likely to belong to a different species than that of a single individual being picked from a different assemblage (Magurran, 2013b). I chose to use Morisita-Horn dissimilarity in this work as it is less affected by species richness than many other abundance-based dissimilarity metrics (Wolda, 1981) and it therefore makes a good choice to quantify compositional change for this work (for further details, equation and illustrative figure see Chapter 2.3.1.2.1).

This chapter is focused on the two Scottish coastal systems. I investigate temporal change in the beta diversity metrics for each coast separately. Morisita-Horn was calculated using the `vegdist` function in the `vegan` package (Oksanen *et al.*, 2017) in R and Jaccard with the `beta.pair` function in the `betapart` package (Baselga *et al.*, 2018). Slopes of change are calculated relative to the second year of the time series, i.e., in these thirty-year time studies, there are twenty nine time points, year two compared to year one, year three to year one, year four to year one and so on.

## 6.2.2 Chao Ricotta approach

In this thesis I decided to structure the taxonomic diversity metrics (see Chapter 3.2) around Hill numbers (Hill, 1973) as it provides a clear statistical framework and can be adjusted to reflect the level of emphasis placed on abundance (Magurran, 2013b; Chao *et al.*, 2014). I therefore chose to quantify species contribution to compositional change using a similar methodology. Chao and Ricotta proposed a novel approach incorporating Hill numbers in this way (Chao & Ricotta, 2019) to investigate structural change in the diversity of systems. This method involves the use of three orders of  $q$ ,  $q_0$ ,  $q_1$  and  $q_2$  (see Chapter 2.3.1.1 and Chapter 3.2 for further details on these measures) and can identify the species that are most influential in the restructuring of their assemblages by linking Jaccard type compositional change measures.

The Chao-Ricotta approach sets out a framework to quantify evenness (or unevenness) within assemblages resulting in a range of five evenness indices. These are given in terms of species richness ( $q_0$ ) and relative abundance measures ( $q_1$  and  $q_2$ ) and reveal the relationships between diversity and evenness. It involves linking beta dissimilarity measures with the unevenness of an assemblage (Chao & Chiu, 2016) based on the first of the evenness indices provided (see Table 1, class 1 in Chao and Ricotta (Chao & Ricotta, 2019)). Species are ‘weighted’ according to their abundance and the resulting measure quantifies the proportion of distinct species within the pooled assemblage (coastal system).

I calculated the contributions of all species to Jaccard type compositional change through the lens of the Hill ( $q$ ) numbers before selecting the top ten contributors to change for  $q_1$  and  $q_2$  ( $q_0$ , which is the equivalent of species



richness contains too many ties to provide any meaningful evaluation). I chose to examine the top ten contributors more closely as the remaining species contribute little to any composition change found (see results section 6.3.2 and Figure 6.5 for illustration). These steps were performed independently for each coastal system.

### 6.2.3 Gotelli framework

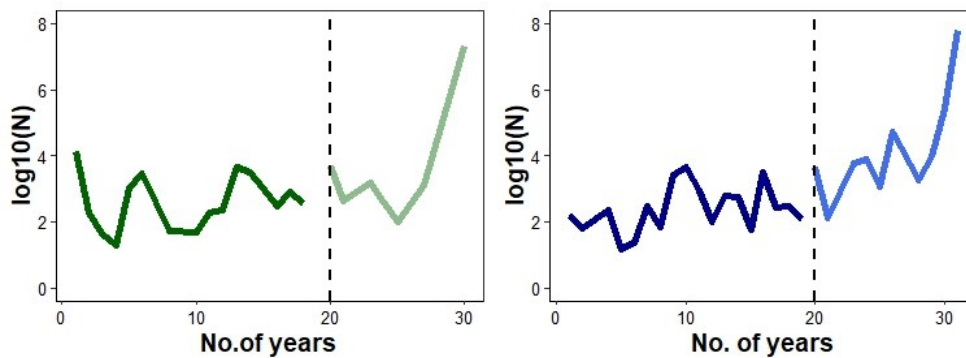
Another recently proposed measure of temporal change (Gotelli *et al.*, 2021) categorises species into distinct classes of temporal dynamics. Each species in an assemblage, i.e., a population, can be classified into one of seven categories of temporal turnover based on the ordered sequence of presences and absences in the assemblage time series following the work in Gotelli et al (Gotelli *et al.*, 2021). To do this, I created matrices of species occurrence per year for each assemblage (coastal system). For each species, the time series was evenly split into an early and a late period (in this work the midpoint is at fifteen years as the time series are of three decades). I then used a contingency table analysis to check for any significant change in incidence through time, either increasing or decreasing. If the contingency test is non-significant, a species may be assigned either to the recurrent or to the random change categories, following a one-tailed runs test (Trapletti A & Hornik K, 2021) to check whether there are unusually small numbers of colonisations and extinctions based on the numbers of presences and absences. Note is also taken of whether a species is present or absent in the first year of the time series. This distinction is important in determining whether the resulting pattern will be one which generates a convergence or a divergence towards the assemblage composition in the baseline year. Thus, each species is classified into one of seven distinct categories of temporal dynamics, which can be either non-directional: no change (always present), random, recurrent, or directional: converging increasing, converging decreasing, diverging increasing or diverging decreasing (see Figure 6.2 for exemplification).



**Figure 6.2:** The figure shows toy examples of each form of classification with species presence coloured by category and absence in white. Whitespace is left after the first year of the time series to highlight the converging/diverging nature of the directional change categories.

## 6.2.4 Core and transient species

The concept of an assemblage being made up of both core and transient species is not new (MacArthur, 1960). Core species, those that are persistent throughout the time series, can often be more abundant and display different forms of species abundance distribution (SAD) (Magurran & Henderson, 2003; Ulrich & Ollik, 2004). The classification of core and transient species is primarily done using a temporal approach, i.e., how persistent through time a species is defines its position on the core to transient scale. Many studies use this type of distinction within assemblages (Magurran & Henderson, 2003; Ulrich & Ollik, 2004; Coyle *et al.*, 2013) and here I partition the species by length of occupancy, i.e., species are considered to be core if they are present in at least two thirds of the time series. To do this I simply created a cut-off point of twenty years (equating to being present for at least two thirds of the time series) and categorised all species meeting this criterion as ‘core’, whilst the remainder were identified as ‘transient’.



**Figure 6.3:** The figure shows log 10 total abundance of all species by the number of years appearing in the system. The dashed lines represent the cut-off point used to designate a species with either core or transient, the paler shades represent the core species, persistent for at least twenty years. As throughout the left panel and green colours show the west coast system whilst the right panel and blue shades are the east.

## 6.2.5 Top quartile of rare species

Taxonomic restrictedness is calculated at the regional scale (in this work this refers to coastal system) and can be generated using the area or extent of species occupancy, in other words how widespread or restricted a species is within a system. The values range between 0 and 1 as the restrictedness is standardised using the most widespread geographic range.

$$Restrictedness_i = 1 - \frac{Ge_i}{Ge_{max}}$$

where  $Ge_i$  is the geographical extent of species  $i$  and  $Ge_{max}$  is the maximum geographical extent

Equation adapted from (Violle *et al.*, 2017)

A low value (tending towards zero) suggests that species are widespread whilst a high (close to 1) value indicates that they have a narrow geographic extent. This metric takes no account of abundance and reflects species occupancy only.

For consistency between forms of rarity in this chapter here I focus on the functional rarity metric with no abundance weighting (functional global distinctiveness (Grenié *et al.*, 2017) and see Chapter 5.2.3). This is calculated by taking the mean pairwise distance between species within the assemblage. It takes all species into account to measure whether a given species is functionally close to its neighbours, i.e., whether it contains a similar or distinct combination of traits. Functional rarity can then be identified as the mean distance in functional space between a species and the others within the assemblage. This measure ranges between 0 and 1, with rarer species tending towards 1 and more common tending towards 0.

$$FunctionalRarity_i = \frac{\sum_{j=1, j \neq i}^N d_{ij}}{N - 1}$$

*N* is the number of species in the community,  $d_{ij}$  is the distance between species *i* and *j*

Equation adapted from (Violle *et al.*, 2017)

In this section I use restrictedness and functional rarity only to identify species as rare or common (functional) and restricted or widespread (taxonomic). This is done by calculating the upper quartile (75%) of each measure by coastal system and then assigning the appropriate values to each species according to their individual scores. The quantile function used here can be located in the `quantreg` (Koenker, 2015) package in R. All those species with restrictedness or functional rarity values greater than the upper quartile, or the top 75% of species will be classified as either rare or restricted accordingly.

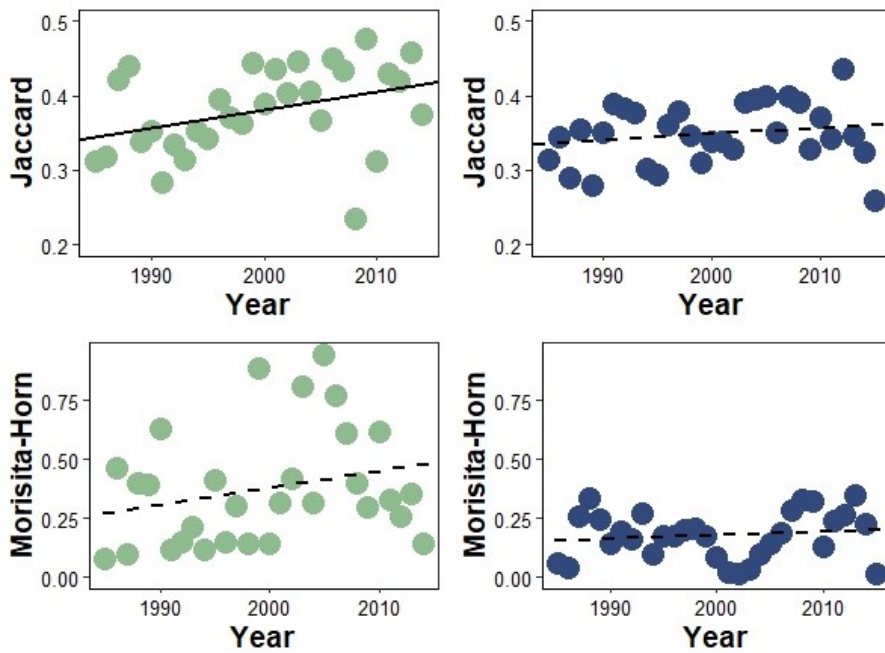
## 6.3 Results

Here I detail the results found for each of the approaches before investigating the connections between several of them.

### 6.3.1 Beta diversity approaches

The results by coastal system show that generally, at the coastal system scale, beta diversity calculated using these metrics is becoming more dissimilar over time, i.e., later years are more different in terms of composition than earlier years. It is clear from Figure 6.4 that although both show positive trends, change in composition differs between coastal system and that this is particularly true when using the abundance weighted measure of Morisita-Horn. There is also greater variance between years on the west coast and the only significant trend is for Jaccard dissimilarity on the west coast. To evaluate this variation between systems I computed the Median absolute deviation (MAD) using the `mad` function from the `stats` package in base R (RCoreTeam, 2021)) of

slopes. The results were as follows: West coast: Jaccard dissimilarity=0.07, Morisita-Horn=0.26, East coast: Jaccard dissimilarity=0.05, Morisita-Horn=0.12.

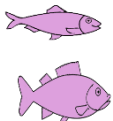
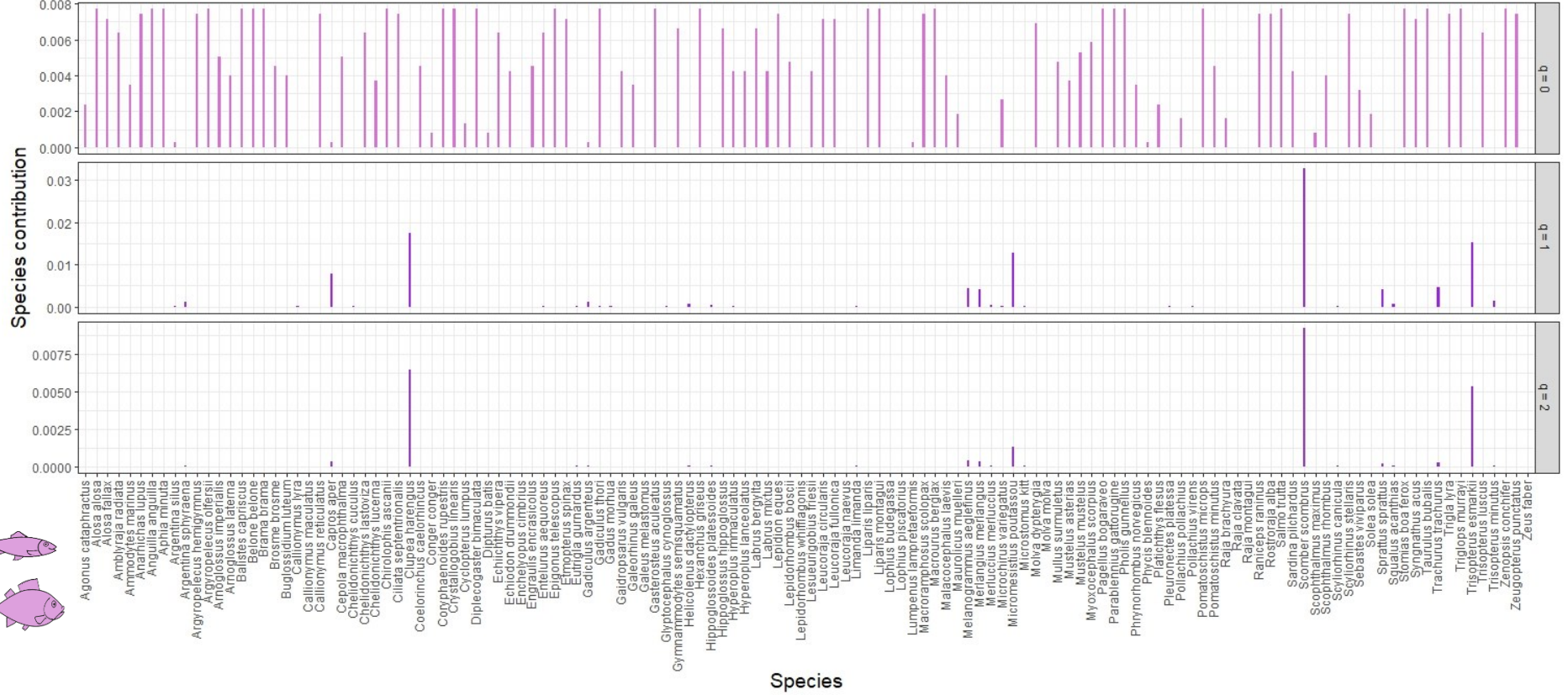


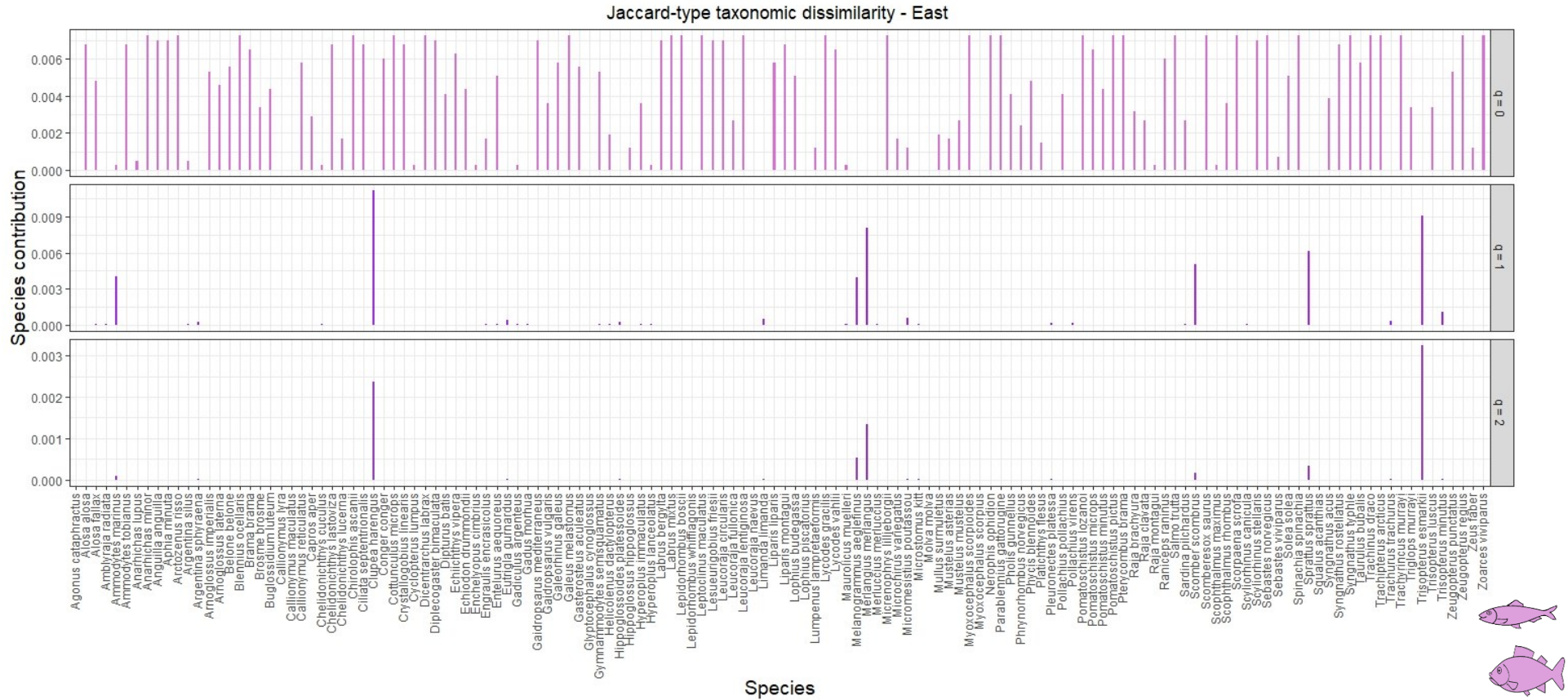
**Figure 6.4:** Yearly dissimilarity measured against the baseline first year of the time series. As throughout this thesis the points are coloured according to coastal system – blue for the east and green for the west. Each point represents the dissimilarity at that time step when compared to the baseline (here the first year of the time series). Points are fitted with a simple linear regression (Ordinary Least Squares) and the lines are solid in the case of a significant trend and dashed for non-significant. Jaccard dissimilarity: west coast – p-value=0.05, Adj.  $R^2=0.1$ ; east coast – p-value=0.3, Adj.  $R^2=0.01$ . Morisita-Horn dissimilarity: west coast – p-value=0.17, Adj.  $R^2=0.03$ ; east coast – p-value=0.46, Adj.  $R^2=-0.02$ .

### 6.3.2 Chao Ricotta approach

When examining the contributions of all species found in each system, there are clear differences between the coasts. The species contributing most to compositional change using  $q_1$  and  $q_2$  are particularly distinct. Additionally, despite the many tied contributions featured in the  $q_0$  results there is only one fish common to both coastal systems in the most influential species category (top ten contributors). This is Yarrell’s blenny, *Chirolophis ascanii* (Walbaum, 1792), which is transient, restricted and functionally rare for both systems.

### Jaccard-type taxonomic dissimilarity - West





**Figure 6.5:** Plots showing the contributions that each species is making to compositional change (Jaccard type dissimilarity) when looking through the lens of the Hill numbers,  $q_0$ ,  $q_1$  and  $q_2$ . Upper panel shows the west coast, and the lower panel shows the east. The top ten contributors for each system as outlined in Table 6.1 can be identified by the height of the visible columns in the  $q_1$  and  $q_2$  plots.



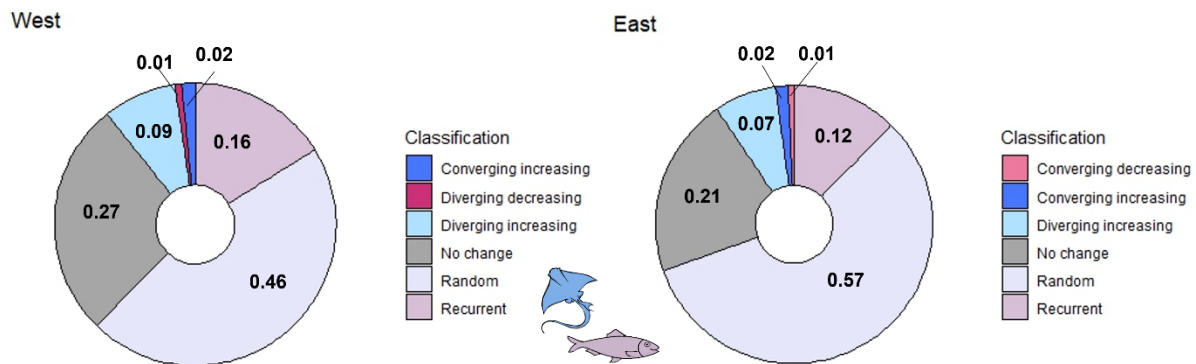
The top ten contributors from  $q_1$  and  $q_2$  differ slightly between systems but are largely consistent between the two metrics, the west coast shows a small change in the ordering between  $q_1$  and  $q_2$ , but both measures share the same species. The east coast introduces one extra species, the grey gurnard, *Eutrigla gurnardus* (Linnaeus, 1758), who appears in the top ten contributors for  $q_2$  but not  $q_1$  whilst the blue whiting, *Micromesistius poutassou* (Risso, 1827), is in  $q_1$  but not  $q_2$ . There are common species to both coasts but also some differences. As expected, all these top contributors are core species and are widespread, and most are in the ‘no change’ category for the Gotelli classification. However, the blue whiting is functionally rare (in the upper quartile – top 75%) in both systems (see Table 6.1 for more detail and Appendix 6.2 for the full table including all species).

**Table 6.1:** The top ten contributors to change in Jaccard type dissimilarity for both Chao-Ricotta  $q_1$  and  $q_2$ , shown here alongside the different categories from other sections, namely the Gotelli classification and the upper quartile (top 75%) of rare species from the functional and taxonomic rarity metrics, (see Appendix 6.1 for details and values of all species).

Coast	Species	Gotelli Class	Core/Transient	Functional Rarity	Taxonomic Rarity	Chao-Ricotta $q_1$ Order	Chao-Ricotta $q_2$ Order
West coast	<i>Scomber scombrus</i>	No change	Core	Common	Widespread	1	1
	<i>Clupea harengus</i>	No change	Core	Common	Widespread	2	2
	<i>Trisopterus esmarkii</i>	No change	Core	Common	Widespread	3	3
	<i>Micromesistius poutassou</i>	No change	Core	Functionally rare	Widespread	4	4
	<i>Melanogrammus aeglefinus</i>	No change	Core	Common	Widespread	7	5
	<i>Merlangius merlangus</i>	No change	Core	Common	Widespread	9	6
	<i>Capros aper</i>	Recurrent	Core	Common	Widespread	5	7
	<i>Trachurus trachurus</i>	No change	Core	Common	Widespread	6	8
	<i>Sprattus sprattus</i>	No change	Core	Common	Widespread	8	9
	<i>Trisopterus minutus</i>	No change	Core	Common	Widespread	10	10
East coast	<i>Trisopterus esmarkii</i>	No change	Core	Common	Widespread	2	1
	<i>Clupea harengus</i>	No change	Core	Common	Widespread	1	2
	<i>Merlangius merlangus</i>	No change	Core	Common	Widespread	3	3
	<i>Melanogrammus aeglefinus</i>	No change	Core	Common	Widespread	7	4
	<i>Sprattus sprattus</i>	No change	Core	Common	Widespread	4	5
	<i>Scomber scombrus</i>	No change	Core	Common	Widespread	5	6
	<i>Ammodytes marinus</i>	Random	Core	Common	Widespread	6	7
	<i>Limanda limanda</i>	No change	Core	Common	Widespread	10	8
	<i>Trisopterus minutus</i>	No change	Core	Common	Widespread	8	9
	<i>Eutrigla gurnardus</i>	No change	Core	Common	Widespread	11	10
	<i>Micromesistius poutassou</i>	Recurrent	Core	Functionally rare	Widespread	9	12

### 6.3.3 Gotelli framework

I generated the classifications for each species according to their presence and absence within the time series (see section 6.2.3 for details), this was done separately for each assemblage. In this section I considered the assemblages as coastal systems (west and east). Firstly, I investigated the proportions of each classification for each coastal system (see Figure 6.6 for pie charts illustrating this). This allowed a comparison of the classes of species found on each coast. As expected, and as suggested by the findings in (Gotelli *et al.*, 2021), most species are random and this is true for both systems. There are, however, subtle differences in the breakdown of species classification as shown in Figure 6.6.

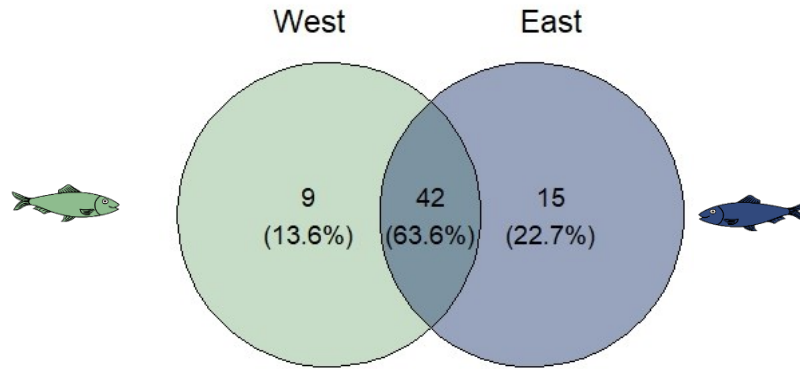


**Figure 6.6:** The pie charts show the proportions of each classification separately for each system. In both systems the random category holds the largest proportion, but this is slightly larger on the east coast whereas the west coast makes up this deficit by holding increased proportions of recurrent and no change species. Although for both coasts the directed change categories consist of approximately 10% of species, there are slight differences between them, whereby the west coast includes only diverging decreasing species and the east coast only converging decreasing species.

### 6.3.4 Core and transient species

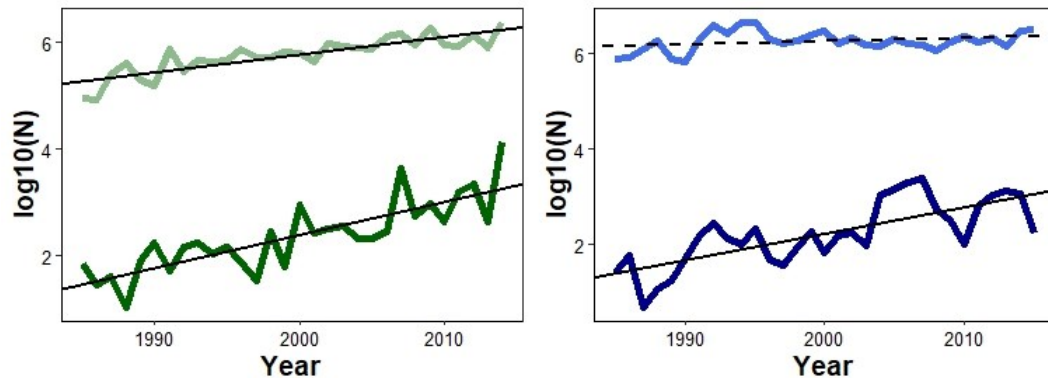
The two coastal systems are similar in terms of the breakdown of species into the core and transient categories with the west coast possessing slightly more transient species (61%) to the east (59%). Most core species are persistent in both systems (64%) as shown in Figure 6.7.





**Figure 6.7:** Venn diagram showing the overlap of core species common to both systems, most core species (64%) are persistent through time for both coasts. West coast shown in green and east in blue.

There are, however, slight spatial differences in the temporal change for the two categories of fish. Although there is a strong positive trend in the total abundance found ( $\log_{10}$ ) each year for transient species in both systems, only the west coast shows a similar strong significant positive trend for core species (see Figure 6.8).

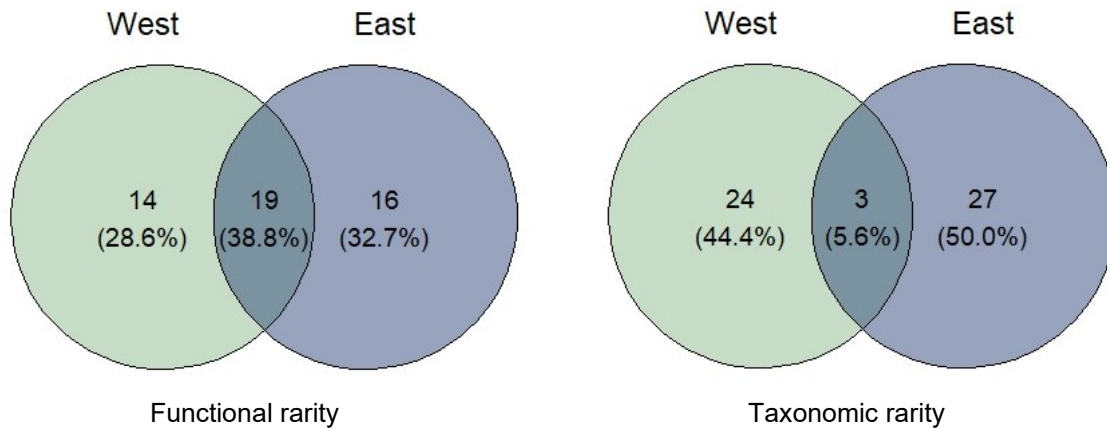


**Figure 6.8:** Figure shows the east and west coast systems with species split into core and transient based on the criteria in the methods section (6.2.4). Here the darker shades represent the transient species (with lower total abundances), and the black lines denote the linear regressions by group. Dashed lines are non-significant and solid significant.

### 6.3.5 Top quartile of rare species

There are nineteen species that are in the upper quartile for functional rarity for both systems, it is interesting to note that they do not always play the same role within their communities as highlighted in Table 6.2. When examining

the species that are taxonomically rare (or restricted) in both systems, there are only three species found, however, these fall into the same category.

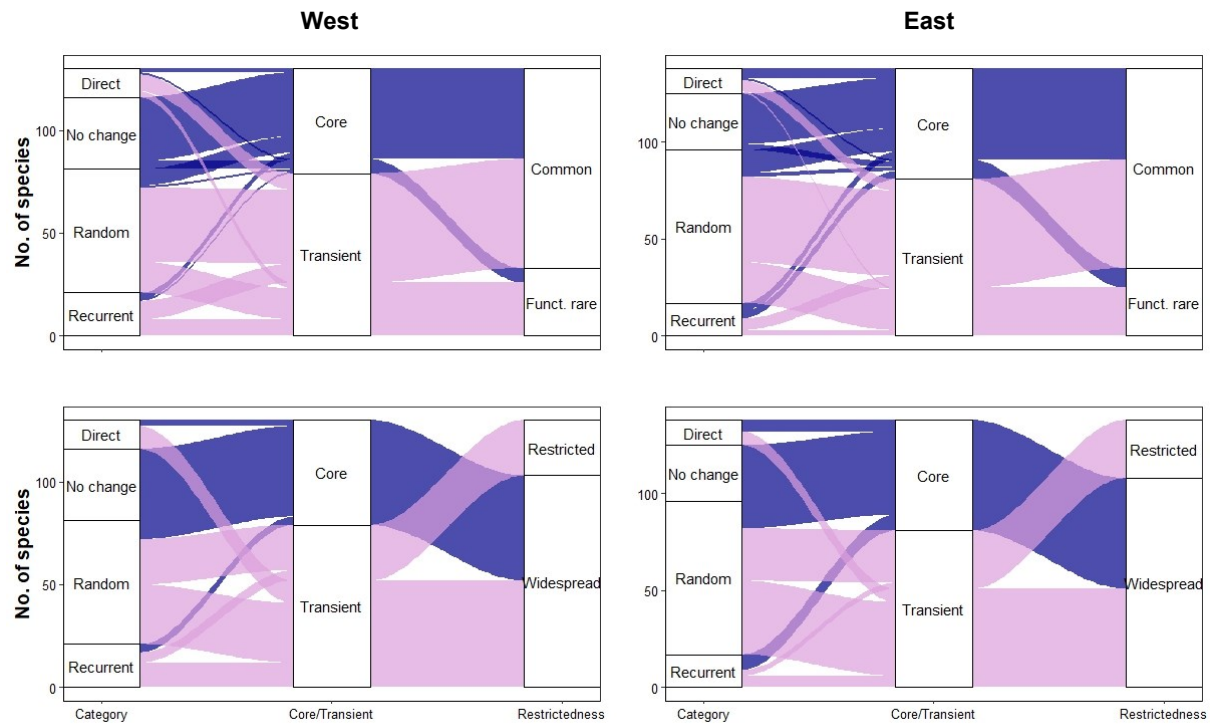


**Figure 6.9:** The left panel Venn diagram shows the numbers of species found in the upper quartile for functional rarity in each system. There is a small overlap (39%) where a species is rare in both systems. The right panel shows the overlap between the systems for taxonomic rarity (restrictedness), only 6% of species are taxonomically rare (upper quartile) in both systems.

**Table 6.2:** Table showing the species in the upper quartile for both systems for functional and taxonomic rarity and the Gotelli categories they fall into for each coastal system.

	West		East	
Species – functional rarity	Gotelli classification	Core/transient	Gotelli classification	Core/transient
<i>Aphia minuta</i>	Recurrent	transient	Random	transient
<i>Brama brama</i>	Random	transient	Recurrent	transient
<i>Chirolophis ascanii</i>	Random	transient	Random	transient
<i>Conger conger</i>	Recurrent	core	Random	transient
<i>Cyclopterus lumpus</i>	Random	core	Random	core
<i>Galeorhinus galeus</i>	Random	transient	Random	transient
<i>Gasterosteus aculeatus</i>	Recurrent	transient	Random	transient
<i>Hippoglossoides platessoides</i>	No change	core	No change	core
<i>Hippoglossus hippoglossus</i>	Random	transient	Recurrent	core
<i>Labrus bergylta</i>	Random	transient	Random	transient
<i>Labrus mixtus</i>	Diverging increasing	transient	Random	transient
<i>Lophius budegassa</i>	No change	core	Diverging increasing	transient
<i>Maurollicus muelleri</i>	Diverging increasing	core	Random	core
<i>Micromesistius poutassou</i>	No change	core	Recurrent	core
<i>Parablennius gattorugine</i>	Random	transient	Random	transient
<i>Salmo trutta</i>	Random	transient	Random	transient
<i>Sardina pilchardus</i>	Diverging increasing	transient	Diverging increasing	core
<i>Squalus acanthias</i>	No change	core	No change	core
<i>Syngnathus acus</i>	Random	transient	Random	transient
<b>Species – restricted</b>				
<i>Chirolophis ascanii</i>	Random	transient	Random	transient
<i>Parablennius gattorugine</i>	Random	transient	Random	transient
<i>Salmo trutta</i>	Random	transient	Random	transient

To better understand the connections between the different classifications the species have been allocated in this work I used alluvial plots to show the flow of species from each of the Gotelli classes to first core and transient and then to the rarity (functional and taxonomic) groupings. Although there are some subtle differences between the coasts, the species perform mainly as expected. For example, all species in the ‘No change’ category also fell into the ‘Core’ group and were ‘Widespread’, although not all were also ‘Common’ as a few fish fell into the functionally rare group despite their persistent and widespread nature. One example of this is the American plaice, *Hippoglossoides platessoides* (Fabricius, 1780), found on both coasts. The European pilchard, *Sardina pilchardus* (Walbaum, 1792), was also slightly unusual in that although it is functionally rare on both coasts, it is also widespread, showing directed change but is more persistent on the east coast where it is classified as core (see Appendix 6.2 for full details).



**Figure 6.10:** The alluvial plots represent the connections between the different Gotelli classifications. The numbers of species falling into the category combinations is used to create ‘flows’ between the columns. The west coast is on the left and east coast on the right. Upper panel represents functional rarity whilst the lower panel is taxonomic rarity in the form of restrictedness. The flows are coloured according to their core status, ‘Core’ in dark blue and ‘Transient’ in plum.

## 6.4 Discussion

One of the key findings from this chapter was the strength and variation between coastal systems when examining the temporal change in beta diversity metrics. This was particularly true for Morisita-Horn, the abundance weighted measure and the result reinforced the apparent importance of numerical abundance in the distinctions between coasts (see previous chapters 3.3.1 and 5.3.4). The other main finding was learning the identities of the species that are most influential in contributing to compositional change and seeing how these differ between both systems and methods. For example, the lesser sand-eel, *Ammodytes marinus* (Raitt, 1934) is among the top contributors to change for the east coast using the Chao-Ricotta method but is not a top contributor on the west. Similarly, the smooth sand-eel, *Gymnammodytes semisquamatus* (Jourdain, 1879) falls into one of the directed change Gotelli classes for the east coast but is in a non-directed change group on the west.

To consider the implications of these results I first discuss the differences between the coasts, then the species’ contribution to compositional change and finally the strengths and weaknesses of these different methods in the understanding of biodiversity change.

### *Differences between coastal systems*

Earlier findings (Magurran *et al.*, 2015b; Moyes & Magurran, 2019) led to the expectation that temporal changes in beta diversity would differ between coastal systems and when considering the distinction between coastal systems this was evident. In fact, the differences in strength of trend mirror those found when examining change in relative dominance (see Chapter 3 and (Moyes & Magurran, 2019) and sea surface temperatures for the areas (see Chapter 2.2, Figure 2.3) (ICES, 2018c, 2019). This suggests that environmental factors such as warming waters could be driving factors in rate and type of compositional change (Baudron *et al.*, 2011; Baudron *et al.*, 2013; Hiddink *et al.*, 2014; Heessen *et al.*, 2015; ICES, 2018c, 2019; Eme *et al.*, 2022).

The results of the Chao-Ricotta method reveal some differences between the systems in terms of the identities of the ten most influential species in the reorganisation of the assemblages. However, these are generally very small differences and for the most part the influential species are shared between systems suggesting that the environmental heterogeneity between coasts may not be an important factor here.

However, the results of the Gotelli classification and the identification of rare species, using either the core/transient framework or selecting the upper quartile of functionally or taxonomically rare species uncover greater differentiation between systems particularly when examining the Gotelli categories. Specifically, I find that the west coast consists of a greater proportion of species that are always present, with more recurrent and fewer random species. Additionally, diverging decreasing species are located only on the west (see Figure 6.6 for illustration). Although there are some core species unique to their own coastal system, most (64%) are common to both (see Figure 6.7 for details). Conversely, when examining the overlap of the rarest species (upper quartile) between systems, the numbers are very low, particularly for taxonomic rarity, suggesting that habitat heterogeneity could be important (see Figure 6.9 for illustration).

### *Species' contribution to compositional change*

#### Chao-Ricotta approach

It is possible to think of an ecological assemblage as being composed of two components, how species rich it is and how evenly distributed those species abundances are (Jost, 2010; Magurran, 2013b). However, this is not always straightforward and a way to differentiate between the influences of rare and abundant species when quantifying change in evenness would be beneficial (Ricotta, 2003). The approach developed by Chao and Ricotta (Chao & Ricotta, 2019) expands on this by quantifying evenness through the lens of three different measures based on Hill numbers (Hill, 1973), namely, species richness ( $q_0$ ), exponential Shannon ( $q_1$ ), and the reciprocal of Simpson ( $q_2$ ). This approach is simple and effective, allowing the user to see how increasing abundance affects the contribution a species makes to compositional change, and crucially, enabling the identification of those species contributing most.

My analyses identified the top ten species contributing to Jaccard type compositional change when examining  $q_1$  and  $q_2$ . Many of these were consistent across systems and most were influential using either metric. Interestingly, with the single exception of the boarfish, *Capros aper*, (Linnaeus, 1758), all species are of commercial interest, either for human consumption or for aquaculture and/or industry (ICES, 2018b, 2020). Consequently, the exploitation of these species by fisheries can affect the compositional change (Trindade-Santos *et al.*, 2020, 2022) of these systems resulting in a cascading effect of predators and prey (Lafferty & Kuris, 2002; Friedland *et al.*, 2019; Hernvann *et al.*, 2020; Wilson & Kimmel, 2021).

### Gotelli framework

The Gotelli framework is a novel approach based on the analyses of long term (at least twenty years) time series, the work undertaken by Gotelli *et al.* (Gotelli *et al.*, 2021) classified species into one of seven categories of temporal change, including directional and non-directional, and is based on the ordered presence and absence of species through time. Their study found that only a small proportion of species contributed to the compositional change found and my work finds similar results. Furthermore, my findings show there may be different drivers of reorganisation at play since there are clear distinctions between systems. For example, only on the west coast do I find species in the ‘diverging decreasing’ category. This group represents species that are decreasing over the time series but that were initially present and this type of change can often be a precursor to local extinction (Tilman *et al.*, 2017; Sánchez-Bayo & Wyckhuys, 2019). One such species is the solenette, *Buglossidium luteum*, (Risso, 1810), which is also in decline on the east coast but was initially absent. Generally, across both systems the directional change species tend to diverge from the baseline, with only five fish falling into any convergent category. Of the direct change species, 67% also fall into the transient category, reinforcing observations that environmental factors or climatic events can be associated with arrivals of new and seldom seen species or those undergoing range expansion or shifts (Diez *et al.*, 2012; Lenoir & Svenning, 2015; Poloczanska *et al.*, 2016; Lenoir *et al.*, 2020).

### Core or transient

An important distinction between species types within an assemblage is how persistent they are through time (Grinnell, 1922), i.e., are they core or transient? Studies have shown that core and transient species contribute to biodiversity in different ways - this can be in terms of how abundant they are or in the shape of their species abundance distributions (Magurran & Henderson, 2003; Helden, 2021). Scale and heterogeneity of environment can be important factors in determining species persistence in an assemblage (Magurran & Henderson, 2003; White & Hurlbert, 2010; Coyle *et al.*, 2013; Umaña *et al.*, 2017) with core species tending to be more abundant and habitat specific than transients (Magurran, 2007). However, in this thesis, despite their distinct habitats, I find a substantial overlap of core species between systems. Nevertheless, it is interesting to note that core species can also be functionally rare, reinforcing the importance of abundance in earlier findings.

## Rare species

It is well documented that any ecological assemblage comprises many rare species and only a few common ones (Preston, 1948; Rabinowitz, 1981; Gaston, 1994; Magurran & Henderson, 2011; Hull *et al.*, 2015; Hewitt *et al.*, 2016; Vermeij & Grosberg, 2018; Enquist *et al.*, 2019), this is true of both functional and taxonomic rarity although the two are not always directly linked (Leitão *et al.*, 2016b; Pavoine & Ricotta, 2021; Tóth *et al.*, 2022; White *et al.*, 2022). Here I choose the upper quartile of species for each system using two simple forms of rarity, how widespread a species is (taxonomic) and how distinct a species' trait combination is in relation to its neighbours (functional) and designate these species as restricted (taxonomic) or rare (functional). Past work has tended to focus on the contributions rare or common species make to species richness patterns, mainly highlighting the greater contributions made by common species (Vázquez & Gaston, 2004; Bregović *et al.*, 2019; Van Schalkwyk *et al.*, 2019). Change in functional diversity, however, tends to be driven by rare species rather than common ones (Mouillot *et al.*, 2013c; Jain *et al.*, 2014; Leitão *et al.*, 2016b; White *et al.*, 2022) although perhaps a more accurate description would be to suggest that rare and common species contribute in different ways to functional diversity (Chapman *et al.*, 2018). Species with more diverse trait combinations such as those described in this work as rare are often considered to contribute positively to ecosystem functioning (Díaz & Cabido, 2001). My analyses suggests that these influential rare species are not only distinct to coastal system but also generally uncoupled with taxonomic rarity.

## Connections

Connections between the classifications of species, particularly when examining functional rarity, are of potential interest as they highlight the perhaps counter intuitive fact that a species can be temporally persistent in an assemblage and yet be functionally rare (or taxonomically rare in some cases). One such species is the previously mentioned American plaice, *Hippoglossoides platessoides* (Fabricius, 1780) which is always present, widespread but functionally rare on both coasts. Another species that exhibits these features on the west coast is the blue whiting, *Micromesistius poutassou*, (Risso, 1827) but although still functionally rare, core and widespread on the east, it is there classified as recurrent (see section 6.2.3 for details and Figure 6.2 for exemplification). Relationships such as these can be potential indicators of future changes, such as the increase of functionally rare (divergent) species to assemblages (Carrington *et al.*, 2021; Ohlert *et al.*, 2022).

## *Strengths and weaknesses of these approaches*

Identifying key rare species in this way and linking them with types of contribution to compositional change in assemblages can prove to be important in the maintenance of sustainable fisheries and successful marine planning (Brown *et al.*, 2015; Nielsen *et al.*, 2018b; Albuquerque & Astudillo-Scalia, 2020). There are additional benefits to be found in the implementation of approaches such as those studied here as they give a fuller picture of what is

happening and who are the strongest in the face of anthropogenic challenges, and the most influential in contributing to compositional change.

However, there are also some limitations in these approaches, for example, the Chao-Ricotta method is less helpful in identifying species contributing to compositional change when considering all species equally ( $q_0$ ). The numbers of species identified as contributing to direct change using the Gotelli framework are small and this approach requires time series of at least twenty years to provide meaningful results (Gotelli *et al.*, 2021) which may not be appropriate for all data. Assigning the values of core and transient to species after applying a selected cut-off, whilst not completely arbitrary is still subjective and a different initial choice could affect results. Similarly, the chosen designation of rarity (use of the upper quartile (75%)) could be narrowed or widened to include more or less species, leading to different results depending on initial user choice.

## 6.5 Conclusion

In conclusion, this chapter describes various methods of quantifying compositional change and the species contributing to it. As with previous chapters, there is evidence of differences between the coastal systems despite their close geographic proximity and similar fish inhabitants. My main findings suggest that only a small number of species contribute to compositional change when considering their contributions through the lens of Hill numbers  $q_1$  (equivalent to exponential Shannon) and  $q_2$  (reciprocal of Simpson) (see Chapter 2.3 for details on these Hill numbers) and show that although levels of contribution differ, the species themselves are largely consistent across systems. Conversely, when looking at the presence absence of species populations in the Gotelli classification, I find subtle differences between systems, with different species being responsible for the directed change categories.

Approaches such as those outlined in this chapter can help to identify key species that are influential in compositional change. These species can be important pointers towards the condition of a system changes in their presence and/or abundance can have cascading effects on the system and their neighbours (Frank *et al.*, 2005; Casini *et al.*, 2009). These are important factors to take account of when planning any conservation or fisheries policies and methods such as the Chao-Ricotta framework take the first steps towards a practical solution to these issues.

This chapter aimed to build on the findings made in the first three research chapters (see Chapters 3, 4 and 5) by looking at species identities and quantifying the contributions made to compositional change in these systems. These methods can help provide accessible frameworks to aid conservation and/or marine planning and fisheries management and underline the importance of a multi-faceted approach to biodiversity assessment (Magurran *et al.*, 2019). I will explore these issues further in the final discussion (see Chapter Seven).



## Chapter Seven – General Discussion



*Buckhaven Harbour, circa 1904*

## Chapter Seven – General Discussion

### 7.1 Background

Human impacts and anthropogenic challenges have led to many changes in marine biodiversity (Bianchi *et al.*, 2000; Gifford *et al.*, 2009; Magurran *et al.*, 2015b; Pecl *et al.*, 2017; Pinheiro *et al.*, 2018; Halpern *et al.*, 2019; Emblemsvåg *et al.*, 2020; Myers *et al.*, 2021; Pacoureau *et al.*, 2021; Oke *et al.*, 2022), which in turn can lead to the restructuring of ecosystems (Magurran, 2016). In this thesis I aimed to gain an understanding of the degree of change taking place in the biodiversity of marine fish assemblages around Scotland and of the potential processes responsible for these patterns. Knowledge behind the patterns and processes in biological diversity (Mouillot *et al.*, 2011a; Gislason *et al.*, 2020) is crucial to aid ecological theory and assist conservation planning and management (Pauly, 2016; Chase *et al.*, 2020).

In my introduction I asked the questions outlined in the following chapters. My overarching question was “how is the biodiversity of these Scottish fish assemblages changing over both time and space?” and each chapter addresses a particular aspect within this theme.

#### 7.1.1 Chapter Three – Taxonomic diversity – changes in diversity over three decades

In this chapter I asked how the taxonomic diversity of two marine fish assemblages from around the Scottish coast has changed over three decades and identified the dominant species in these systems. My results suggest that despite the close geographic proximity of the coastal systems (Heessen *et al.*, 2015), temporal trends in taxonomic diversity are spatially heterogeneous, with differences in both direction and strength of patterns found. Additionally, this chapter points to the fact that there have been marked temporal changes in the dominance structure of Scottish marine assemblages over the last three decades (Moyes & Magurran, 2019). These changes include not only shifts in the abundance of the most dominant species but also in the identities of these important species.

This chapter highlights the importance of tracking changes in complementary taxonomic diversity measures such as the Hill (Hill, 1973) numbers framework used here, in addition to the identities of the species most dominant through time. A practical approach such as the one I adopted shows that there is still a lot to learn regarding the changes taking place within these fish assemblages and also reinforces the importance of the application of science in the conservation and management of fish resources (Obregón *et al.*, 2018). My approach illustrates changes sometimes hidden when examining with single metric analyses. Furthermore, it highlights the importance of multi-species analyses of harvested stocks and has implications not just for fisheries management (see section 7.2 for details) but also for consumer choices (Godfray *et al.*, 2010; Engelhard *et al.*, 2019).

### **7.1.2 Chapter Four – Functional diversity – patterns of change over thirty years**

In this second research chapter I expanded on the work of Chapter 3 by using functional diversity measures to quantify changes in the two coastal systems. I asked how these functional diversity metrics: richness, evenness and divergence (Villéger *et al.*, 2017; Magneville *et al.*, 2021), changed over the thirty years and explored the relationships between these and the taxonomic metrics used in Chapter 3. My results suggest that despite the close geographic proximity of the Celtic Sea (west) and North Sea (east) systems, their contrasting environmental and structural features (Heessen *et al.*, 2015; ICES, 2018c, 2019) lead to differences in the way that functional diversity responds at the assemblage level.

This chapter also examined the correlations between selected taxonomic diversity measures and the functional diversity metrics, revealing changes in the hierarchical clustering over the three decades. This chapter reinforces the view that examining the basic biology and trait combinations of fish species can help to improve our understanding of their ability to adapt and thrive leading in turn, to better sustainability (Hammer *et al.*, 1993; Winemiller, 2005; Karp *et al.*, 2019). This is of particular importance in current times (van Gemert *et al.*, 2018; Cochrane, 2021) as there are many anthropogenic challenges facing fish species including overfishing (Frank *et al.*, 2016; Trindade-Santos *et al.*, 2020) and climate change (Jacobs *et al.*, 2018).

### **7.1.3 Chapter Five – Temporal and spatial rarity – geographical patterns and changes through time**

In this chapter I asked how rarity, both taxonomic and functional, is changing over time. My results suggest that there are subtle but important differences in how trends in functional rarity relate to trends in the structural properties of the assemblages. These results also suggest that, in a departure from a null expectation, these assemblages are maintaining levels of functionality, i.e., consistent combinations of traits, even as assemblage size increases or decreases. A clearer understanding of the potential drivers of change in functional rarity can assist with more targeted conservation plans and fisheries management and it is already clear that shifts in community rarity have implications for ecosystem resilience (Mouillot *et al.*, 2013c; Leitão *et al.*, 2016a; Albuquerque & Astudillo-Scalia, 2020; Loiseau *et al.*, 2020). The findings in this chapter underline the importance of taking an integrative approach to protect, maintain and sustain fishes of higher functional rarity (Davies *et al.*, 2022; Trindade-Santos *et al.*, 2022).

The results of this chapter further highlight the importance of measuring both taxonomic and functional dimensions of diversity, in this case rarity, in any assessment processes. They also point to a theoretical deficit in biodiversity science, in relation to predicting the consequences of restructured trait abundance distributions for trends in functional diversity and ecosystem health.

### 7.1.4 Chapter Six – Compositional change and rarity

In this my final research chapter I investigated the compositional changes found in these systems. To do this I used a range of approaches, including classical beta diversity indices (Jaccard, 1908; Morisita, 1959) and two recently developed methods by Chao et al. and Gotelli et al (Chao & Ricotta, 2019; Gotelli *et al.*, 2021) which identify those species contributing most to change. Here I also categorised species according to their roles within the assemblage, i.e., their functional rarity; their spatial distribution, i.e., their taxonomic rarity; and their temporal persistence, i.e., whether they are core (present for at least two thirds of the time series) or transient (present for less than two thirds of the time series).

My results show evidence of differences between the coastal systems despite their close geographic proximity and similar fish populations (Heessen *et al.*, 2015; ICES, 2018b, 2020). Furthermore, I have demonstrated that only a small number of species contribute to compositional change when considering their contributions through the lens of Hill numbers and established that although levels of contribution differ, the species themselves are largely consistent across systems. However, the Gotelli classification found subtle differences between systems, and identified different species falling into the directed change categories. The methods illustrated here can help provide accessible frameworks to aid conservation and/or marine planning and fisheries management and underline the importance of a multi-faceted approach to biodiversity assessment (Fitzgerald *et al.*, 2022).

## 7.2 Summary

The results uncovered in this thesis highlighted the importance of focusing on assemblage level rather than species level diversity changes, not only as providing a greater understanding of the processes underlying biodiversity change but also as better indicators of sustainable fisheries and successful marine planning.

The current biodiversity crisis (Pimm *et al.*, 2014; Steffen *et al.*, 2015a; Steffen *et al.*, 2015b) is the consequence of a combination of anthropogenic impacts including over-exploitation and climate change. These factors can be seen as important drivers of community reorganisation and a better understanding of these trends can contribute to improved fisheries management practices as they examine the whole assemblage, combining the maintenance of functioning within the system whilst protecting and sustaining fish resources (Jennings *et al.*, 2014). Thus it is imperative (Bridgewater, 2016) that we balance the realities of human impact and human needs in order to keep our oceans both sustained and sustainable. It seems clear that biodiversity trends (Elahi *et al.*, 2015) are affected by various drivers and rarely by a single factor. It is crucial to regard fish assemblages as a complete ecosystem incorporating other socio-economic aims (Rodríguez-Rodríguez *et al.*, 2016) in order to be better informed in marine planning decisions and creating climate change targets. This appears to be a sound basis for the inclusion of multiple aspects of biodiversity measurement. My work suggests that species abundances could be an important factor in the diversity changes found. This is supported by a recent study examining the changes in fish abundances

by Simpson and Sims (Simpson & Sims, 2016) showing how some stocks are recovering only for us to lose others. This could, in part, be due to warming waters having an effect on marine assemblages (Simpson *et al.*, 2011) and could potentially lead to changes in the availability of fish populations such as cod (O'Brien *et al.*, 2000; Beaugrand *et al.*, 2003). This again highlights the importance of assessing whole fish assemblages as an understanding of their functioning is key to responsible fisheries (O'Connor *et al.*, 2009; Harborne & Mumby, 2011).

Current fisheries management policies (Government, 2013, 2014; Commission, 2015; Government, 2021) are largely based on the population level assessments (Government, 2013, 2014; Froese *et al.*, 2018; Government, 2021), but there is a suggestion that an ecosystem based approach could provide a better strategy (Trochta *et al.*, 2018; Piet *et al.*, 2019). This type of ecosystem based approach including both functional and taxonomic aspects often provides a better indicator of the sustainability of marine systems (Rincón-Díaz *et al.*, 2021). An understanding of the interactions and subsequent changes within marine fish assemblages (Aune *et al.*, 2018; McLean *et al.*, 2019c; Pecuchet *et al.*, 2019) can be a valuable tool in the creation of marine and fisheries policies.

### 7.3 Future directions for the field

In this thesis I have focused only on taxonomic and functional diversity but there is a third component of biodiversity, namely phylogenetic diversity which is becoming increasingly popular in biodiversity assessments (Tucker *et al.*, 2017). This aspect of biological diversity is an important one as phylogenetic diversity considers not only species identities but also their evolutionary history to ascertain how evolutionarily distinct they are from each other (Harvey & Pagel, 1991). Thus, an assemblage containing three species of fish belonging to the Gadidae family, Atlantic cod *Gadus morhua* (Linnaeus, 1758), haddock *Melanogrammus aeglefinus* (Linnaeus, 1758) and whiting *Merlangius merlangus* (Linnaeus, 1758) will be less diverse than one with three species from different families. For example, a Thornback ray *Raja clavata* (Linnaeus, 1758) from the Rajidae family, a Lemon sole *Microstomus kitt* (Walbaum, 1792) from the Pleuronectidae family and an Atlantic mackerel *Scomber scombrus* (Linnaeus, 1758) from the Scombridae family. Phylogenetic distance (or difference) is measured by calculating the sums of the branch lengths between one species and another, there are numerous methods available to do this (Webb *et al.*, 2002; Webb *et al.*, 2008; Chao *et al.*, 2010; Mouquet *et al.*, 2012; Tucker *et al.*, 2017). A recent paper introduced the concept of an integrated framework for alpha diversity (Chao *et al.*, 2021). This approach combines the three dimensions of diversity as a unified framework of Hill numbers and provides a statistically robust method to compare change in the different facets.

Although there have been studies examining changes in the phylogenetic diversity of terrestrial taxon such as plants (Winter *et al.*, 2009; Li *et al.*, 2019; Crockett *et al.*, 2022; Doby *et al.*, 2022) or birds (Monnet *et al.*, 2014; Voskamp *et al.*, 2017) and in freshwater fishes (Alberdi & Gilbert, 2019; Lin *et al.*, 2021; Cano-Barbacid *et al.*, 2022; Liu *et al.*, 2022) where phylogenies are well resolved, there has been less work in the marine realm. However, the advent of resources such as the Fish Tree of Life (Rabosky *et al.*, 2018) and the Open Tree of Life

(<https://tree.opentreeoflife.org/about/open-tree-of-life>) along with R packages, fishtree (Chang *et al.*, 2019) and rotl (Michonneau *et al.*, 2016) to interact with them mean that it is now much easier to access fish phylogenies and investigate the evolutionary change within marine assemblages such as the coastal regions of Scotland. The addition of this third dimension of diversity adds an extra layer to assemblage level assessments of biodiversity change and can lead to an improved understanding of the interactions taking place within these regions (Doxa *et al.*, 2016; Jarzyna & Jetz, 2016; Smiley *et al.*, 2020; Liu *et al.*, 2022; Qiao *et al.*, 2022).

This thesis does not examine the possible socio-economic consequences of fisheries decline; however, this remains a possible avenue for future research. Worldwide, the consequences of overfishing have had a catastrophic effect on many fish populations and there is a real need to examine fishing policies alongside human needs (Cochrane, 2021; Williams *et al.*, 2021). Although this is of a more critical need in parts of the world where fish is the main source of protein in the diet (Stoffle), it is also important in regions where fishing as a commercial industry is historically the main source of employment (Smith, 2012). It is important to be able to relate to the inherent cultures (McGoodwin, 2001) in fishing communities and to differentiate between those. In many developing countries fishing is essential for survival (Stoffle) whilst in developed countries such as the UK the fishing industry has been the main means of livelihood in many coastal communities (Brookfield *et al.*, 2005) and is also important for economic prosperity. Aside from the obvious survival and prosperity there are often many other reasons for fishing (Young *et al.*, 2016), whether it is based on family ties (van der Valk & De Vos, 2016), the coastal landscape (Smith *et al.*, 2016) or simply the lack of other career opportunities in the area.

Historically, much of Scotland's coastal region was dominated by the fishing industry (Smith, 2012) and it was the career of choice for many either through desire or necessity. This landscape has changed dramatically since the mid-20<sup>th</sup> century, and it seems unlikely that the fishing industry is a top choice of occupation for many at the current time. Nevertheless, fish plays a large role in Scotland's economy and if we want this to continue it is critical that we do our utmost to preserve the trade, and for this to happen we need first to address the issues affecting it. Ultimately the understanding of the underlying dynamics of the communities is vital in order to properly plan and manage for future sustainability (Stead, 2005), particularly if we are to avoid any decline in the deprivation measure (Noble *et al.*, 2006) around these coastal areas. Future work in this sector could include the assessment of socio-economic impacts (Stead, 2005) in the coastal regions analysed in this thesis. There are extensive landings and vessel information for the last hundred years available from Scottish Government (Government, 2017), in addition to socio-economic studies (Government, 2002) and these could be used to map fisheries declines to socio-economic status in these regions. There are also data available from Scottish Government on the deprivation index of Scottish areas (Scottish Index of Multiple Deprivation (SIMD)) (Government, 2016), these can highlight potential areas where the loss of the fishing industry has had detrimental impacts on the human populations therein. The Social Market Foundation (<https://www.smf.co.uk/publications/>) report in 2017 found that some coastal areas of Scotland were among the most deprived in the United Kingdom. Although there have been studies into the socio-economic effects of the decline of the fishing industry undertaken from a social science point of view (Brookfield *et al.*, 2005;

Nadel-Klein, 2020), including a Scottish Government publication in 2009 (Jamieson *et al.*, 2009), it would be interesting to examine the relationship between the fishing industry and the biodiversity of these regions. The maintenance of fish diversity is of the utmost importance, but this should be done in a manner that is sustainable and beneficial for both the fish communities and their human counterparts (Stead, 2005; Symes & Phillipson, 2009; Ban, 2019).

This thesis aimed to quantify biodiversity change in the coastal assemblages of marine fish around Scotland and understand if systems on the east and west coasts exhibit similar patterns of change despite the heterogeneity of their habitats. My work identified key differences between the two coastal systems including changes in the dominance structure over the thirty year period and uncovered links with the underlying structure of assemblages and the rarity of species. The results of my thesis reinforce the importance of taking a whole assemblage view of fisheries assessments as they underline the cascading effects of changing species richness within a community and provide stronger links with the conservation priorities for marine fish biodiversity (Jennings *et al.*, 2014). I hope that future work can continue this trend and therefore provide a basis for strong, sustainable fisheries that will protect and maintain these valuable natural resources.

This thesis fills an important gap in the current knowledge and understanding around fisheries science, by applying a range of metrics and frameworks that inform diversity change, both spatial and temporal, as applied to the assemblage level. This work can provide the basis for an integrated practical solution to the issues raised around ineffective fisheries management and conservation/marine protection plans. One potential application for some of my work could address the possible consequences for an assemblage if key species such as those most influential in compositional change as suggested in Chapter 6 – Chao-Ricotta approach (Chao & Ricotta, 2019) and Gotelli framework (Gotelli *et al.*, 2021) are removed or introduced to assemblages. Gaining an understanding of the potential outcomes can clarify key questions around fishing practices such as total allowable catches within certain areas and the policies around no-take or multiple-use zones in marine protected areas.

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## Appendices



*Stornoway Harbour, circa 1921*

## Appendix 2

```
# Load Libraries
library(tidyverse)
library(knitr)

# Resampling code
rarefysamples<-function(Year, SampleID, Species, Abundance,
                        resamps) {

  rareftab<-data.frame(array(NA,dim=c(0,3)))
  # getting vector with number of samples per year
  nsamples<-c()
  for(y in unique(Year)){
    nsamples<-c(nsamples, length(unique(SampleID[Year==y])))
  }
  t<-1
  minsample<-min(nsamples)
  for(repeats in 1:resamps){
    raref<-data.frame(array(NA,dim=c(1,3)))
    names(raref)<-c("Year","Species","Abundance")
    for(y in unique(Year)){
      # getting samples for this year
      samps<-unique(SampleID[Year==y])
      # re-sampling samples to equalise number of samples
      sam<-as.character(sample(samps,minsample,replace=T))
      # getting data that belongs to bootstrapped samples
      rarefyear<-data.frame(SampleID[which(SampleID %in% sam & Year == y)],Species[which(Sa
mpleID %in% sam & Year == y)],Abundance[which(SampleID %in% sam & Year == y)])
      names(rarefyear)<-c("SampleID", "Species", "Abundance")
      # calculating pooled abundances of each species to store
      spabun<-tapply(as.numeric(rarefyear[,3]),as.character(rarefyear[,2]),sum)
      spar<-data.frame(rep(y, length(spabun)),names(spabun),spabun, row.names=NULL)
      names(spar)<-c("Year", "Species", "Abundance")
      raref<-rbind(raref,spar)
    }
    # calculating year by species table of abundance
    rareftab<-rbind(rareftab,cbind(rep(repeats,dim(raref)[1]),raref))
  }
  return(rareftab)
}

# Read the data
TSall<-read.csv("ScottishFish2016.csv")

# Call the function
TS2<-select(TSall, coast, Year, Species, tot, lat)
TS2$samplat<-paste(TS2$coast, TS2$Year, TS2$lat)
TS<-as.data.frame(TS2 %>% group_by(Year, Species, lat, samplat) %>% summarise(totN=sum(to
t)))

TSrf<-list()
IDs<-unique(TS$lat)
```

```

for(i in 1:length(IDs)){
  data<-TS[TS$lat==IDs[i],]
  TSrf[[i]]<-rarefysamples(data$Year, data$samplat, data$Species, data$totN, 1)
}
names(TSrf)<-IDs

rf<-do.call(rbind, TSrf)
rf<-data.frame(rf, ID=rep(names(TSrf), times=unlist(lapply(TSrf, nrow))))
rf<-rf[!is.na(rf$Year),-1]

# Save output as rds file for use in each chapter
saveRDS(rf, "resampledData.rds")

```

**Appendix 2.1** Code block shows the resampling code common to all research chapters (3, 4, 5 and 6)

Species	Coast
<i>Agonus cataphractus</i>	Both
<i>Alosa alosa</i>	Both
<i>Alosa fallax</i>	Both
<i>Amblyraja radiata</i>	Both
<i>Ammodytes marinus</i>	Both
<i>Ammodytes tobianus</i>	East
<i>Anarhichas lupus</i>	Both
<i>Anarhichas minor</i>	East
<i>Anguilla anguilla</i>	Both
<i>Aphia minuta</i>	Both
<i>Arctozenus risso</i>	East
<i>Argentina silus</i>	Both
<i>Argentina sphyraena</i>	Both
<i>Argyropelecus hemigymnus</i>	West
<i>Argyropelecus olfersii</i>	West
<i>Arnoglossus imperialis</i>	Both
<i>Arnoglossus laterna</i>	Both
<i>Balistes capriscus</i>	West
<i>Belone belone</i>	Both
<i>Blennius ocellaris</i>	East
<i>Brama brama</i>	Both
<i>Brosme brosme</i>	Both
<i>Buglossidium luteum</i>	Both
<i>Callionymus lyra</i>	Both
<i>Callionymus maculatus</i>	Both
<i>Callionymus reticulatus</i>	Both
<i>Capros aper</i>	Both

<b>Species</b>	<b>Coast</b>
<i>Cepola macrophthalmalma</i>	West
<i>Chelidonichthys cuculus</i>	Both
<i>Chelidonichthys lastoviza</i>	Both
<i>Chelidonichthys lucerna</i>	Both
<i>Chirolophis ascanii</i>	Both
<i>Ciliata septentrionalis</i>	Both
<i>Clupea harengus</i>	Both
<i>Coelorinchus caelorhincus</i>	West
<i>Conger conger</i>	Both
<i>Coryphaenoides rupestris</i>	West
<i>Cottunculus microps</i>	East
<i>Crystallogobius linearis</i>	Both
<i>Cyclopterus lumpus</i>	Both
<i>Dicentrarchus labrax</i>	East
<i>Diplecogaster bimaculata</i>	Both
<i>Dipturus batis</i>	Both
<i>Echiichthys vipera</i>	Both
<i>Echiodon drummondii</i>	Both
<i>Enchelyopus cimbrius</i>	Both
<i>Engraulis encrasicolus</i>	Both
<i>Entelurus aequoreus</i>	Both
<i>Epigonus telescopus</i>	West
<i>Etmopterus spinax</i>	West
<i>Eutrigla gurnardus</i>	Both
<i>Gadiculus argenteus</i>	Both
<i>Gadiculus thori</i>	West
<i>Gadus morhua</i>	Both
<i>Gaidropsarus mediterraneus</i>	East
<i>Gaidropsarus vulgaris</i>	Both
<i>Galeorhinus galeus</i>	Both
<i>Galeus melastomus</i>	Both
<i>Gasterosteus aculeatus</i>	Both
<i>Glyptocephalus cynoglossus</i>	Both
<i>Gymnammodytes semisquamatus</i>	Both
<i>Helicolenus dactylopterus</i>	Both
<i>Hexanchus griseus</i>	West
<i>Hippoglossoides platessoides</i>	Both
<i>Hippoglossus hippoglossus</i>	Both
<i>Hyperoplus immaculatus</i>	Both
<i>Hyperoplus lanceolatus</i>	Both

<b>Species</b>	<b>Coast</b>
<i>Labrus bergylta</i>	Both
<i>Labrus mixtus</i>	Both
<i>Lepidion eques</i>	West
<i>Lepidorhombus boscii</i>	Both
<i>Lepidorhombus whiffiagonis</i>	Both
<i>Leptoclinus maculatus</i>	East
<i>Lesueurigobius friesii</i>	Both
<i>Leucoraja circularis</i>	Both
<i>Leucoraja fullonica</i>	Both
<i>Leucoraja lentiginosa</i>	East
<i>Leucoraja naevus</i>	Both
<i>Limanda limanda</i>	Both
<i>Liparis liparis</i>	Both
<i>Liparis montagui</i>	Both
<i>Lophius budegassa</i>	Both
<i>Lophius piscatorius</i>	Both
<i>Lumpenus lampretaeformis</i>	Both
<i>Lycodes gracilis</i>	East
<i>Lycodes vahlII</i>	East
<i>Macroramphosus scolopax</i>	West
<i>Macrourus berglax</i>	West
<i>Malacocephalus laevis</i>	West
<i>Maurolicus muelleri</i>	Both
<i>Melanogrammus aeglefinus</i>	Both
<i>Merlangius merlangus</i>	Both
<i>Merluccius merluccius</i>	Both
<i>Micrenophrys lilljeborgii</i>	East
<i>Microchirus variegatus</i>	Both
<i>Micromesistius poutassou</i>	Both
<i>Microstomus kitt</i>	Both
<i>Molva dypterygia</i>	West
<i>Molva molva</i>	Both
<i>Mullus surmuletus</i>	Both
<i>Mustelus asterias</i>	Both
<i>Mustelus mustelus</i>	Both
<i>Myoxocephalus scorpioides</i>	East
<i>Myoxocephalus scorpius</i>	Both
<i>Nerophis ophidion</i>	East
<i>Pagellus bogaraveo</i>	West
<i>Parablennius gattorugine</i>	Both

<b>Species</b>	<b>Coast</b>
<i>Pholis gunnellus</i>	Both
<i>Phrynorhombus norvegicus</i>	Both
<i>Phycis blennoides</i>	Both
<i>Platichthys flesus</i>	Both
<i>Pleuronectes platessa</i>	Both
<i>Pollachius pollachius</i>	Both
<i>Pollachius virens</i>	Both
<i>Pomatoschistus lozanoi</i>	East
<i>Pomatoschistus microps</i>	Both
<i>Pomatoschistus minutus</i>	Both
<i>Pomatoschistus pictus</i>	East
<i>Pterycombus brama</i>	East
<i>Raja brachyura</i>	Both
<i>Raja clavata</i>	Both
<i>Raja montagui</i>	Both
<i>Raniceps raninus</i>	Both
<i>Rostroraja alba</i>	West
<i>Salmo trutta</i>	Both
<i>Sardina pilchardus</i>	Both
<i>Scomber scombrus</i>	Both
<i>Scomberesox saurus</i>	East
<i>Scophthalmus maximus</i>	Both
<i>Scophthalmus rhombus</i>	Both
<i>Scorpaena scrofa</i>	East
<i>Scyliorhinus canicula</i>	Both
<i>Scyliorhinus stellaris</i>	Both
<i>Sebastes norvegicus</i>	East
<i>Sebastes viviparus</i>	Both
<i>Solea solea</i>	Both
<i>Spinachia spinachia</i>	East
<i>Sprattus sprattus</i>	Both
<i>Squalus acanthias</i>	Both
<i>Stomias boa ferox</i>	West
<i>Syngnathus acus</i>	Both
<i>Syngnathus rostellatus</i>	East
<i>Syngnathus typhle</i>	East
<i>Taurulus bubalis</i>	Both
<i>Trachinus draco</i>	East
<i>Trachipterus arcticus</i>	East
<i>Trachurus trachurus</i>	Both

<b>Species</b>	<b>Coast</b>
<i>Trachyrincus murrayi</i>	East
<i>Trigla lyra</i>	West
<i>Triglops murrayi</i>	Both
<i>Trisopterus esmarkii</i>	Both
<i>Trisopterus luscus</i>	Both
<i>Trisopterus minutus</i>	Both
<i>Zenopsis conchifer</i>	West
<i>Zeugopterus punctatus</i>	Both
<i>Zeugopterus regius</i>	East
<i>Zeus faber</i>	Both
<i>Zoarces viviparus</i>	East

**Appendix 2.2** List of species used in this thesis with Coast column populated according to location, and, where only found in one system, shaded by colour (blue for the east coast and green for the west).



	<b>K</b>	<b>Lm</b>	<b>QB</b>	<b>Troph</b>	<b>Depth</b>	<b>Temp</b>	<b>Gen Time</b>	<b>Rep Guild</b>	<b>Body Shape</b>	<b>Swim Mode</b>	<b>Position Water Col</b>
<b>K</b>	NA	-0.37	0.29	-0.38	-0.26	0.18	-0.58	-0.16	-0.15	0.13	-0.08
<b>Lm</b>	-0.37	NA	-0.38	0.46	0.33	-0.1	0.72	0.07	0	-0.12	0.17
<b>QB</b>	0.29	-0.38	NA	-0.35	-0.25	0.18	-0.34	-0.01	-0.08	0.19	-0.14
<b>Troph</b>	-0.38	0.46	-0.35	NA	0.18	-0.02	0.29	0.02	0.06	-0.11	0.14
<b>Depth</b>	-0.26	0.33	-0.25	0.18	NA	-0.38	0.37	0.05	0.02	-0.42	0.24
<b>Temp</b>	0.18	-0.1	0.18	-0.02	-0.38	NA	-0.24	0.04	0.14	0.25	-0.05
<b>Gen Time</b>	-0.58	0.72	-0.34	0.29	0.37	-0.24	NA	0.05	0.08	-0.14	0.07
<b>Rep Guild</b>	-0.16	0.07	-0.01	0.02	0.05	0.04	0.05	NA	0.37	0.05	0.19
<b>Body Shape</b>	-0.15	0	-0.08	0.06	0.02	0.14	0.08	0.37	NA	0.09	-0.07
<b>Swim Mode</b>	0.13	-0.12	0.19	-0.11	-0.42	0.25	-0.14	0.05	0.09	NA	-0.1
<b>Position Water Col</b>	-0.08	0.17	-0.14	0.14	0.24	-0.05	0.07	0.19	-0.07	-0.1	NA

**Appendix 2.3** Table of pairwise correlations (Pearson) between trait values in functional analyses.

## Appendix 3

```
# Load Libraries
library(tidyverse)
library(vegan)
library(hillR)
library(GGally)
library(knitr)

# Functions

# Change format of data from Long to wide
doPivot<-function(t1) {
  m1<-as.data.frame(pivot_wider(t1, names_from=Species, values_from=Abundance))
  m1[is.na(m1)]<-0
  return(m1)
}

# Function to calculate each of the five metrics
# Here I used two methods to calculate q1 and q2
# This was just done as a double check
getAlpha<-function(x, id) {

  yr<-unique(x[, 1])
  x<-x[,-1]
  # species richness
  S=apply(x>0, 1, sum)
  # numerical abundance
  N=apply(x, 1, sum)
  # maximum abundance per species for dominance/qinf calculations
  mx=apply(x, 1, max)
  # exponential Shannon
  expShan=apply(x, 1, function(s){n<-sum(s);
    exp(-sum(s/n*ifelse(s==0,0,log(s/n))))})
  # inverse Simpson
  getInvS<-diversity(x, "inv")
  # Hill numbers h0, h1 and h2, equivalent to species richness,
# exponential Shannon and inverse Simpson respectively
  getH0<-hill_taxa(x, q=0)
  getH1<-hill_taxa(x, q=1)
  getH2<-hill_taxa(x, q=2)
  invS<-c(1, getInvS[1:(nrow(x))])[-1]
  h0<-c(1, getH0[1:(nrow(x))])[-1]
  h1<-c(1, getH1[1:(nrow(x))])[-1]
  h2<-c(1, getH2[1:(nrow(x))])[-1]

  # output data frame
  df_out<-data.frame(Year=yr, S=S, expShan=expShan, invS=invS,
    h0=h0, h1=h1, h2=h2, ID=id, N=N, mx=mx)
  return(df_out)
}

# Function to return summary statistics for printing
```

```

getSummStatistics<-function(fit, metric, lat) {
  getInt<-round(fit$coef[1], 3)
  getS1<-round(fit$coef[2], 3)
  getPval<-round(summary(fit)$coefficients[2,4], 3)
  getAdjR<-round(summary(fit)$adj.r.squared, 3)
  v<-c("metric"=metric, "intercept"=getInt,
       "slope"=getS1, "p-value"=getPval,
       "adjusted R2"=getAdjR, "latitude"=lat)
  return(v)
}

# calling the function to calculate the metrics
xd<-data.frame()

for(getID in unique(lats$ID)) {
  t11<-subset(lats, ID==getID)
  t1<-select(t11, Year, Species, Abundance)
  x<-getAlpha(doPivot(t1), getID)
  xd<-rbind(xd, x)
}
# adding the q infinity Hill number and dominance (Berger-Parker)
xd$hinf<-1/(xd$mx/xd$N)
xd$Berg<-xd$mx/xd$N

# calculating slopes and p-values for each metric
dft<-data.frame()

for(id in unique(xd$ID)){

  dfits<-c()
  f1<-subset(xd, ID==id)
  fitd<-lm(f1$h0~f1$Year)
  fits<-lm(f1$h1~f1$Year)
  fitt<-lm(f1$h2~f1$Year)
  fite<-lm(f1$N~f1$Year)
  fitf<-lm(f1$hinf~f1$Year)
  dfits<-c(dfits, id, fitd$coef[2], summary(fitd)$coefficients[2,4],
          fits$coef[2], summary(fits)$coefficients[2,4], fitt$coef[2],
          summary(fitt)$coefficients[2,4], fite$coef[2],
          summary(fite)$coefficients[2,4], fitf$coef[2],
          summary(fitf)$coefficients[2,4])
  dft<-rbind(dft, dfits)

  colnames(dft)<-c("latBand", "q0Slope", "q0Pval", "q1Slope", "q1Pval",
                 "q2Slope", "q2Pval", "NSlope", "NPval",
                 "qinfSlope", "qinfPval")
}
# ensuring the variables are numeric
k<-c(2,3,4,5,6,7,8,9,10,11)
dft[,k]<-apply(dft[,k], 2, function(x) as.numeric(as.character(x)))

# split the column to extract the coast
dft<-separate(data=dft, col=latBand, into=c("coast", "Band"),
             sep="_")
# rebuild the latitudinal band field

```

```

dft$latBand<-paste(dft$coast, dft$Band, sep="_")

# select the fields needed for the pairs correlation plot
forPairs<-select(dft, coast, q0Slope, q1Slope, q2Slope, NSlope,
                qinfSlope)

colnames(forPairs)<-c("coast", "q0", "q1", "q2", "N", "qInf")

# generate the pairs plot coloured by coastal system
dp2<-ggpairs(forPairs, columns=2:6, upper=list(continuous=wrap("cor",
                                                             size=4),lower=list(continuou
s=wrap("points", alpha=.5))),
             ggplot2::aes(colour=coast))

for(i in 1:5) {
  for(j in 1:5){
    dp2[i,j]<-dp2[i,j] +
      scale_fill_manual(values=c("#31497d", "darkseagreen")) +
      scale_colour_manual(values=c("#31497d", "darkseagreen"))
  }
}

# call the summary statistics function and print table
all<-data.frame()

for(id in unique(xd$ID)){

  f1<-subset(xd, ID==id)
  fitd<-lm(f1$h0~f1$Year)
  fits<-lm(f1$h1~f1$Year)
  fitt<-lm(f1$h2~f1$Year)
  fite<-lm(f1$N~f1$Year)
  fitf<-lm(f1$hinf~f1$Year)

  v<-getSummStatistics(fite, "N", id)
  all<-rbind(all, v)
  v<-getSummStatistics(fitd, "q0", id)
  all<-rbind(all, v)
  v<-getSummStatistics(fits, "q1", id)
  all<-rbind(all, v)
  v<-getSummStatistics(fitt, "q2", id)
  all<-rbind(all, v)
  v<-getSummStatistics(fitf, "qinf", id)
  all<-rbind(all, v)

  colnames(all)<-c("Metric", "Intercept", "Slope",
                 "p-value", "Adjusted R2", "Latitudinal Band")
}
k<-c(2,3,4,5)
all[,k]<-apply(all[,k], 2, function(x) as.numeric(as.character(x)))

```

**Appendix 3.1** Code block showing functions used in this chapter

<b>Metric</b>	<b>Intercept</b>	<b>Slope</b>	<b>p-value</b>	<b>Adjusted R2</b>	<b>Latitudinal Band</b>
N	-15055595.806	7610.444	0.014	0.165	e_10
q0	-1057.355	0.547	0.000	0.447	e_10
q1	104.148	-0.050	0.004	0.222	e_10
q2	121.879	-0.060	0.000	0.481	e_10
qinf	80.416	-0.039	0.000	0.451	e_10
N	-5642625.112	2844.324	0.010	0.204	e_11
q0	-1019.785	0.522	0.000	0.586	e_11
q1	-12.568	0.008	0.838	-0.038	e_11
q2	8.832	-0.003	0.919	-0.040	e_11
qinf	12.578	-0.005	0.734	-0.035	e_11
N	-7618036.433	3832.998	0.000	0.366	e_12
q0	-428.539	0.230	0.029	0.129	e_12
q1	114.213	-0.055	0.205	0.023	e_12
q2	95.539	-0.046	0.082	0.072	e_12
qinf	57.613	-0.028	0.038	0.115	e_12
N	-3915698.243	1974.542	0.051	0.101	e_13
q0	-389.187	0.207	0.116	0.055	e_13
q1	54.887	-0.026	0.523	-0.021	e_13
q2	47.026	-0.022	0.341	-0.002	e_13
qinf	33.647	-0.016	0.199	0.026	e_13
N	-17395.387	74.683	0.967	-0.034	e_3
q0	-1294.097	0.663	0.000	0.709	e_3
q1	-168.198	0.087	0.001	0.320	e_3
q2	-113.564	0.059	0.007	0.197	e_3
qinf	-54.123	0.028	0.058	0.088	e_3
N	-10596105.903	5354.928	0.015	0.160	e_4
q0	-890.645	0.461	0.000	0.370	e_4
q1	-90.572	0.048	0.100	0.059	e_4
q2	-63.549	0.034	0.176	0.030	e_4
qinf	-26.593	0.015	0.333	-0.001	e_4
N	6518540.226	-3188.904	0.284	0.006	e_5
q0	-881.903	0.457	0.000	0.531	e_5
q1	-68.633	0.037	0.169	0.032	e_5
q2	-25.608	0.015	0.508	-0.019	e_5
qinf	2.307	0.000	0.992	-0.034	e_5
N	-2709391.677	1556.538	0.698	-0.029	e_6
q0	-556.968	0.300	0.001	0.296	e_6
q1	-9.993	0.007	0.633	-0.026	e_6
q2	33.936	-0.015	0.338	-0.002	e_6
qinf	39.054	-0.018	0.152	0.038	e_6

<b>Metric</b>	<b>Intercept</b>	<b>Slope</b>	<b>p-value</b>	<b>Adjusted R2</b>	<b>Latitudinal Band</b>
N	5770510.452	-2683.519	0.686	-0.029	e_7
q0	-358.323	0.202	0.050	0.096	e_7
q1	-16.570	0.010	0.574	-0.023	e_7
q2	29.947	-0.014	0.380	-0.007	e_7
qinf	27.630	-0.013	0.228	0.017	e_7
N	7544902.290	-3605.401	0.460	-0.015	e_8
q0	-623.290	0.332	0.001	0.290	e_8
q1	32.060	-0.014	0.444	-0.013	e_8
q2	72.844	-0.035	0.019	0.148	e_8
qinf	55.683	-0.027	0.006	0.204	e_8
N	-388142.129	291.165	0.898	-0.034	e_9
q0	-695.355	0.369	0.000	0.335	e_9
q1	-62.752	0.034	0.169	0.032	e_9
q2	22.099	-0.009	0.580	-0.023	e_9
qinf	39.172	-0.019	0.066	0.081	e_9
N	-7890436.887	3979.864	0.003	0.254	w_1
q0	-843.260	0.441	0.002	0.277	w_1
q1	-28.425	0.017	0.732	-0.031	w_1
q2	-24.877	0.014	0.687	-0.030	w_1
qinf	-5.679	0.004	0.848	-0.034	w_1
N	-15385109.186	7748.457	0.000	0.358	w_2
q0	-1228.956	0.633	0.000	0.378	w_2
q1	44.519	-0.020	0.656	-0.028	w_2
q2	29.060	-0.013	0.632	-0.027	w_2
qinf	1.641	0.000	0.986	-0.036	w_2
N	-11135504.110	5606.580	0.001	0.307	w_3
q0	-932.326	0.486	0.000	0.390	w_3
q1	17.093	-0.006	0.917	-0.035	w_3
q2	17.671	-0.007	0.863	-0.035	w_3
qinf	13.155	-0.005	0.800	-0.033	w_3
N	-14951686.784	7519.100	0.000	0.344	w_4
q0	-1269.715	0.654	0.000	0.390	w_4
q1	-125.390	0.065	0.124	0.050	w_4
q2	-95.834	0.050	0.091	0.067	w_4
qinf	-45.513	0.024	0.124	0.050	w_4
N	-6450124.332	3244.963	0.000	0.391	w_5
q0	-965.740	0.499	0.000	0.370	w_5
q1	175.374	-0.085	0.069	0.088	w_5
q2	131.126	-0.064	0.052	0.104	w_5
qinf	58.766	-0.028	0.067	0.089	w_5

<b>Metric</b>	<b>Intercept</b>	<b>Slope</b>	<b>p-value</b>	<b>Adjusted R2</b>	<b>Latitudinal Band</b>
N	-7245903.186	3681.402	0.088	0.071	w_6
q0	-464.508	0.252	0.033	0.127	w_6
q1	74.237	-0.035	0.307	0.003	w_6
q2	88.406	-0.043	0.092	0.068	w_6
qinf	60.226	-0.029	0.049	0.103	w_6
N	-10358346.439	5236.778	0.011	0.182	w_7
q0	-702.844	0.374	0.000	0.362	w_7
q1	80.324	-0.038	0.288	0.006	w_7
q2	85.439	-0.041	0.127	0.048	w_7
qinf	51.064	-0.024	0.144	0.041	w_7
N	-8813066.517	4450.216	0.003	0.243	w_8
q0	-991.262	0.513	0.000	0.445	w_8
q1	-169.399	0.087	0.032	0.123	w_8
q2	-101.874	0.053	0.085	0.070	w_8
qinf	-51.404	0.027	0.105	0.059	w_8
N	-12169904.595	6124.101	0.001	0.305	w_9
q0	-1430.549	0.732	0.000	0.726	w_9
q1	-28.896	0.017	0.680	-0.029	w_9
q2	22.064	-0.010	0.712	-0.031	w_9
qinf	23.744	-0.011	0.455	-0.015	w_9

**Appendix 3.2** Table of summary statistics for slopes of change used in this chapter

## Appendix 4

```
# Load Libraries
library(tidyverse)
library(mFD)
library(knitr)

# Functions

# Change format of data from Long to wide
doPivot<-function(t1) {
  m1<-as.data.frame(pivot_wider(t1, names_from=Species, values_from=Abundance))
  m1[is.na(m1)]<-0
  return(m1)
}

getFunctional<-function(fx, trxa) {

  fx3<-subset(fx, Species %in% trxa$Species)
  trx<-subset(trxa, Species %in% fx$Species)

  xsp<-as.data.frame(spread(fx3, key="gID", value="Abundance"))
  xsp[is.na(xsp)]<-0

  ## organise the categorical variables
  tr2<-trx
  tr2<-tr2[-1]
  vr<-as.vector(unique(tr2$BodyShapIII_combined))
  rg<-as.vector(unique(tr2$RepGuildCombined))
  pwc<-as.vector(unique(tr2$PositionWaterColumn))
  sm<-as.vector(unique(tr2$SwimMode))
  tr3<-tr2[-1]

  ## convert to species x trait matrix
  tr4<-as.data.frame( matrix(NA, nrow(tr3), ncol(tr3),      dimnames=list(row.names(tr3),
names(tr3))))
  tr4[, "K"]<-as.numeric( tr3[, "K" ] )
  tr4[, "Lm"]<-as.numeric( tr3[, "Lm" ] )
  tr4[, "QB"]<-as.numeric( tr3[, "QB" ] )
  tr4[, "Troph"]<-as.numeric( tr3[, "Troph" ] )
  tr4[, "DepthMax"]<-as.numeric( tr3[, "DepthMax" ] )
  tr4[, "TempPrefMean"]<-as.numeric( tr3[, "TempPrefMean" ] )
  tr4[, "Generation_time"]<-as.numeric( tr3[, "Generation_time" ] )
  tr4[, "BodyShapIII_combined"]<-factor(tr3[, "BodyShapIII_combined"], levels=vr)
  tr4[, "RepGuildCombined"]<-factor(tr3[, "RepGuildCombined"], levels=rg)
  tr4[, "PositionWaterColumn"]<-factor(tr3[, "PositionWaterColumn"], levels=pwc)
  tr4[, "SwimMode"]<-factor(tr3[, "SwimMode"], levels=sm)
  tr4<-tr4[-1]
  row.names(tr4)<-tr3[,1]

  xsp<-setNames(data.frame(t(xsp[, -1])), xsp[,1])
  xsp1<-as.matrix(xsp)
  rownames(xsp1)<-1985
```



```

qx<-quality_funct_space(tr4, traits_weights=NULL,
                        nbdim=4, metric="Gower", dendro=FALSE, plot=NA)
qtr<-qx$details_funct_space$mat_coord[,1:3]
mfd<-multidimFD(qtr, xsp1)
return(list("funDiv"=mfd, "coords"=qtr))
}

# Function to return summary statistics for printing
getSummStatistics<-function(fit, metric, lat) {
  getInt<-round(fit$coef[1], 3)
  getS1<-round(fit$coef[2], 3)
  getPval<-round(summary(fit)$coefficients[2,4], 3)
  getAdjR<-round(summary(fit)$adj.r.squared, 3)
  v<-c("metric"=metric, "intercept"=getInt,
        "slope"=getS1, "p-value"=getPval,
        "adjusted R2"=getAdjR, "latitude"=lat)
  return(v)
}

# calculating slopes and p-values for each metric
dft<-data.frame()

for(id in unique(getFun$ID)){

  dfits<-c()
  f1<-subset(getFun, ID==id)
  fitd<-lm(f1$FRic~f1$Year)
  fits<-lm(f1$FDiv~f1$Year)
  fitt<-lm(f1$FEve~f1$Year)
  dfits<-c(dfits, id, fitd$coef[2], summary(fitd)$coefficients[2,4],
           fits$coef[2], summary(fits)$coefficients[2,4], fitt$coef[2],
           summary(fitt)$coefficients[2,4])
  dft<-rbind(dft, dfits)

  colnames(dft)<-c("latBand", "FRSlope", "FRPval", "FDSlope", "FDPval",
                  "FESlope", "FEPval")

}

k<-c(2,3,4,5,6,7)
dft[,k]<-apply(dft[,k], 2, function(x) as.numeric(as.character(x)))

# call the summary statistics function and print table
all<-data.frame()

for(id in unique(xd$ID)){

  f1<-subset(xd, ID==id)
  fitd<-lm(f1$FRic~f1$Year)
  fits<-lm(f1$FDiv~f1$Year)
  fitt<-lm(f1$FEve~f1$Year)

```

```

v<-getSummStatistics(fitd, "Fun. Richness", id)
all<-rbind(all, v)
v<-getSummStatistics(fits, "Fun. Divergence", id)
all<-rbind(all, v)
v<-getSummStatistics(fitt, "Fun. Evenness", id)
all<-rbind(all, v)

colnames(all)<-c("Metric", "Intercept", "Slope",
                "p-value", "Adjusted R2", "Latitudinal Band")
}
k<-c(2,3,4,5)
all[,k]<-apply(all[,k], 2, function(x) as.numeric(as.character(x)))

```

**Appendix 4.1** Code block for functions in this chapter

<b>Metric</b>	<b>Intercept</b>	<b>Slope</b>	<b>p-value</b>	<b>Adjusted R2</b>	<b>Latitudinal Band</b>
Functional Richness	-7.272	0.004	0.000	0.344	e_10
Functional Richness	-11.041	0.006	0.005	0.251	e_11
Functional Richness	-2.962	0.002	0.101	0.061	e_12
Functional Richness	-5.390	0.003	0.096	0.066	e_13
Functional Richness	-13.984	0.007	0.000	0.573	e_3
Functional Richness	-13.085	0.007	0.000	0.410	e_4
Functional Richness	-12.711	0.007	0.000	0.555	e_5
Functional Richness	-9.001	0.005	0.000	0.430	e_6
Functional Richness	-4.753	0.003	0.005	0.212	e_7
Functional Richness	-7.343	0.004	0.000	0.342	e_8
Functional Richness	-9.205	0.005	0.000	0.418	e_9
Functional Richness	-4.308	0.002	0.096	0.063	w_1
Functional Richness	-10.654	0.006	0.015	0.166	w_2
Functional Richness	-6.992	0.004	0.001	0.320	w_3
Functional Richness	-16.607	0.009	0.000	0.371	w_4
Functional Richness	-11.980	0.006	0.003	0.260	w_5
Functional Richness	-7.719	0.004	0.021	0.152	w_6
Functional Richness	-8.219	0.004	0.000	0.367	w_7
Functional Richness	-13.144	0.007	0.000	0.392	w_8
Functional Richness	-15.502	0.008	0.000	0.421	w_9
Functional Evenness	4.313	-0.002	0.105	0.056	e_10
Functional Evenness	-0.322	0.000	0.805	-0.037	e_11
Functional Evenness	1.450	-0.001	0.736	-0.031	e_12
Functional Evenness	5.112	-0.002	0.155	0.039	e_13
Functional Evenness	-6.895	0.004	0.001	0.281	e_3

<b>Metric</b>	<b>Intercept</b>	<b>Slope</b>	<b>p-value</b>	<b>Adjusted R2</b>	<b>Latitudinal Band</b>
Functional Evenness	-5.109	0.003	0.045	0.102	e_4
Functional Evenness	-2.807	0.002	0.153	0.037	e_5
Functional Evenness	0.106	0.000	0.900	-0.034	e_6
Functional Evenness	3.111	-0.001	0.188	0.027	e_7
Functional Evenness	1.657	-0.001	0.503	-0.018	e_8
Functional Evenness	-0.930	0.001	0.537	-0.021	e_9
Functional Evenness	2.859	-0.001	0.278	0.008	w_1
Functional Evenness	10.830	-0.005	0.000	0.463	w_2
Functional Evenness	6.126	-0.003	0.016	0.160	w_3
Functional Evenness	8.082	-0.004	0.008	0.197	w_4
Functional Evenness	7.278	-0.003	0.028	0.140	w_5
Functional Evenness	0.290	0.000	0.978	-0.037	w_6
Functional Evenness	0.745	0.000	0.779	-0.033	w_7
Functional Evenness	6.281	-0.003	0.018	0.155	w_8
Functional Evenness	5.860	-0.003	0.048	0.101	w_9
Functional Divergence	-7.968	0.004	0.023	0.137	e_10
Functional Divergence	-14.048	0.007	0.026	0.151	e_11
Functional Divergence	-16.330	0.009	0.000	0.339	e_12
Functional Divergence	-12.062	0.006	0.047	0.107	e_13
Functional Divergence	0.218	0.000	0.883	-0.034	e_3
Functional Divergence	-4.625	0.003	0.170	0.032	e_4
Functional Divergence	-2.056	0.001	0.490	-0.017	e_5
Functional Divergence	-3.940	0.002	0.066	0.082	e_6
Functional Divergence	-5.711	0.003	0.030	0.123	e_7
Functional Divergence	-4.587	0.003	0.034	0.116	e_8
Functional Divergence	-1.596	0.001	0.425	-0.012	e_9
Functional Divergence	3.672	-0.001	0.441	-0.014	w_1
Functional Divergence	3.683	-0.001	0.602	-0.026	w_2
Functional Divergence	9.111	-0.004	0.071	0.080	w_3
Functional Divergence	2.925	-0.001	0.721	-0.031	w_4
Functional Divergence	-10.903	0.006	0.064	0.092	w_5
Functional Divergence	0.706	0.000	0.980	-0.037	w_6
Functional Divergence	-1.686	0.001	0.484	-0.017	w_7
Functional Divergence	-3.788	0.002	0.366	-0.005	w_8
Functional Divergence	-9.780	0.005	0.044	0.106	w_9

**Appendix 4.2** Table of summary statistics for slopes of change used in this chapter

## Appendix 5

```
# Load Libraries
library(tidyverse)
library(funrar)
library(vegan)
library(knitr)
library(moments)
library(quantreg)

set.seed(123)

# Functions

# Function to calculate the three forms of rarity
getRarity<-function(fx, trxa) {

  fx3<-subset(fx, Species %in% trxa$Species)
  trx<-subset(trxa, Species %in% fx$Species)

  xsp<-as.data.frame(spread(fx3, key="gID", value="Abundance"))
  xsp[is.na(xsp)]<-0

  ## organise the categorical variables
  tr2<-trx
  tr2<-tr2[-1]
  vr<-as.vector(unique(tr2$BodyShapIII_combined))
  rg<-as.vector(unique(tr2$RepGuildCombined))
  pwc<-as.vector(unique(tr2$PositionWaterColumn))
  sm<-as.vector(unique(tr2$SwimMode))
  tr3<-tr2[-1]

  ## convert to species x trait matrix
  tr4<-as.data.frame( matrix(NA, nrow(tr3), ncol(tr3),      dimnames=list(row.names(tr3),
names(tr3))))
  tr4[, "K"]<-as.numeric( tr3[, "K"] )
  tr4[, "Lm"]<-as.numeric( tr3[, "Lm"] )
  tr4[, "QB"]<-as.numeric( tr3[, "QB"] )
  tr4[, "Troph"]<-as.numeric( tr3[, "Troph"] )
  tr4[, "DepthMax"]<-as.numeric( tr3[, "DepthMax"] )
  tr4[, "TempPrefMean"]<-as.numeric( tr3[, "TempPrefMean"] )
  tr4[, "Generation_time"]<-as.numeric( tr3[, "Generation_time"] )
  tr4[, "BodyShapIII_combined"]<-factor(tr3[, "BodyShapIII_combined"], levels=vr)
  tr4[, "RepGuildCombined"]<-factor(tr3[, "RepGuildCombined"], levels=rg)
  tr4[, "PositionWaterColumn"]<-factor(tr3[, "PositionWaterColumn"], levels=pwc)
  tr4[, "SwimMode"]<-factor(tr3[, "SwimMode"], levels=sm)
  tr4<-tr4[-1]
  row.names(tr4)<-tr3[,1]

  traitT<-compute_dist_matrix(tr4, metric="gower", center=FALSE, scale=FALSE)

  ## covert to matrix and prepare for funrar function
  xsp<-setNames(data.frame(t(xsp[, -1])), xsp[, 1])
```

```

xsp1<-as.matrix(xsp)
specT<-make_relative(xsp1)

scotFun<-funrar(specT, traitT, rel_abund=TRUE)
gd<-distinctiveness_global(traitT, di_name="global_di")
si<-mean(scotFun$Si)
dix<-as.data.frame(t(scotFun$Di))$V1
frku<-moments::kurtosis(dix)
frsk<-moments::skewness(dix)
gdku<-moments::kurtosis(gd$global_di)
gdsk<-moments::skewness(gd$global_di)
return(list("di"=mean(scotFun$Di), "gd"=mean(gd), "si"=si, "kurt"=frku, "skew"=frsk, "g
dKu"=gdku, "gdsk"=gdsk))
}

# function to calculate functional evenness
getFunCoords<-function(fx, trxar) {

fx3<-subset(fx, Species %in% trxa$Species)
trx<-subset(trxa, Species %in% fx$Species)

xsp<-as.data.frame(spread(fx3, key="gID", value="Abundance"))
xsp[is.na(xsp)]<-0

## organise the categorical variables
tr2<-trx
tr2<-tr2[-1]
vr<-as.vector(unique(tr2$BodyShapIII_combined))
rg<-as.vector(unique(tr2$RepGuildCombined))
pwc<-as.vector(unique(tr2$PositionWaterColumn))
sm<-as.vector(unique(tr2$SwimMode))
tr3<-tr2[-1]

## convert to species x trait matrix
tr4<-as.data.frame( matrix(NA, nrow(tr3), ncol(tr3),      dimnames=list(row.names(tr3),
names(tr3))))
tr4[, "K"]<-as.numeric( tr3[, "K"] )
tr4[, "Lm"]<-as.numeric( tr3[, "Lm"] )
tr4[, "QB"]<-as.numeric( tr3[, "QB"] )
tr4[, "Troph"]<-as.numeric( tr3[, "Troph"] )
tr4[, "DepthMax"]<-as.numeric( tr3[, "DepthMax"] )
tr4[, "TempPrefMean"]<-as.numeric( tr3[, "TempPrefMean"] )
tr4[, "Generation_time"]<-as.numeric( tr3[, "Generation_time"] )
tr4[, "BodyShapIII_combined"]<-factor(tr3[, "BodyShapIII_combined"], levels=vr)
tr4[, "RepGuildCombined"]<-factor(tr3[, "RepGuildCombined"], levels=rg)
tr4[, "PositionWaterColumn"]<-factor(tr3[, "PositionWaterColumn"], levels=pwc)
tr4[, "SwimMode"]<-factor(tr3[, "SwimMode"], levels=sm)
tr4<-tr4[-1]
row.names(tr4)<-tr3[,1]

xsp<-setNames(data.frame(t(xsp[, -1])), xsp[,1])
xsp1<-as.matrix(xsp)
rownames(xsp1)<-1985

qx<-quality_funct_space(tr4, traits_weights=NULL,

```

```

                                nbdim=4, metric="Gower", dendro=FALSE, plot=NA)
qtr<-qx$details_func_space$mat_coord[,1:3]
mfd<-multidimFD(qtr, xsp1)
feve<-mfd[,17]
return(feve)
}

# Function to convert from long to wide format
doPivot<-function(t1) {
  m1<-as.data.frame(pivot_wider(t1, names_from=Species, values_from=Abundance))
  m1[is.na(m1)]<-0
  return(m1)
}

# Function to assign species identities based on
# random selection (xz) for the null model
getSpeciesIdentity<-function(cl) {
  Species<-case_when(between(cl, xz$tsum[1], xz$csum[1]) ~ xz$Species[1],
    between(cl, xz$tsum[2], xz$csum[2]) ~ xz$Species[2],
    between(cl, xz$tsum[3], xz$csum[3]) ~ xz$Species[3],
    between(cl, xz$tsum[4], xz$csum[4]) ~ xz$Species[4],
    between(cl, xz$tsum[5], xz$csum[5]) ~ xz$Species[5],
    between(cl, xz$tsum[6], xz$csum[6]) ~ xz$Species[6],
    between(cl, xz$tsum[7], xz$csum[7]) ~ xz$Species[7],
    between(cl, xz$tsum[8], xz$csum[8]) ~ xz$Species[8],
    between(cl, xz$tsum[9], xz$csum[9]) ~ xz$Species[9],
    between(cl, xz$tsum[10], xz$csum[10]) ~ xz$Species[10],
    between(cl, xz$tsum[11], xz$csum[11]) ~ xz$Species[11],
    between(cl, xz$tsum[12], xz$csum[12]) ~ xz$Species[12],
    between(cl, xz$tsum[13], xz$csum[13]) ~ xz$Species[13],
    between(cl, xz$tsum[14], xz$csum[14]) ~ xz$Species[14],
    between(cl, xz$tsum[15], xz$csum[15]) ~ xz$Species[15],
    between(cl, xz$tsum[16], xz$csum[16]) ~ xz$Species[16],
    between(cl, xz$tsum[17], xz$csum[17]) ~ xz$Species[17],
    between(cl, xz$tsum[18], xz$csum[18]) ~ xz$Species[18],
    between(cl, xz$tsum[19], xz$csum[19]) ~ xz$Species[19],
    between(cl, xz$tsum[20], xz$csum[20]) ~ xz$Species[20],
    between(cl, xz$tsum[21], xz$csum[21]) ~ xz$Species[21],
    between(cl, xz$tsum[22], xz$csum[22]) ~ xz$Species[22],
    between(cl, xz$tsum[23], xz$csum[23]) ~ xz$Species[23],
    between(cl, xz$tsum[24], xz$csum[24]) ~ xz$Species[24],
    between(cl, xz$tsum[25], xz$csum[25]) ~ xz$Species[25],
    between(cl, xz$tsum[26], xz$csum[26]) ~ xz$Species[26],
    between(cl, xz$tsum[27], xz$csum[27]) ~ xz$Species[27],
    between(cl, xz$tsum[28], xz$csum[28]) ~ xz$Species[28],
    between(cl, xz$tsum[29], xz$csum[29]) ~ xz$Species[29],
    between(cl, xz$tsum[30], xz$csum[30]) ~ xz$Species[30],
    between(cl, xz$tsum[31], xz$csum[31]) ~ xz$Species[31],
    between(cl, xz$tsum[32], xz$csum[32]) ~ xz$Species[32],
    between(cl, xz$tsum[33], xz$csum[33]) ~ xz$Species[33],
    between(cl, xz$tsum[34], xz$csum[34]) ~ xz$Species[34],
    between(cl, xz$tsum[35], xz$csum[35]) ~ xz$Species[35],
    between(cl, xz$tsum[36], xz$csum[36]) ~ xz$Species[36],
    between(cl, xz$tsum[37], xz$csum[37]) ~ xz$Species[37],
    between(cl, xz$tsum[38], xz$csum[38]) ~ xz$Species[38],

```

```

between(c1, xz$tsum[39], xz$csum[39]) ~ xz$Species[39],
between(c1, xz$tsum[40], xz$csum[40]) ~ xz$Species[40],
between(c1, xz$tsum[41], xz$csum[41]) ~ xz$Species[41],
between(c1, xz$tsum[42], xz$csum[42]) ~ xz$Species[42],
between(c1, xz$tsum[43], xz$csum[43]) ~ xz$Species[43],
between(c1, xz$tsum[44], xz$csum[44]) ~ xz$Species[44],
between(c1, xz$tsum[45], xz$csum[45]) ~ xz$Species[45],
between(c1, xz$tsum[46], xz$csum[46]) ~ xz$Species[46],
between(c1, xz$tsum[47], xz$csum[47]) ~ xz$Species[47],
between(c1, xz$tsum[48], xz$csum[48]) ~ xz$Species[48],
between(c1, xz$tsum[49], xz$csum[49]) ~ xz$Species[49],
between(c1, xz$tsum[50], xz$csum[50]) ~ xz$Species[50],
between(c1, xz$tsum[51], xz$csum[51]) ~ xz$Species[51],
between(c1, xz$tsum[52], xz$csum[52]) ~ xz$Species[52],
between(c1, xz$tsum[53], xz$csum[53]) ~ xz$Species[53],
between(c1, xz$tsum[54], xz$csum[54]) ~ xz$Species[54],
between(c1, xz$tsum[58], xz$csum[58]) ~ xz$Species[55])
return(Species)
}

# Loop for null model
its<-1000

df<-as.data.frame(xz$Species)
colnames(df)<- "Species"

tot<-sum(xz$Abundance)

for(k in 1:its) {
  res<-c()
  res2<-c()
  res3<-c()
  nc<-c()
  sf<-c()
  ev<-c()
  fe<-c()
  ku<-c()
  sk<-c()
  ku2<-c()
  sk2<-c()
  trxx<-trx[4:14]
  trxx[]<-lapply(trxx, sample)
  trxx$oldspecies<-trx$oldspecies
  trxx$coast<-trx$coast
  trxx$Species<-trx$Species
  trxr2<-trxx[, c(12, 13, 14, 1,2,3,4,5,6,7,8,9,10,11)]
  for(n in unique(nseq)) {
    c1<-sample(1:tot, n, replace=FALSE)
    d1<-as.data.frame(getSpeciesIdentity(c1))
    d1$Abundance<-1
    colnames(d1)<-c("Species", "Abundance")
    fx<-as.data.frame(d1 %>% group_by(Species) %>%
      summarise(Abundance=sum(Abundance)))
    trxr<-subset(trxr2, Species %in% fx$Species)
    siEv<-diversity(doPivot(fx), "inv")
  }
}

```

```

fx$gID<-1985
res<-c(res, getRarityDi(fx, trxar))
res2<-c(res2, getRarity(fx, trxar)$si)
res3<-c(res3, getRarityGD(fx, trxar))
fco<-getFunCoords(fx, trxar)
ku<-c(ku, getRarity(fx, trxar)$kurt)
sk<-c(sk, getRarity(fx, trxar)$skew)
ku2<-c(ku2, getRarity(fx, trxar)$gdKu)
sk2<-c(sk2, getRarity(fx, trxar)$gdsK)
sf<-c(sf, length(fx$Species))
ev<-c(ev, siEv)
nc<-c(nc, n)
fe<-c(fe, fco)
print(k)

resf<-as.data.frame(res)
resb<-as.data.frame(res2)
resg<-as.data.frame(res3)
resc<-as.data.frame(sf)
resd<-as.data.frame(ev)
resn<-as.data.frame(nc)
resfe<-as.data.frame(fe)
resku<-as.data.frame(ku)
ressk<-as.data.frame(sk)
resgdk<-as.data.frame(ku2)
resgds<-as.data.frame(sk2)
all<-cbind(resb, resf, resg, resd, resn, resfe, resku,
           ressk, resgdk, resgds)
colnames(all)<-c("Scarc", "Dist", "G1Dist", "spR", "simpInv", "n", "FEve",
               "kurt", "skew", "glKurt", "glSkew")
all$iter<-k
}
alldf<-rbind(alldf, all)
}

alldf$simpEv<-alldf$simpInv/alldf$spR

# Function to return summary statistics for printing
getSummStatistics<-function(fit, metric, lat) {
  getInt<-round(fit$coef[1], 3)
  getS1<-round(fit$coef[2], 3)
  getPval<-round(summary(fit)$coefficients[2,4], 3)
  getAdjR<-round(summary(fit)$adj.r.squared, 3)
  v<-c("metric"=metric, "intercept"=getInt,
       "slope"=getS1, "p-value"=getPval,
       "adjusted R2"=getAdjR, "latitude"=lat)
  return(v)
}

# call the summary statistics function and print table
all<-data.frame()

for(id in unique(xd$latBand)){

  f1<-subset(xd, latBand==id)
  fitd<-lm(f1$distinct~f1$Year)

```



```

fits<-lm(f1$scarcity~f1$Year)
fitt<-lm(f1$S~f1$Year)
fite<-lm(f1$N~f1$Year)
fitp<-lm(f1$glDist~f1$Year)
fitf<-lm(f1$SimpEven~f1$Year)

v<-getSummStatistics(fite, "N", id)
all<-rbind(all, v)
v<-getSummStatistics(fitd, "Fun", id)
all<-rbind(all, v)
v<-getSummStatistics(fits, "Tax", id)
all<-rbind(all, v)
v<-getSummStatistics(fitt, "S", id)
all<-rbind(all, v)
v<-getSummStatistics(fitp, "FunNoAb", id)
all<-rbind(all, v)
v<-getSummStatistics(fitf, "SimpEven", id)
all<-rbind(all, v)

colnames(all)<-c("Metric", "Intercept", "Slope",
               "p-value", "Adjusted R2", "Latitudinal Band")
}

k<-c(2,3,4,5)
all[,k]<-apply(all[,k], 2, function(x) as.numeric(as.character(x)))

```

**Appendix 5.1** Code block including null model

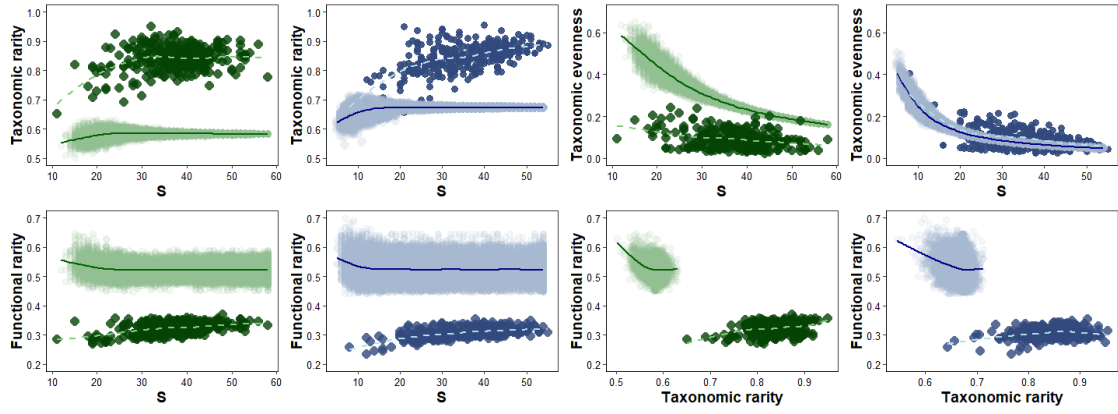
<b>Metric</b>	<b>Intercept</b>	<b>Slope</b>	<b>p-value</b>	<b>Adjusted R2</b>	<b>Latitudinal Band</b>
N	-15055595.806	7610.444	0.014	0.165	e_10
Fun	-1.775	0.001	0.000	0.360	e_10
Tax	-3.072	0.002	0.007	0.196	e_10
S	-1057.355	0.547	0.000	0.447	e_10
FunNoAb	2.290	-0.001	0.000	0.398	e_10
SimpEven	5.263	-0.003	0.000	0.431	e_10
N	-5642625.112	2844.324	0.010	0.204	e_11
Fun	-1.751	0.001	0.021	0.163	e_11
Tax	-5.238	0.003	0.023	0.159	e_11
S	-1019.785	0.522	0.000	0.586	e_11
FunNoAb	1.711	-0.001	0.042	0.122	e_11
SimpEven	6.467	-0.003	0.057	0.103	e_11
N	-7618036.433	3832.998	0.000	0.366	e_12
Fun	-1.070	0.001	0.032	0.124	e_12
Tax	-3.705	0.002	0.066	0.084	e_12

<b>Metric</b>	<b>Intercept</b>	<b>Slope</b>	<b>p-value</b>	<b>Adjusted R2</b>	<b>Latitudinal Band</b>
S	-428.539	0.230	0.029	0.129	e_12
FunNoAb	0.392	0.000	0.977	-0.036	e_12
SimpEven	3.398	-0.002	0.057	0.092	e_12
N	-3915698.243	1974.542	0.051	0.101	e_13
Fun	-0.621	0.000	0.308	0.003	e_13
Tax	-3.952	0.002	0.118	0.054	e_13
S	-389.187	0.207	0.116	0.055	e_13
FunNoAb	0.616	0.000	0.715	-0.032	e_13
SimpEven	4.063	-0.002	0.137	0.046	e_13
N	-17395.387	74.683	0.967	-0.034	e_3
Fun	-0.639	0.000	0.052	0.094	e_3
Tax	0.328	0.000	0.670	-0.028	e_3
S	-1294.097	0.663	0.000	0.709	e_3
FunNoAb	2.306	-0.001	0.000	0.516	e_3
SimpEven	-0.466	0.000	0.714	-0.030	e_3
N	-10596105.903	5354.928	0.015	0.160	e_4
Fun	-1.623	0.001	0.000	0.343	e_4
Tax	-0.882	0.001	0.183	0.028	e_4
S	-890.645	0.461	0.000	0.370	e_4
FunNoAb	1.773	-0.001	0.001	0.281	e_4
SimpEven	0.316	0.000	0.910	-0.034	e_4
N	6518540.226	-3188.904	0.284	0.006	e_5
Fun	-0.697	0.000	0.090	0.065	e_5
Tax	-0.043	0.000	0.535	-0.021	e_5
S	-881.903	0.457	0.000	0.531	e_5
FunNoAb	2.038	-0.001	0.003	0.242	e_5
SimpEven	1.492	-0.001	0.351	-0.003	e_5
N	-2709391.677	1556.538	0.698	-0.029	e_6
Fun	-0.781	0.001	0.035	0.114	e_6
Tax	0.807	0.000	0.923	-0.034	e_6
S	-556.968	0.300	0.001	0.296	e_6
FunNoAb	0.559	0.000	0.695	-0.029	e_6
SimpEven	1.500	-0.001	0.185	0.027	e_6
N	5770510.452	-2683.519	0.686	-0.029	e_7
Fun	-0.385	0.000	0.149	0.039	e_7
Tax	1.891	-0.001	0.223	0.018	e_7
S	-358.323	0.202	0.050	0.096	e_7
FunNoAb	1.763	-0.001	0.003	0.236	e_7
SimpEven	0.837	0.000	0.347	-0.003	e_7
N	7544902.290	-3605.401	0.460	-0.015	e_8

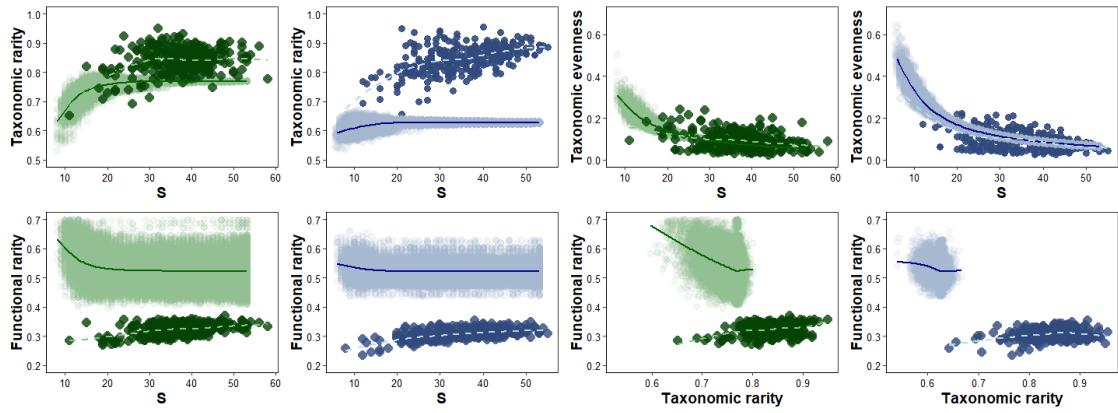
<b>Metric</b>	<b>Intercept</b>	<b>Slope</b>	<b>p-value</b>	<b>Adjusted R2</b>	<b>Latitudinal Band</b>
Fun	-0.162	0.000	0.200	0.023	e_8
Tax	0.327	0.000	0.491	-0.017	e_8
S	-623.290	0.332	0.001	0.290	e_8
FunNoAb	2.014	-0.001	0.000	0.480	e_8
SimpEven	2.241	-0.001	0.029	0.125	e_8
N	-388142.129	291.165	0.898	-0.034	e_9
Fun	-0.924	0.001	0.001	0.313	e_9
Tax	2.271	-0.001	0.183	0.028	e_9
S	-695.355	0.369	0.000	0.335	e_9
FunNoAb	1.242	0.000	0.088	0.066	e_9
SimpEven	1.210	-0.001	0.217	0.019	e_9
N	-7890436.887	3979.864	0.003	0.254	w_1
Fun	-0.435	0.000	0.177	0.031	w_1
Tax	-1.631	0.001	0.139	0.044	w_1
S	-843.260	0.441	0.002	0.277	w_1
FunNoAb	0.921	0.000	0.170	0.033	w_1
SimpEven	1.156	-0.001	0.529	-0.021	w_1
N	-15385109.186	7748.457	0.000	0.358	w_2
Fun	-0.743	0.001	0.167	0.034	w_2
Tax	-4.404	0.003	0.033	0.122	w_2
S	-1228.956	0.633	0.000	0.378	w_2
FunNoAb	2.563	-0.001	0.002	0.281	w_2
SimpEven	3.056	-0.001	0.077	0.075	w_2
N	-11135504.110	5606.580	0.001	0.307	w_3
Fun	-1.737	0.001	0.003	0.256	w_3
Tax	-1.484	0.001	0.229	0.017	w_3
S	-932.326	0.486	0.000	0.390	w_3
FunNoAb	1.525	-0.001	0.002	0.273	w_3
SimpEven	1.329	-0.001	0.519	-0.020	w_3
N	-14951686.784	7519.100	0.000	0.344	w_4
Fun	-3.523	0.002	0.000	0.437	w_4
Tax	-0.614	0.001	0.400	-0.009	w_4
S	-1269.715	0.654	0.000	0.390	w_4
FunNoAb	1.586	-0.001	0.014	0.167	w_4
SimpEven	0.051	0.000	0.984	-0.036	w_4
N	-6450124.332	3244.963	0.000	0.391	w_5
Fun	-0.670	0.000	0.323	0.001	w_5
Tax	-6.034	0.003	0.005	0.243	w_5
S	-965.740	0.499	0.000	0.370	w_5
FunNoAb	0.691	0.000	0.469	-0.017	w_5

<b>Metric</b>	<b>Intercept</b>	<b>Slope</b>	<b>p-value</b>	<b>Adjusted R2</b>	<b>Latitudinal Band</b>
SimpEven	5.961	-0.003	0.019	0.164	w_5
N	-7245903.186	3681.402	0.088	0.071	w_6
Fun	-1.148	0.001	0.054	0.098	w_6
Tax	-0.893	0.001	0.225	0.019	w_6
S	-464.508	0.252	0.033	0.127	w_6
FunNoAb	0.484	0.000	0.804	-0.035	w_6
SimpEven	2.325	-0.001	0.177	0.032	w_6
N	-10358346.439	5236.778	0.011	0.182	w_7
Fun	-0.674	0.000	0.142	0.043	w_7
Tax	-0.604	0.001	0.260	0.011	w_7
S	-702.844	0.374	0.000	0.362	w_7
FunNoAb	1.204	0.000	0.057	0.092	w_7
SimpEven	1.824	-0.001	0.207	0.022	w_7
N	-8813066.517	4450.216	0.003	0.243	w_8
Fun	-2.318	0.001	0.001	0.288	w_8
Tax	1.163	0.000	0.852	-0.034	w_8
S	-991.262	0.513	0.000	0.445	w_8
FunNoAb	1.732	-0.001	0.015	0.166	w_8
SimpEven	-0.732	0.000	0.630	-0.027	w_8
N	-12169904.595	6124.101	0.001	0.305	w_9
Fun	-3.593	0.002	0.000	0.465	w_9
Tax	-1.555	0.001	0.218	0.020	w_9
S	-1430.549	0.732	0.000	0.726	w_9
FunNoAb	1.389	0.000	0.035	0.118	w_9
SimpEven	3.668	-0.002	0.065	0.085	w_9

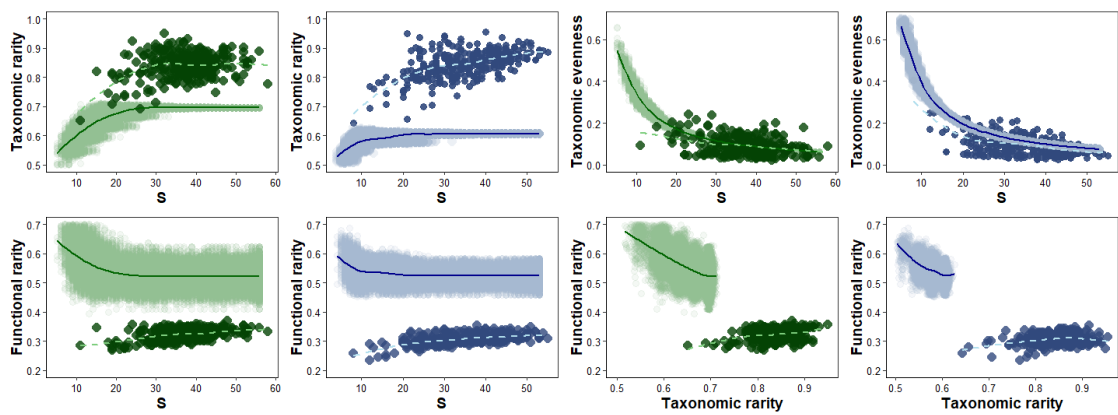
**Appendix 5.2** Table of summary statistics



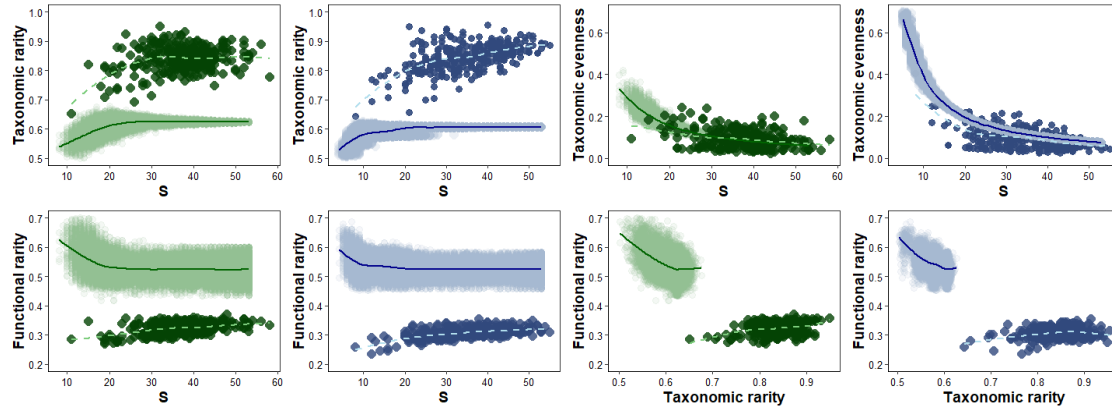
Random sample 1



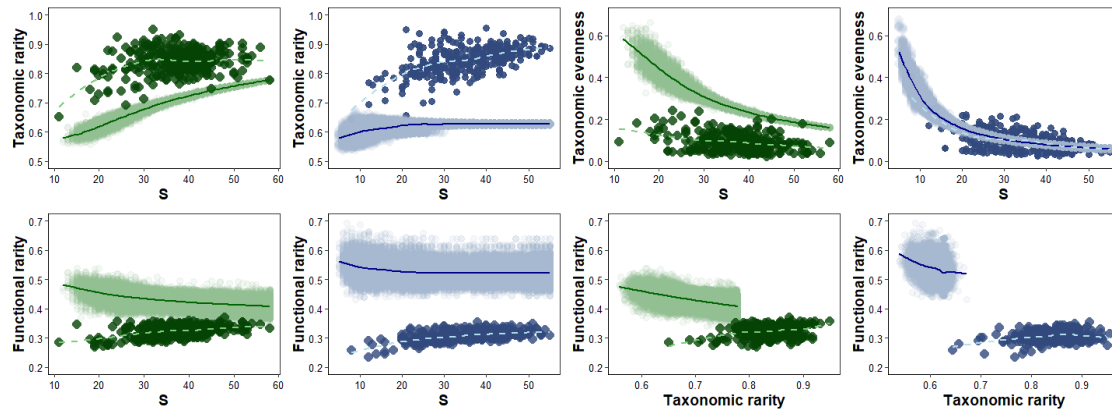
Random sample 2



Random sample 3



**Random sample 4**



**Random sample 5**

**Appendix 5.3:** Results of five different starting samples of the gamma assemblage

## Appendix 6

```
# Load Libraries
library(tidyverse)
library(tseries)
library(ade4)
library(reshape2)
library(ggpubr)
library(phytools)
library(ape)
library(funrar)
library(betapart)
library(vegan)
library(grid)
library(gridExtra)
library(ggalluvial)

# Functions

# functions to calculate the Chao Ricotta contributions, these are based on the code
provided by the 2019 Chao Ricotta paper [1]

qD <- function(p,q){
  p <- p[p>0]
  if(q!=1){
    (sum(p^q))^(1/(1-q))
  }else{
    exp(-sum(p*log(p)))
  }
}

#' new_fun computes all six classes of evenness measures.
#' @param x is an observed species abundance or frequency vector.
#' @param q.order is a vector of diversity orders: user must specify a sequence (sugg
ested range is from 0 to 2 in an increment of 0.05).
#' @return the profiles of all six classes of evenness indices listed in Table 1; see
Figure 2 for output.
new_fun <- function(x,q.order){
  FUN <- qD
  n <- sum(x)
  p <- x/n
  q_profile_evenness <- function(q){
    qDest <- FUN(p,q)
    #S <- sum(x>0)
    S <- sum(x>0)
    E1 <- ifelse(q!=1, (1-qDest^(1-q))/(1-S^(1-q)), log(qDest)/log(S))
    E2 <- ifelse(q!=1, (1-qDest^(q-1))/(1-S^(q-1)), log(qDest)/log(S))
    E3 <- (qDest-1)/(S-1)
    E4 <- (1-1/qDest)/(1-1/S)
    E5 <- log(qDest)/log(S)
    if(q==0){
      p <- p[p>0]
      nu <- abs(p - (1/S))
    }
  }
}
```

```

    nu <- nu[nu > 0]
    sub1 <- (sum(log(abs(nu)))/sum(nu>0)-(log(1-1/S)+(1-S)*log(S))/S)
    E6 <- 1-exp(sub1)
  }else{
    p <- p[p>0]
    E6 <- 1-(sum(abs(p-1/S)^q)/((1-1/S)^q+(S-1)*S^(-q)))^(1/q)
  }

  #E6 <- ifelse(q=1, 1-sum(abs(p-1/S)^(1-q))/(abs(1-1/S)^(1-q)+
  return(c(E1,E2,E3,E4,E5,E6))
}
out <- as.matrix(t(sapply(q.order, q_profile_evenness)))
colnames(out) <- c("E1", "E2", "E3", "E4", "E5", "E6")
out
}

tax_q_profile <- function(x, name1){
  x <- as.data.frame(x)
  x$q.order <- as.character(q)
  x1 <- melt(x, id.vars = c("q.order"))
  names(x1) <- c("q", "Habitat", "evenness")
  ggplot(x1, aes(q, evenness))+
    geom_line(aes(color = Habitat, group = Habitat, linetype = Habitat), size = 1.1)+
    scale_linetype_manual(values=c("dashed", "1111", "solid"))+
    theme_bw()+
    theme(axis.title = element_text(size = 14),
          axis.text = element_text(size = 12),
          legend.title = element_text(size = 14),
          legend.text = element_text(size = 12),
          strip.text = element_text(size = 14),
          legend.position = "bottom")+
    scale_x_discrete(breaks=seq(0, 2, 0.5))+
    theme(legend.key.width = unit(2,"cm"))+
    theme(plot.title = element_text(size=20, face="bold.italic",hjust = 0.5))+
    ggtitle(name1)+
    xlab("Diversity order q")
  #ylim(c(0, 1))
}

#' Gini_even computes the two Gini evenness indices mentioned in the Discussion section and in Appendix S4.
#' @param x is an observed species abundance or frequency vector.
#' @return a vector of two Gini evenness indices (non-normalized and normalized).
Gini_even <- function(x){
  x <- sort(x[x>0], decreasing = T)/sum(x)
  S <- length(x)
  ipi <- sapply(1:S, function(i) i*x[i]) %>% sum
  c("Non-normalized Gini" = (2*ipi-1)/S, "Normalized Gini" = (2*ipi-2)/(S-1))
}

dis1 <- function(x, q, type = "tax", type2 = "species", tree = NULL){
  if(type2 == "species"){
    FUN <- rowSums
  }else{
    FUN <- colSums
  }
}

```



```

if(type == "tax"){
  x <- as.matrix(x)
  x <- x[rowSums(x)>0, ]
  N <- ncol(x)
  zbar <- rowSums(x)/N
  x1 <- x[zbar>0, ]
  zbar1 <- zbar[zbar>0]
  if(q==0){
    UqN <- FUN(x==0)/((N-1)*(sum(rowSums(x)>0)))
    CqN <- FUN(x==0)/((N-1)*(sum(apply(x, 2, function(i){sum(i>0)}))))
  }else if(q==2){
    UqN <- FUN((x1-zbar1)^2)/((N^q-N)*sum(zbar1^q))
    CqN <- FUN((x1-zbar1)^2)/((1-N^(1-q))*sum(x1^q))
  }else if(q!=1){
    UqN <- FUN((x1)^q-(zbar1)^q)/((N^q-N)*sum(zbar1^q))
    CqN <- FUN((x1)^q-(zbar1)^q)/((1-N^(1-q))*sum(x1^q))
  }else{
    x2 <- x1/zbar1
    UqN <- FUN(x1*log(x2), na.rm = T)/((sum(x)*log(N)))
    CqN <- UqN
  }
}else{
  Li <- c(tree1$leaves, tree1$nodes)
  cumtree = function(a, tree){
    a <- a[names(tree$leaves)]
    for(i in 1:length(tree$parts)){
      a[1+length(a)] <- sum(a[tree$parts[[i]]])
      names(a)[length(a)] <- names(tree$parts)[i]
    }
    a
  }
  ai <- apply(x, 2, cumtree, tree1)
  wt <- apply(ai, 1, function(x1)(sum(x1))^q/sum(Li*rowSums(ai, na.rm = T)^q))
  N <- ncol(ai)
  zbar <- rowSums(ai)/N
  x1 <- ai[zbar>0, ]
  zbar1 <- zbar[zbar>0]
  Li <- Li[zbar>0]
  T1 <- sum(rowSums(x1)*Li)
  if(q==0){
    if(type2 == "species"){
      rn <- nrow(x1)
      UqN <- sapply(1:rn, function(i){(Li[i]*sum(x1[i, ]==0))})/((N-1)*sum(Li))
      CqN <- sapply(1:rn, function(i){(Li[i]*sum(x1[i, ]==0))})/((N-1)*sum(Li*rowSums(x1!
=0))))}
    }else{
      UqN <- apply(x1, 2, function(x){sum(Li[x==0])})/((N-1)*sum(Li))
      CqN <- apply(x1, 2, function(x){sum(Li[x==0])})/((N-1)*sum(Li*colSums(x1!=0)))}
    }
  }else if(q==2){
    UqN <- FUN(Li*((x1-zbar1)^2), na.rm = T)/((N^q-N)*sum(Li*zbar1^q))
    CqN <- FUN(Li*((x1-zbar1)^2), na.rm = T)/((1-N^(1-q))*sum(Li*x1^q))
  }else if(q!=1){
    UqN <- FUN(Li*((x1)^q-(zbar1)^q), na.rm = T)/((N^q-N)*sum(Li*zbar1^q))
  }
}

```

```

    CqN <- FUN(Li*((x1)^q-(zbar1)^q), na.rm = T)/((1-N^(1-q))*sum(Li*x1^q))
  }else{
    x2 <- x1/zbar1
    UqN <- FUN(Li*x1*log(x2), na.rm = T)/(T1*log(N))
    CqN <- UqN
  }
}

# c(sum(UqN), sum(CqN))
rbind(UqN, CqN)
}

#' draw_dis_spe plots the contribution of each species/node to dissimilarity (Jaccard
-type dissimilarity and Sorensen-type dissimilarity).
#' @param data is a merged table of output values with three columns corresponding to
output for q = 0, 1, 2.
#' @param title_name is the title name of plot.
#' @type indicates the type of contribution: "tax" for taxonomic and "phy" for phylog
enetic
#' @return the plot of the contribution of each species/node.
draw_dis_spe <- function(data, title_name, type = "tax"){
  colnames(data) <- c("q = 0", "q = 1", "q = 2")
  data <- melt(data)
  g <- ggplot(data, aes(x = as.factor(Var1), y = value, fill = Var2))+
  geom_col(width = 0.2)+
  facet_grid(Var2~., scales = "free_y")+
  theme_bw()+
  # ylim(c(0, max(data[, 3])))
  theme(axis.text.x = element_text(angle = 90, hjust = 1, vjust = .3),
        axis.title = element_text(size = 14),
        plot.title = element_text(hjust = 0.5))+
  guides(fill="none")+
  ggtitle(title_name)

  if(type == "tax"){
    g <- g +
    xlab("Species")+
    ylab("Species contribution")+
    scale_fill_manual(values=c("orchid", "purple", "darkorchid"))
  }else{
    g <- g +
    xlab("Species/node")+
    ylab("Species/node contribution")+
    scale_fill_manual(values=c("orchid", "purple", "darkorchid"))
  }
  return(g)
}

getMat<-function(f1) {
  widenedf<-f1 %>% spread(key=Year,value=relAbund)
  widenedf[is.na(widenedf)]<-0
  return(widenedf)
}
#####

```

```

# function to calculate Gotelli trends

getTrends<-function(x) {

  time <- rep("late",length(x))
  time[1:(round(length(x)/2))] <- "early"

  # tabulate f
  z_x <- table(x,time)

  tslen<-length(x)
  tssum<-sum(x)
  l<-c()

  for(k in 1:(tslen-1)){
    j<-abs(x[k+1]-x[k])
    l<-c(l, j)
    v<-sum(l)
  }

  bsline<-x[1]

  if(tslen>tssum) {

    rownames(z_x) <- c("absent","present")
    # get p value
    p_val <- chisq.test(z_x)$p.val

    # get early and late fractions
    f_early <- z_x["present","early"]/sum(z_x[,1])
    f_late <- z_x["present","late"]/sum(z_x[,2])

    if((f_early > f_late) & (p_val <= 0.05)) trend<--1
    if((f_early < f_late) & (p_val <= 0.05)) trend<-1
    if(p_val > 0.05) trend<-0
    runsPV<-runs.test(as.factor(x),alternative="less")
    runsTestPV<-runsPV$p.value
    if(runsTestPV<0.05) trendPlus<-10
    if(runsTestPV>0.05)trendPlus<-5
  }
  if(tslen==tssum) {
    p_val <- NA
    f_early <- NA
    f_late <- NA
    runsTestPV<-NA
    trend<-NA
    trendPlus<-NA
  }

  statSumm<-list("trendPlus"=trendPlus, "chiPval"=p_val, "runsPval"=runsTestPV,
                "trend"=trend, "bsline"=bsline)
  return(statSumm)
}
#####

```

```
# functions to calculate beta diversity metrics
```

```
getForBeta<-function(spec_df, rfid) {  
  
  yr<-unique(spec_df[, 1])  
  spec_df<-spec_df[,-1]  
  spec_df[spec_df>0]<-1  
  getBas<-beta.pair(spec_df, index.family="jac")$beta.jac  
  getT0<-beta.pair(spec_df, index.family="jac")$beta.jtu  
  getN<-beta.pair(spec_df, index.family="jac")$beta.jne  
  
  basJac<-c(1, getBas[1:(nrow(spec_df)-1)])  
  tover<-c(1, getT0[1:(nrow(spec_df)-1)])  
  nested<-c(1, getN[1:(nrow(spec_df)-1)])  
  
  df_out<-data.frame(Year=yr, J=basJac, T0=tover, N=nested, coast=rfid)  
  
  df_out<-df_out[-1,]  
  return(df_out)  
}  
  
doPivot<-function(t1) {  
  
  m1<-as.data.frame(pivot_wider(t1, names_from=Species, values_from=Abundance))  
  m1[is.na(m1)]<-0  
  return(m1)  
}  
  
getBeta<-function(x, cst) {  
  
  yr<-unique(x[, 1])  
  x<-x[,-1]  
  x2<-x  
  x2[x2>1]<-1  
  getj<-vegdist(x2, "jaccard")  
  getmh<-vegdist(x, "horn")  
  
  jacc<-c(1, getj[1:(nrow(x))])[-1]  
  mh<-c(1, getmh[1:(nrow(x))])[-1]  
  
  df_out<-data.frame(Year=yr, coast=cst, jaccD=jacc, mhorn=mh)  
  return(df_out)  
}
```

```
#####
```

```
# Function to calculate rarity
```

```
getRarity<-function(fx, trxa) {  
  
  fx3<-subset(fx, Species %in% trxa$Species)  
  trx<-subset(trxa, Species %in% fx$Species)  
  
  xsp<-as.data.frame(spread(fx3, key="gID", value="Abundance"))  
  xsp[is.na(xsp)]<-0
```

```

## organise the categorical variables
tr2<-trx
tr2<-tr2[-1]
vr<-as.vector(unique(tr2$BodyShapIII_combined))
rg<-as.vector(unique(tr2$RepGuildCombined))
pwc<-as.vector(unique(tr2$PositionWaterColumn))
sm<-as.vector(unique(tr2$SwimMode))
tr3<-tr2[-1]

## convert to species x trait matrix
tr4<-as.data.frame( matrix(NA, nrow(tr3), ncol(tr3),      dimnames=list(row.names(tr3),
names(tr3))))
tr4[, "K"]<-as.numeric( tr3[, "K"] )
tr4[, "Lm"]<-as.numeric( tr3[, "Lm"] )
tr4[, "QB"]<-as.numeric( tr3[, "QB"] )
tr4[, "Troph"]<-as.numeric( tr3[, "Troph"] )
tr4[, "DepthMax"]<-as.numeric( tr3[, "DepthMax"] )
tr4[, "TempPrefMean"]<-as.numeric( tr3[, "TempPrefMean"] )
tr4[, "Generation_time"]<-as.numeric( tr3[, "Generation_time"] )
tr4[, "BodyShapIII_combined"]<-factor(tr3[, "BodyShapIII_combined"], levels=vr)
tr4[, "RepGuildCombined"]<-factor(tr3[, "RepGuildCombined"], levels=rg)
tr4[, "PositionWaterColumn"]<-factor(tr3[, "PositionWaterColumn"], levels=pwc)
tr4[, "SwimMode"]<-factor(tr3[, "SwimMode"], levels=sm)
tr4<-tr4[-1]
row.names(tr4)<-tr3[,1]

traitT<-compute_dist_matrix(tr4, metric="gower", center=FALSE, scale=FALSE)

## convert to matrix and prepare for funrar function
xsp<-setNames(data.frame(t(xsp[, -1])), xsp[, 1])
xsp1<-as.matrix(xsp)
specT<-make_relative(xsp1)

scotFun<-funrar(specT, traitT, rel_abund=TRUE)

return(scotFun)
}

#####
# call the functions to calculate Chao Ricotta

allTops<-data.frame()

for(lb in unique(fish2$coast)) {

  f1<-subset(fish2, coast==lb)
  dft<-f1 %>% group_by(Year) %>% mutate(relAbund=Abundance/sum(Abundance))
  dft2<-select(dft, Year, Species, relAbund)
  data2<-as.data.frame(getMat(dft2))
  n1<-(length(data2)-1)

  data3<-matrix(as.numeric(as.matrix(data2[-1])), ncol=n1)
  rownames(data3)<-as.matrix(data2)[,1]

```

```

# calculate the contribution of each species to
# taxonomic dissimilarity and then plot
t01<- t(dis1(data3, 0, type = "tax", type2 = "species"))
t11 <- t(dis1(data3, 1, type = "tax", type2 = "species"))
t21 <- t(dis1(data3, 2, type = "tax", type2 = "species"))

tax_UqN_r <- cbind(t01[, 1], t11[, 1], t21[, 1])
tax_CqN_r <- cbind(t01[, 2], t11[, 2], t21[, 2])
print(draw_dis_spe(tax_UqN_r, paste("Jaccard-type taxonomic dissimilarity ", lb)))
jq<-as.data.frame(tax_UqN_r)
jq$coast<-lb
jq$Species<-rownames(jq)
allTops<-rbind(allTops, jq)
}

```

#####

```

# call the function to assign the Gotelli trends

ids<-unique(fish$coast)
df<-data.frame()
idplace<-1
for(id in ids){
  dfa<-c()
  # getting data for relevant rarefyID
  data<-fish[fish$coast==id,]
  groups<-data.frame(as.character(data$Species),as.numeric(data$Year))
  data.mat<- tapply(data$Abundance,groups, FUN=sum)
  # formatting data into species by time matrix
  data.mat[is.na(data.mat)]<-0
  #removing species that are always absent
  numSp<-dim(data.mat)[1]
  bindf<- data.mat
  bindf[bindf>0]<-1
  # create data frame to hold results
  if(!is.matrix(bindf)) bindf<-t(bindf)

  if(dim(bindf)[1]>0){
    # Loop through the data
    for (i in 1:nrow(bindf)) {
      # Extract data for a species, do the new test, save output
      z<-bindf[i,]
      trn<-getTrends(z)
      dfa<-c(id, rownames(bindf)[i],trn$chiPval, trn$trend,
            trn$runsPval, trn$trendPlus, trn$bsline, trn$tssum, trn$tslen)
      df<-rbind(df, dfa)
    }
  }
  print(id)
  data.mat<-t(apply(data.mat,1,scale))
  idplace<-idplace+numSp
}

```

```

colnames(df)<-c("coast", "Species", "chiPVal", "trend", "runsPval",
              "trendPlus", "bsline")
k<-c(3,4,5,6,7)
df[,k]<-apply(df[,k], 2, function(x) as.numeric(as.character(x)))

# assign correct names
dft<-df[1:7]

dfspN<-as.data.frame(dft %>%
  mutate(catClass=case_when(
    trend==1 & bsline==0 ~ "Diverging increasing",
    trend==1 & bsline==1 ~ "Converging increasing",
    trend==-1 & bsline==0 ~ "Converging decreasing",
    trend==-1 & bsline==1 ~ "Diverging decreasing",
    is.na(trend) ~ "No change",
    trend==0 & trendPlus==10 ~ "Recurrent",
    trend==0 & trendPlus==5 ~ "Random"
  )
)
#####

# assign core and transient
fishCT<-as.data.frame(fish %>% group_by(coast, Species) %>%
  summarise(years=n_distinct(Year)))
fishCT$coreT<-"all"
fishCTr<-as.data.frame(fishCT %>% mutate(coreT=if_else(years>19,
  "core", "transient")))
#####

# call the beta diversity functions

dffx<-data.frame()

for(cst in unique(fish2$coast)) {
  xs1<-subset(fish2, coast==cst)
  xs1<-select(xs1, Year, Species, Abundance)
  xsp<-as.data.frame(spread(xs1, key="Species", value="Abundance"))
  xsp[is.na(xsp)]<-0
  tff<-getForBeta(xsp, cst)
  dffx<-rbind(dffx, tff)
}

xd<-data.frame()

for(cst in unique(fish2$coast)) {
  t11<-subset(fish2, coast==cst)
  t1<-select(t11, Year, Species, Abundance)
  x<-getBeta(doPivot(t1), cst)
  xd<-rbind(xd, x)
}

```

```

xd<-merge(xd, dffx, by=c("Year", "coast"), all=T)

# to produce slopes for each coast

df<-data.frame()

for(cst in unique(xd$coast)) {
  x<-subset(xd, coast==cst)
  dfits<-c()
  fitd<-lm(x$jaccD~x$Year)
  fits<-lm(x$mhorn~x$Year)
  dfits<-c(dfits, cst, fitd$coef[[2]],
           summary(fitd)$coefficients[2,4], fits$coef[[2]],
           summary(fits)$coefficients[2,4])
  df<-rbind(df, dfits)
}

colnames(df)<-c("coast", "JDSlope",
               "JDPval", "MHSlope", "MHPval")

```

**Appendix 6.1** Code block showing functions used in this chapter



Coast	Species	q0	q1	q2	Gotelli Classification	Functional Rarity Value	Restricted-ness Value	Core/Transient	Functional Rarity West	Functional Rarity East	Restricted-ness West	Restricted-ness East	q0 Order	q1 Order	q2 Order
e	<i>Agonus cataphractus</i>	0.0000	0.0000	0.0000	No change	0.328	0.000	Core	Common	Common	Widespread	Widespread	110	49	46
w	<i>Agonus cataphractus</i>	0.0024	0.0000	0.0000	Random	0.331	0.300	Core	Common	Common	Widespread	Widespread	81	57	56
e	<i>Alosa alosa</i>	0.0068	0.0000	0.0000	Random	0.394	0.903	Transient	Common	Common	Widespread	Widespread	39	116	121
w	<i>Alosa alosa</i>	0.0077	0.0000	0.0000	Random	0.392	0.967	Transient	Common	Common	Restricted	Widespread	1	126	126
e	<i>Alosa fallax</i>	0.0048	0.0000	0.0000	Random	0.380	0.645	Transient	Common	Common	Widespread	Widespread	64	32	34
w	<i>Alosa fallax</i>	0.0072	0.0000	0.0000	Random	0.375	0.900	Transient	Common	Common	Widespread	Widespread	39	107	108
e	<i>Amblyraja radiata</i>	0.0000	0.0000	0.0000	No change	0.395	0.000	Core	Common	Common	Widespread	Widespread	111	30	28
w	<i>Amblyraja radiata</i>	0.0064	0.0000	0.0000	Random	0.396	0.800	Transient	Common	Common	Widespread	Widespread	49	61	62
e	<i>Ammodytes marinus</i>	0.0002	0.0041	0.0001	Random	0.372	0.032	Core	Common	Common	Widespread	Widespread	101	6	7
w	<i>Ammodytes marinus</i>	0.0034	0.0000	0.0000	Recurrent	0.371	0.433	Transient	Common	Common	Widespread	Widespread	78	39	40
e	<i>Ammodytes tobianus</i>	0.0068	0.0000	0.0000	Random	0.365	0.903	Transient	Common	Common	Widespread	Widespread	40	64	63
e	<i>Anarhichas lupus</i>	0.0005	0.0000	0.0000	Recurrent	0.351	0.065	Core	Common	Common	Widespread	Widespread	100	60	59
w	<i>Anarhichas lupus</i>	0.0074	0.0000	0.0000	Random	0.348	0.933	Transient	Common	Common	Widespread	Widespread	28	106	105
e	<i>Anarhichas minor</i>	0.0072	0.0000	0.0000	Random	0.377	0.968	Transient	Common	Common	Widespread	Restricted	1	130	130
e	<i>Anguilla anguilla</i>	0.0070	0.0000	0.0000	Random	0.324	0.935	Transient	Common	Common	Widespread	Widespread	31	112	112
w	<i>Anguilla anguilla</i>	0.0077	0.0000	0.0000	Random	0.324	0.967	Transient	Common	Common	Restricted	Widespread	2	128	128
e	<i>Aphia minuta</i>	0.0070	0.0000	0.0000	Random	0.497	0.935	Transient	Common	Funct. rare	Widespread	Widespread	32	82	84
w	<i>Aphia minuta</i>	0.0077	0.0000	0.0000	Recurrent	0.504	0.967	Transient	Funct. rare	Common	Restricted	Widespread	23	115	114
e	<i>Arctozenus risso</i>	0.0072	0.0000	0.0000	Random	0.451	0.968	Transient	Common	Funct. rare	Widespread	Restricted	2	122	120
e	<i>Argentina silus</i>	0.0005	0.0000	0.0000	Random	0.397	0.065	Core	Common	Common	Widespread	Widespread	99	23	22
w	<i>Argentina silus</i>	0.0003	0.0002	0.0000	Random	0.387	0.033	Core	Common	Common	Widespread	Widespread	91	20	23
e	<i>Argentina sphyraena</i>	0.0000	0.0002	0.0000	No change	0.372	0.000	Core	Common	Common	Widespread	Widespread	112	13	14
w	<i>Argentina sphyraena</i>	0.0000	0.0012	0.0000	No change	0.362	0.000	Core	Common	Common	Widespread	Widespread	96	11	11
w	<i>Argyropelecus hemigymnus</i>	0.0074	0.0000	0.0000	Recurrent	0.466	0.933	Transient	Funct. rare	Common	Widespread	Widespread	35	100	100
w	<i>Argyropelecus olfersii</i>	0.0077	0.0000	0.0000	Random	0.425	0.967	Transient	Funct. rare	Common	Restricted	Widespread	3	112	111
e	<i>Arnoglossus imperialis</i>	0.0053	0.0000	0.0000	Random	0.312	0.710	Transient	Common	Common	Widespread	Widespread	59	86	88
w	<i>Arnoglossus imperialis</i>	0.0050	0.0000	0.0000	Diverging increasing	0.317	0.633	Transient	Common	Common	Widespread	Widespread	55	85	87
e	<i>Arnoglossus laterna</i>	0.0046	0.0000	0.0000	Diverging increasing	0.311	0.613	Transient	Common	Common	Widespread	Widespread	66	67	68
w	<i>Arnoglossus laterna</i>	0.0040	0.0000	0.0000	Random	0.316	0.500	Transient	Common	Common	Widespread	Widespread	72	80	80
w	<i>Balistes capriscus</i>	0.0077	0.0000	0.0000	Random	0.458	0.967	Transient	Funct. rare	Common	Restricted	Widespread	4	99	97
e	<i>Belone belone</i>	0.0056	0.0000	0.0000	Random	0.374	0.742	Transient	Common	Common	Widespread	Widespread	56	69	70
w	<i>Belone belone</i>	0.0077	0.0000	0.0000	Random	0.375	0.967	Transient	Common	Common	Restricted	Widespread	5	123	123
e	<i>Blennius ocellaris</i>	0.0072	0.0000	0.0000	Random	0.334	0.968	Transient	Common	Common	Widespread	Restricted	3	128	128
e	<i>Brama brama</i>	0.0065	0.0000	0.0000	Recurrent	0.433	0.871	Transient	Common	Funct. rare	Widespread	Widespread	47	94	97
w	<i>Brama brama</i>	0.0077	0.0000	0.0000	Random	0.422	0.967	Transient	Funct. rare	Common	Restricted	Widespread	6	125	125

E	<i>Brosme brosme</i>	0.0034	0.0000	0.0000	Random	0.336	0.452	Transient	Common	Common	Widespread	Widespread	77	79	80
w	<i>Brosme brosme</i>	0.0045	0.0000	0.0000	Random	0.332	0.567	Transient	Common	Common	Widespread	Widespread	61	74	77
e	<i>Buglossidium luteum</i>	0.0043	0.0000	0.0000	Converging decreasing	0.354	0.581	Transient	Common	Common	Widespread	Widespread	67	66	67
w	<i>Buglossidium luteum</i>	0.0040	0.0000	0.0000	Diverging decreasing	0.358	0.500	Transient	Common	Common	Widespread	Widespread	71	44	48
e	<i>Callionymus lyra</i>	0.0000	0.0000	0.0000	No change	0.305	0.000	Core	Common	Common	Widespread	Widespread	113	38	35
w	<i>Callionymus lyra</i>	0.0000	0.0000	0.0000	No change	0.309	0.000	Core	Common	Common	Widespread	Widespread	97	31	27
e	<i>Callionymus maculatus</i>	0.0000	0.0000	0.0000	No change	0.328	0.000	Core	Common	Common	Widespread	Widespread	114	43	39
w	<i>Callionymus maculatus</i>	0.0000	0.0000	0.0000	No change	0.329	0.000	Core	Common	Common	Widespread	Widespread	98	34	33
e	<i>Callionymus reticulatus</i>	0.0058	0.0000	0.0000	Random	0.295	0.774	Transient	Common	Common	Widespread	Widespread	52	54	54
w	<i>Callionymus reticulatus</i>	0.0074	0.0000	0.0000	Random	0.299	0.933	Transient	Common	Common	Widespread	Widespread	29	105	104
e	<i>Capros aper</i>	0.0029	0.0000	0.0000	Random	0.346	0.387	Transient	Common	Common	Widespread	Widespread	81	78	78
w	<i>Capros aper</i>	0.0003	0.0078	0.0003	Recurrent	0.343	0.033	Core	Common	Common	Widespread	Widespread	93	5	7
w	<i>Cepola macrophthalmia</i>	0.0050	0.0000	0.0000	Random	0.315	0.633	Transient	Common	Common	Widespread	Widespread	56	65	66
e	<i>Chelidonichthys cuculus</i>	0.0002	0.0000	0.0000	Random	0.318	0.032	Core	Common	Common	Widespread	Widespread	102	26	24
w	<i>Chelidonichthys cuculus</i>	0.0000	0.0001	0.0000	No change	0.320	0.000	Core	Common	Common	Widespread	Widespread	99	24	24
e	<i>Chelidonichthys lastoviza</i>	0.0068	0.0000	0.0000	Random	0.357	0.903	Transient	Common	Common	Widespread	Widespread	41	101	100
w	<i>Chelidonichthys lastoviza</i>	0.0064	0.0000	0.0000	Random	0.360	0.800	Transient	Common	Common	Widespread	Widespread	50	73	75
e	<i>Chelidonichthys lucerna</i>	0.0017	0.0000	0.0000	Random	0.312	0.226	Core	Common	Common	Widespread	Widespread	92	39	44
w	<i>Chelidonichthys lucerna</i>	0.0037	0.0000	0.0000	Random	0.317	0.467	Transient	Common	Common	Widespread	Widespread	75	86	88
e	<i>Chirolophis ascanii</i>	0.0072	0.0000	0.0000	Random	0.400	0.968	Transient	Common	Funct. rare	Widespread	Restricted	4	133	133
w	<i>Chirolophis ascanii</i>	0.0077	0.0000	0.0000	Random	0.398	0.967	Transient	Funct. rare	Common	Restricted	Widespread	7	124	124
e	<i>Ciliata septentrionalis</i>	0.0068	0.0000	0.0000	Random	0.324	0.903	Transient	Common	Common	Widespread	Widespread	42	113	115
w	<i>Ciliata septentrionalis</i>	0.0074	0.0000	0.0000	Random	0.326	0.933	Transient	Common	Common	Widespread	Widespread	30	93	92
e	<i>Clupea harengus</i>	0.0000	0.0112	0.0024	No change	0.382	0.000	Core	Common	Common	Widespread	Widespread	115	1	2
w	<i>Clupea harengus</i>	0.0000	0.0173	0.0065	No change	0.380	0.000	Core	Common	Common	Widespread	Widespread	100	2	2
w	<i>Coelorinchus caelorhincus</i>	0.0045	0.0000	0.0000	Converging increasing	0.409	0.567	Transient	Funct. rare	Common	Widespread	Widespread	59	33	41
e	<i>Conger conger</i>	0.0060	0.0000	0.0000	Random	0.445	0.806	Transient	Common	Funct. rare	Widespread	Widespread	50	98	99
w	<i>Conger conger</i>	0.0008	0.0000	0.0000	Recurrent	0.425	0.100	Core	Funct. rare	Common	Widespread	Widespread	90	72	68
w	<i>Coryphaenoides rupestris</i>	0.0077	0.0000	0.0000	Random	0.452	0.967	Transient	Funct. rare	Common	Restricted	Widespread	8	81	81
e	<i>Cottunculus microps</i>	0.0072	0.0000	0.0000	Random	0.448	0.968	Transient	Common	Funct. rare	Widespread	Restricted	5	91	90
e	<i>Crystallogobius linearis</i>	0.0068	0.0000	0.0000	Random	0.384	0.903	Transient	Common	Common	Widespread	Widespread	43	80	81
w	<i>Crystallogobius linearis</i>	0.0077	0.0000	0.0000	Random	0.397	0.967	Transient	Common	Common	Restricted	Widespread	9	50	53
e	<i>Cyclopterus lumpus</i>	0.0002	0.0000	0.0000	Random	0.437	0.032	Core	Common	Funct. rare	Widespread	Widespread	103	72	65
w	<i>Cyclopterus lumpus</i>	0.0013	0.0000	0.0000	Random	0.432	0.167	Core	Funct. rare	Common	Widespread	Widespread	87	76	71
e	<i>Dicentrarchus labrax</i>	0.0072	0.0000	0.0000	Random	0.352	0.968	Transient	Common	Common	Widespread	Restricted	6	119	117

e	<i>Diplecogaster bimaculata</i>	0.0070	0.0000	0.0000	Random	0.359	0.935	Transient	Common	Common	Widespread	Widespread	33	118	122
w	<i>Diplecogaster bimaculata</i>	0.0077	0.0000	0.0000	Random	0.372	0.967	Transient	Common	Common	Restricted	Widespread	10	119	119
e	<i>Dipturus batis</i>	0.0041	0.0000	0.0000	Random	0.417	0.548	Transient	Common	Funct. rare	Widespread	Widespread	71	97	96
w	<i>Dipturus batis</i>	0.0008	0.0000	0.0000	Random	0.395	0.100	Core	Common	Common	Widespread	Widespread	88	60	58
e	<i>Echiichthys vipera</i>	0.0063	0.0000	0.0000	Random	0.313	0.839	Transient	Common	Common	Widespread	Widespread	49	96	95
w	<i>Echiichthys vipera</i>	0.0064	0.0000	0.0000	Recurrent	0.317	0.800	Transient	Common	Common	Widespread	Widespread	52	90	93
e	<i>Echiodon drummondii</i>	0.0043	0.0000	0.0000	Recurrent	0.364	0.581	Transient	Common	Common	Widespread	Widespread	68	76	79
w	<i>Echiodon drummondii</i>	0.0042	0.0000	0.0000	Random	0.363	0.533	Transient	Common	Common	Widespread	Widespread	66	82	83
e	<i>Enchelyopus cimbrius</i>	0.0002	0.0000	0.0000	Random	0.300	0.032	Core	Common	Common	Widespread	Widespread	104	46	43
w	<i>Enchelyopus cimbrius</i>	0.0000	0.0000	0.0000	No change	0.298	0.000	Core	Common	Common	Widespread	Widespread	101	37	37
e	<i>Engraulis encrasicolus</i>	0.0017	0.0000	0.0000	Diverging increasing	0.377	0.226	Core	Common	Common	Widespread	Widespread	90	21	23
w	<i>Engraulis encrasicolus</i>	0.0045	0.0000	0.0000	Diverging increasing	0.371	0.567	Transient	Common	Common	Widespread	Widespread	60	36	39
e	<i>Entelurus aequoreus</i>	0.0051	0.0001	0.0000	Diverging increasing	0.375	0.677	Transient	Common	Common	Widespread	Widespread	61	19	21
w	<i>Entelurus aequoreus</i>	0.0064	0.0001	0.0000	Diverging increasing	0.392	0.800	Transient	Common	Common	Widespread	Widespread	48	27	30
w	<i>Epigonus telescopus</i>	0.0077	0.0000	0.0000	Random	0.415	0.967	Transient	Funct. rare	Common	Restricted	Widespread	11	118	117
w	<i>Etmopterus spinax</i>	0.0072	0.0000	0.0000	Recurrent	0.421	0.900	Transient	Funct. rare	Common	Widespread	Widespread	42	78	79
e	<i>Eutrigla gurnardus</i>	0.0000	0.0004	0.0000	No change	0.313	0.000	Core	Common	Common	Widespread	Widespread	116	11	10
w	<i>Eutrigla gurnardus</i>	0.0000	0.0003	0.0000	No change	0.319	0.000	Core	Common	Common	Widespread	Widespread	102	17	17
e	<i>Gadiculus argenteus</i>	0.0002	0.0000	0.0000	Random	0.375	0.032	Core	Common	Common	Widespread	Widespread	105	22	20
w	<i>Gadiculus argenteus</i>	0.0003	0.0010	0.0000	Recurrent	0.366	0.033	Core	Common	Common	Widespread	Widespread	94	12	12
w	<i>Gadiculus thori</i>	0.0077	0.0002	0.0000	Recurrent	0.371	0.967	Transient	Common	Common	Restricted	Widespread	24	21	25
e	<i>Gadus morhua</i>	0.0000	0.0000	0.0000	No change	0.377	0.000	Core	Common	Common	Widespread	Widespread	117	20	18
w	<i>Gadus morhua</i>	0.0000	0.0001	0.0000	No change	0.358	0.000	Core	Common	Common	Widespread	Widespread	103	26	26
e	<i>Gaidropsarus mediterraneus</i>	0.0070	0.0000	0.0000	Random	0.346	0.935	Transient	Common	Common	Widespread	Widespread	34	109	109
e	<i>Gaidropsarus vulgaris</i>	0.0036	0.0000	0.0000	Random	0.308	0.484	Transient	Common	Common	Widespread	Widespread	75	58	60
w	<i>Gaidropsarus vulgaris</i>	0.0042	0.0000	0.0000	Recurrent	0.308	0.533	Transient	Common	Common	Widespread	Widespread	68	64	65
e	<i>Galeorhinus galeus</i>	0.0058	0.0000	0.0000	Random	0.437	0.774	Transient	Common	Funct. rare	Widespread	Widespread	53	95	94
w	<i>Galeorhinus galeus</i>	0.0034	0.0000	0.0000	Random	0.415	0.433	Transient	Funct. rare	Common	Widespread	Widespread	76	84	85
e	<i>Galeus melastomus</i>	0.0072	0.0000	0.0000	Random	0.332	0.968	Transient	Common	Common	Widespread	Restricted	7	131	131
w	<i>Galeus melastomus</i>	0.0000	0.0000	0.0000	No change	0.324	0.000	Core	Common	Common	Widespread	Widespread	104	48	44
e	<i>Gasterosteus aculeatus</i>	0.0056	0.0000	0.0000	Random	0.422	0.742	Transient	Common	Funct. rare	Widespread	Widespread	57	100	101
w	<i>Gasterosteus aculeatus</i>	0.0077	0.0000	0.0000	Recurrent	0.423	0.967	Transient	Funct. rare	Common	Restricted	Widespread	25	130	130
e	<i>Glyptocephalus cynoglossus</i>	0.0000	0.0000	0.0000	No change	0.360	0.000	Core	Common	Common	Widespread	Widespread	118	34	33

w	<i>Glyptocephalus cynoglossus</i>	0.0000	0.0000	0.0000	No change	0.358	0.000	Core	Common	Common	Widespread	Widespread	105	29	28
e	<i>Gymnammodytes semisquamatus</i>	0.0053	0.0000	0.0000	Diverging increasing	0.379	0.710	Transient	Common	Common	Widespread	Widespread	58	28	30
w	<i>Gymnammodytes semisquamatus</i>	0.0066	0.0000	0.0000	Random	0.388	0.833	Transient	Common	Common	Widespread	Widespread	45	42	43
e	<i>Helicolenus dactylopterus</i>	0.0019	0.0000	0.0000	Recurrent	0.385	0.258	Core	Common	Common	Widespread	Widespread	88	25	26
w	<i>Helicolenus dactylopterus</i>	0.0000	0.0006	0.0000	No change	0.374	0.000	Core	Common	Common	Widespread	Widespread	106	14	16
w	<i>Hexanchus griseus</i>	0.0077	0.0000	0.0000	Random	0.533	0.967	Transient	Funct. rare	Common	Restricted	Widespread	12	127	127
e	<i>Hippoglossoides platessoides</i>	0.0000	0.0002	0.0000	No change	0.422	0.000	Core	Common	Funct. rare	Widespread	Widespread	119	14	11
w	<i>Hippoglossoides platessoides</i>	0.0000	0.0005	0.0000	No change	0.416	0.000	Core	Funct. rare	Common	Widespread	Widespread	107	15	14
e	<i>Hippoglossus hippoglossus</i>	0.0012	0.0000	0.0000	Recurrent	0.502	0.161	Core	Common	Funct. rare	Widespread	Widespread	94	77	69
w	<i>Hippoglossus hippoglossus</i>	0.0066	0.0000	0.0000	Random	0.479	0.833	Transient	Funct. rare	Common	Widespread	Widespread	46	103	106
e	<i>Hyperoplus immaculatus</i>	0.0036	0.0000	0.0000	Diverging increasing	0.339	0.484	Transient	Common	Common	Widespread	Widespread	74	29	29
w	<i>Hyperoplus immaculatus</i>	0.0042	0.0000	0.0000	Diverging increasing	0.346	0.533	Transient	Common	Common	Widespread	Widespread	63	28	31
e	<i>Hyperoplus lanceolatus</i>	0.0002	0.0000	0.0000	Random	0.328	0.032	Core	Common	Common	Widespread	Widespread	106	31	31
w	<i>Hyperoplus lanceolatus</i>	0.0042	0.0000	0.0000	Random	0.336	0.533	Transient	Common	Common	Widespread	Widespread	67	63	63
e	<i>Labrus bergylta</i>	0.0070	0.0000	0.0000	Random	0.428	0.935	Transient	Common	Funct. rare	Widespread	Widespread	35	117	116
w	<i>Labrus bergylta</i>	0.0066	0.0000	0.0000	Random	0.427	0.833	Transient	Funct. rare	Common	Widespread	Widespread	47	97	98
e	<i>Labrus mixtus</i>	0.0072	0.0000	0.0000	Random	0.422	0.968	Transient	Common	Funct. rare	Widespread	Restricted	8	105	103
w	<i>Labrus mixtus</i>	0.0042	0.0000	0.0000	Diverging increasing	0.422	0.533	Transient	Funct. rare	Common	Widespread	Widespread	64	83	82
w	<i>Lepidion eques</i>	0.0074	0.0000	0.0000	Recurrent	0.410	0.933	Transient	Funct. rare	Common	Widespread	Widespread	36	54	59
e	<i>Lepidorhombus boscii</i>	0.0072	0.0000	0.0000	Random	0.312	0.968	Transient	Common	Common	Widespread	Restricted	9	73	73
w	<i>Lepidorhombus boscii</i>	0.0048	0.0000	0.0000	Diverging increasing	0.315	0.600	Transient	Common	Common	Widespread	Widespread	57	68	70
e	<i>Lepidorhombus whiffiagonis</i>	0.0000	0.0000	0.0000	No change	0.385	0.000	Core	Common	Common	Widespread	Widespread	120	36	36
w	<i>Lepidorhombus whiffiagonis</i>	0.0000	0.0000	0.0000	No change	0.375	0.000	Core	Common	Common	Widespread	Widespread	108	35	29
e	<i>Leptoclinus maculatus</i>	0.0072	0.0000	0.0000	Recurrent	0.372	0.968	Transient	Common	Common	Widespread	Restricted	28	135	135
e	<i>Lesueurigobius friesii</i>	0.0070	0.0000	0.0000	Random	0.388	0.935	Transient	Common	Common	Widespread	Widespread	36	107	108
w	<i>Lesueurigobius friesii</i>	0.0042	0.0000	0.0000	Recurrent	0.400	0.533	Transient	Funct. rare	Common	Widespread	Widespread	69	43	45
e	<i>Leucoraja circularis</i>	0.0070	0.0000	0.0000	Random	0.352	0.935	Transient	Common	Common	Widespread	Widespread	37	102	104

w	<i>Leucoraja circularis</i>	0.0072	0.0000	0.0000	Recurrent	0.346	0.900	Transient	Common	Common	Widespread	Widespread	43	95	96
e	<i>Leucoraja fullonica</i>	0.0027	0.0000	0.0000	Recurrent	0.402	0.355	Core	Common	Funct. rare	Widespread	Widespread	85	85	83
w	<i>Leucoraja fullonica</i>	0.0072	0.0000	0.0000	Random	0.386	0.900	Transient	Common	Common	Widespread	Widespread	40	101	103
e	<i>Leucoraja lentiginosa</i>	0.0072	0.0000	0.0000	Random	0.371	0.968	Transient	Common	Common	Widespread	Restricted	10	137	137
e	<i>Leucoraja naevus</i>	0.0000	0.0000	0.0000	No change	0.341	0.000	Core	Common	Common	Widespread	Widespread	121	48	41
w	<i>Leucoraja naevus</i>	0.0000	0.0000	0.0000	No change	0.340	0.000	Core	Common	Common	Widespread	Widespread	109	59	51
e	<i>Limanda limanda</i>	0.0000	0.0005	0.0000	No change	0.309	0.000	Core	Common	Common	Widespread	Widespread	122	10	8
w	<i>Limanda limanda</i>	0.0000	0.0002	0.0000	No change	0.313	0.000	Core	Common	Common	Widespread	Widespread	110	18	18
e	<i>Liparis liparis</i>	0.0058	0.0000	0.0000	Random	0.347	0.774	Transient	Common	Common	Widespread	Widespread	54	90	91
w	<i>Liparis liparis</i>	0.0077	0.0000	0.0000	Random	0.357	0.967	Transient	Common	Common	Restricted	Widespread	13	77	78
e	<i>Liparis montagui</i>	0.0068	0.0000	0.0000	Random	0.324	0.903	Transient	Common	Common	Widespread	Widespread	44	104	107
w	<i>Liparis montagui</i>	0.0077	0.0000	0.0000	Recurrent	0.331	0.967	Transient	Common	Common	Restricted	Widespread	26	116	115
e	<i>Lophius budegassa</i>	0.0051	0.0000	0.0000	Diverging increasing	0.429	0.677	Transient	Common	Funct. rare	Widespread	Widespread	62	88	89
w	<i>Lophius budegassa</i>	0.0000	0.0000	0.0000	No change	0.406	0.000	Core	Funct. rare	Common	Widespread	Widespread	111	79	69
e	<i>Lophius piscatorius</i>	0.0000	0.0000	0.0000	No change	0.412	0.000	Core	Common	Funct. rare	Widespread	Widespread	123	51	45
w	<i>Lophius piscatorius</i>	0.0000	0.0000	0.0000	No change	0.389	0.000	Core	Common	Common	Widespread	Widespread	112	45	42
e	<i>Lumpenus lampretaeformis</i>	0.0012	0.0000	0.0000	Recurrent	0.362	0.161	Core	Common	Common	Widespread	Widespread	95	63	58
w	<i>Lumpenus lampretaeformis</i>	0.0003	0.0000	0.0000	Recurrent	0.379	0.033	Core	Common	Common	Widespread	Widespread	95	38	35
e	<i>Lycodes gracilis</i>	0.0072	0.0000	0.0000	Random	0.373	0.968	Transient	Common	Common	Widespread	Restricted	11	83	86
e	<i>Lycodes vahlii</i>	0.0065	0.0000	0.0000	Random	0.444	0.871	Transient	Common	Funct. rare	Widespread	Widespread	46	68	72
w	<i>Macroramphosus scolopax</i>	0.0074	0.0000	0.0000	Random	0.377	0.933	Transient	Common	Common	Widespread	Widespread	31	114	116
w	<i>Macrourus berglax</i>	0.0077	0.0000	0.0000	Recurrent	0.434	0.967	Transient	Funct. rare	Common	Restricted	Widespread	27	62	61
w	<i>Malacocephalus laevis</i>	0.0040	0.0000	0.0000	Converging increasing	0.377	0.500	Transient	Common	Common	Widespread	Widespread	70	52	55
e	<i>Maurolucus muelleri</i>	0.0002	0.0000	0.0000	Random	0.480	0.032	Core	Common	Funct. rare	Widespread	Widespread	107	33	32
w	<i>Maurolucus muelleri</i>	0.0019	0.0000	0.0000	Diverging increasing	0.472	0.233	Core	Funct. rare	Common	Widespread	Widespread	83	46	49
e	<i>Melanogrammus aeglefinus</i>	0.0000	0.0040	0.0005	No change	0.308	0.000	Core	Common	Common	Widespread	Widespread	124	7	4
w	<i>Melanogrammus aeglefinus</i>	0.0000	0.0044	0.0004	No change	0.304	0.000	Core	Common	Common	Widespread	Widespread	113	7	5
e	<i>Merlangius merlangus</i>	0.0000	0.0081	0.0013	No change	0.361	0.000	Core	Common	Common	Widespread	Widespread	125	3	3
w	<i>Merlangius merlangus</i>	0.0000	0.0041	0.0003	No change	0.350	0.000	Core	Common	Common	Widespread	Widespread	114	9	6
e	<i>Merluccius merluccius</i>	0.0000	0.0001	0.0000	No change	0.318	0.000	Core	Common	Common	Widespread	Widespread	126	17	19
w	<i>Merluccius merluccius</i>	0.0000	0.0004	0.0000	No change	0.311	0.000	Core	Common	Common	Widespread	Widespread	115	16	15
e	<i>Micrenophrys lilljeborgii</i>	0.0072	0.0000	0.0000	Random	0.334	0.968	Transient	Common	Common	Widespread	Restricted	12	125	125

e	<i>Microchirus variegatus</i>	0.0017	0.0000	0.0000	Converging increasing	0.344	0.226	Core	Common	Common	Widespread	Widespread	89	53	52
w	<i>Microchirus variegatus</i>	0.0027	0.0000	0.0000	Diverging increasing	0.348	0.333	Core	Common	Common	Widespread	Widespread	80	30	32
e	<i>Micromesistius poutassou</i>	0.0012	0.0005	0.0000	Recurrent	0.438	0.161	Core	Common	Funct. rare	Widespread	Widespread	96	9	12
w	<i>Micromesistius poutassou</i>	0.0000	0.0128	0.0013	No change	0.423	0.000	Core	Funct. rare	Common	Widespread	Widespread	116	4	4
e	<i>Microstomus kitt</i>	0.0000	0.0001	0.0000	No change	0.313	0.000	Core	Common	Common	Widespread	Widespread	127	18	16
w	<i>Microstomus kitt</i>	0.0000	0.0001	0.0000	No change	0.317	0.000	Core	Common	Common	Widespread	Widespread	117	22	19
w	<i>Molva dypterygia</i>	0.0069	0.0000	0.0000	Random	0.341	0.867	Transient	Common	Common	Widespread	Widespread	44	98	99
e	<i>Molva molva</i>	0.0000	0.0000	0.0000	No change	0.369	0.000	Core	Common	Common	Widespread	Widespread	128	45	38
w	<i>Molva molva</i>	0.0000	0.0000	0.0000	No change	0.350	0.000	Core	Common	Common	Widespread	Widespread	118	56	50
e	<i>Mullus surmuletus</i>	0.0019	0.0000	0.0000	Converging increasing	0.345	0.258	Core	Common	Common	Widespread	Widespread	87	42	50
w	<i>Mullus surmuletus</i>	0.0048	0.0000	0.0000	Recurrent	0.350	0.600	Transient	Common	Common	Widespread	Widespread	58	91	91
e	<i>Mustelus asterias</i>	0.0017	0.0000	0.0000	Diverging increasing	0.340	0.226	Core	Common	Common	Widespread	Widespread	91	40	48
w	<i>Mustelus asterias</i>	0.0037	0.0000	0.0000	Diverging increasing	0.338	0.467	Transient	Common	Common	Widespread	Widespread	74	70	73
e	<i>Mustelus mustelus</i>	0.0027	0.0000	0.0000	Diverging increasing	0.368	0.355	Core	Common	Common	Widespread	Widespread	82	62	62
w	<i>Mustelus mustelus</i>	0.0053	0.0000	0.0000	Recurrent	0.364	0.667	Transient	Common	Common	Widespread	Widespread	54	88	89
e	<i>Myoxocephalus scorpioides</i>	0.0072	0.0000	0.0000	Random	0.356	0.968	Transient	Common	Common	Widespread	Restricted	13	106	105
e	<i>Myoxocephalus scorpius</i>	0.0000	0.0000	0.0000	No change	0.368	0.000	Core	Common	Common	Widespread	Widespread	129	47	47
w	<i>Myoxocephalus scorpius</i>	0.0058	0.0000	0.0000	Random	0.372	0.733	Transient	Common	Common	Widespread	Widespread	53	87	86
e	<i>Nerophis ophidion</i>	0.0072	0.0000	0.0000	Random	0.417	0.968	Transient	Common	Funct. rare	Widespread	Restricted	14	126	126
w	<i>Pagellus bogaraveo</i>	0.0077	0.0000	0.0000	Random	0.339	0.967	Transient	Common	Common	Restricted	Widespread	14	66	67
e	<i>Parablennius gattorugine</i>	0.0072	0.0000	0.0000	Random	0.409	0.968	Transient	Common	Funct. rare	Widespread	Restricted	15	134	134
w	<i>Parablennius gattorugine</i>	0.0077	0.0000	0.0000	Random	0.419	0.967	Transient	Funct. rare	Common	Restricted	Widespread	15	104	102
e	<i>Pholis gunnellus</i>	0.0041	0.0000	0.0000	Diverging increasing	0.348	0.548	Transient	Common	Common	Widespread	Widespread	70	61	64
w	<i>Pholis gunnellus</i>	0.0077	0.0000	0.0000	Random	0.365	0.967	Transient	Common	Common	Restricted	Widespread	16	120	120
e	<i>Phrynorhombus norvegicus</i>	0.0024	0.0000	0.0000	Random	0.396	0.323	Core	Common	Common	Widespread	Widespread	86	75	71
w	<i>Phrynorhombus norvegicus</i>	0.0034	0.0000	0.0000	Random	0.390	0.433	Transient	Common	Common	Widespread	Widespread	77	71	72
e	<i>Phycis blennoides</i>	0.0048	0.0000	0.0000	Random	0.360	0.645	Transient	Common	Common	Widespread	Widespread	65	92	93
w	<i>Phycis blennoides</i>	0.0003	0.0000	0.0000	Random	0.344	0.033	Core	Common	Common	Widespread	Widespread	92	47	46

e	<i>Platichthys flesus</i>	0.0014	0.0000	0.0000	Recurrent	0.316	0.194	Core	Common	Common	Widespread	Widespread	93	44	49
w	<i>Platichthys flesus</i>	0.0024	0.0000	0.0000	Random	0.322	0.300	Core	Common	Common	Widespread	Widespread	82	75	76
e	<i>Pleuronectes platessa</i>	0.0000	0.0002	0.0000	No change	0.345	0.000	Core	Common	Common	Widespread	Widespread	130	15	15
w	<i>Pleuronectes platessa</i>	0.0000	0.0001	0.0000	No change	0.346	0.000	Core	Common	Common	Widespread	Widespread	119	23	22
e	<i>Pollachius pollachius</i>	0.0041	0.0000	0.0000	Random	0.367	0.548	Transient	Common	Common	Widespread	Widespread	72	55	56
w	<i>Pollachius pollachius</i>	0.0016	0.0000	0.0000	Random	0.353	0.200	Core	Common	Common	Widespread	Widespread	85	51	52
e	<i>Pollachius virens</i>	0.0000	0.0001	0.0000	No change	0.328	0.000	Core	Common	Common	Widespread	Widespread	131	16	17
w	<i>Pollachius virens</i>	0.0000	0.0002	0.0000	No change	0.322	0.000	Core	Common	Common	Widespread	Widespread	120	19	21
e	<i>Pomatoschistus lozanoi</i>	0.0072	0.0000	0.0000	Random	0.398	0.968	Transient	Common	Common	Widespread	Restricted	16	65	66
e	<i>Pomatoschistus microps</i>	0.0065	0.0000	0.0000	Recurrent	0.367	0.871	Transient	Common	Common	Widespread	Widespread	48	56	55
w	<i>Pomatoschistus microps</i>	0.0077	0.0000	0.0000	Random	0.377	0.967	Transient	Common	Common	Restricted	Widespread	17	58	60
e	<i>Pomatoschistus minutus</i>	0.0043	0.0000	0.0000	Recurrent	0.381	0.581	Transient	Common	Common	Widespread	Widespread	69	52	53
w	<i>Pomatoschistus minutus</i>	0.0045	0.0000	0.0000	Random	0.392	0.567	Transient	Common	Common	Widespread	Widespread	62	32	38
e	<i>Pomatoschistus pictus</i>	0.0072	0.0000	0.0000	Random	0.418	0.968	Transient	Common	Funct. rare	Widespread	Restricted	17	123	123
e	<i>Pterycombus brama</i>	0.0072	0.0000	0.0000	Random	0.418	0.968	Transient	Common	Funct. rare	Widespread	Restricted	18	124	124
e	<i>Raja brachyura</i>	0.0031	0.0000	0.0000	Recurrent	0.345	0.419	Transient	Common	Common	Widespread	Widespread	80	57	57
w	<i>Raja brachyura</i>	0.0016	0.0000	0.0000	Random	0.340	0.200	Core	Common	Common	Widespread	Widespread	86	53	54
e	<i>Raja clavata</i>	0.0027	0.0000	0.0000	Random	0.364	0.355	Core	Common	Common	Widespread	Widespread	84	59	61
w	<i>Raja clavata</i>	0.0000	0.0000	0.0000	No change	0.355	0.000	Core	Common	Common	Widespread	Widespread	121	49	47
e	<i>Raja montagui</i>	0.0002	0.0000	0.0000	Random	0.339	0.032	Core	Common	Common	Widespread	Widespread	108	35	37
w	<i>Raja montagui</i>	0.0000	0.0000	0.0000	No change	0.336	0.000	Core	Common	Common	Widespread	Widespread	122	41	34
e	<i>Raniceps raninus</i>	0.0060	0.0000	0.0000	Random	0.301	0.806	Transient	Common	Common	Widespread	Widespread	51	111	111
w	<i>Raniceps raninus</i>	0.0074	0.0000	0.0000	Random	0.302	0.933	Transient	Common	Common	Widespread	Widespread	32	117	118
w	<i>Rostroraja alba</i>	0.0074	0.0000	0.0000	Recurrent	0.409	0.933	Transient	Funct. rare	Common	Widespread	Widespread	37	102	101
e	<i>Salmo trutta</i>	0.0072	0.0000	0.0000	Random	0.448	0.968	Transient	Common	Funct. rare	Widespread	Restricted	19	120	118
w	<i>Salmo trutta</i>	0.0077	0.0000	0.0000	Random	0.442	0.967	Transient	Funct. rare	Common	Restricted	Widespread	18	96	95
e	<i>Sardina pilchardus</i>	0.0027	0.0000	0.0000	Diverging increasing	0.463	0.355	Core	Common	Funct. rare	Widespread	Widespread	83	24	27
w	<i>Sardina pilchardus</i>	0.0042	0.0000	0.0000	Diverging increasing	0.464	0.533	Transient	Funct. rare	Common	Widespread	Widespread	65	69	74
e	<i>Scomber scombrus</i>	0.0000	0.0050	0.0001	No change	0.390	0.000	Core	Common	Common	Widespread	Widespread	132	5	6
w	<i>Scomber scombrus</i>	0.0000	0.0327	0.0092	No change	0.382	0.000	Core	Common	Common	Widespread	Widespread	123	1	1
e	<i>Scomberesox saurus</i>	0.0072	0.0000	0.0000	Recurrent	0.432	0.968	Transient	Common	Funct. rare	Widespread	Restricted	29	108	106
e	<i>Scophthalmus maximus</i>	0.0002	0.0000	0.0000	Random	0.360	0.032	Core	Common	Common	Widespread	Widespread	109	89	77
w	<i>Scophthalmus maximus</i>	0.0008	0.0000	0.0000	Random	0.364	0.100	Core	Common	Common	Widespread	Widespread	89	92	84
e	<i>Scophthalmus rhombus</i>	0.0036	0.0000	0.0000	Recurrent	0.361	0.484	Transient	Common	Common	Widespread	Widespread	76	74	74
w	<i>Scophthalmus rhombus</i>	0.0040	0.0000	0.0000	Random	0.365	0.500	Transient	Common	Common	Widespread	Widespread	73	89	90
e	<i>Scorpaena scrofa</i>	0.0072	0.0000	0.0000	Random	0.369	0.968	Transient	Common	Common	Widespread	Restricted	20	103	102
e	<i>Scyliorhinus canicula</i>	0.0000	0.0000	0.0000	No change	0.316	0.000	Core	Common	Common	Widespread	Widespread	133	27	25
w	<i>Scyliorhinus canicula</i>	0.0000	0.0001	0.0000	No change	0.308	0.000	Core	Common	Common	Widespread	Widespread	124	25	20
e	<i>Scyliorhinus stellaris</i>	0.0070	0.0000	0.0000	Random	0.399	0.935	Transient	Common	Common	Widespread	Widespread	38	99	98
w	<i>Scyliorhinus stellaris</i>	0.0074	0.0000	0.0000	Random	0.378	0.933	Transient	Common	Common	Widespread	Widespread	33	110	110

e	<i>Sebastes norvegicus</i>	0.0072	0.0000	0.0000	Random	0.455	0.968	Transient	Common	Funct. rare	Widespread	Restricted	21	114	113
e	<i>Sebastes viviparus</i>	0.0007	0.0000	0.0000	Random	0.385	0.097	Core	Common	Common	Widespread	Widespread	98	37	42
w	<i>Sebastes viviparus</i>	0.0032	0.0000	0.0000	Random	0.388	0.400	Transient	Common	Common	Widespread	Widespread	79	55	57
e	<i>Solea solea</i>	0.0051	0.0000	0.0000	Random	0.324	0.677	Transient	Common	Common	Widespread	Widespread	63	70	75
w	<i>Solea solea</i>	0.0019	0.0000	0.0000	Diverging increasing	0.331	0.233	Core	Common	Common	Widespread	Widespread	84	67	64
e	<i>Spinachia spinachia</i>	0.0072	0.0000	0.0000	Random	0.418	0.968	Transient	Common	Funct. rare	Widespread	Restricted	22	127	127
e	<i>Sprattus sprattus</i>	0.0000	0.0061	0.0003	No change	0.396	0.000	Core	Common	Common	Widespread	Widespread	134	4	5
w	<i>Sprattus sprattus</i>	0.0000	0.0041	0.0002	No change	0.395	0.000	Core	Common	Common	Widespread	Widespread	125	8	9
e	<i>Squalus acanthias</i>	0.0000	0.0000	0.0000	No change	0.433	0.000	Core	Common	Funct. rare	Widespread	Widespread	135	41	40
w	<i>Squalus acanthias</i>	0.0000	0.0007	0.0000	No change	0.417	0.000	Core	Funct. rare	Common	Widespread	Widespread	126	13	13
w	<i>Stomias boa ferox</i>	0.0077	0.0000	0.0000	Random	0.390	0.967	Transient	Common	Common	Restricted	Widespread	19	121	121
e	<i>Syngnathus acus</i>	0.0039	0.0000	0.0000	Random	0.409	0.516	Transient	Common	Funct. rare	Widespread	Widespread	73	81	82
w	<i>Syngnathus acus</i>	0.0072	0.0000	0.0000	Random	0.430	0.900	Transient	Funct. rare	Common	Widespread	Widespread	41	108	109
e	<i>Syngnathus rostellatus</i>	0.0068	0.0000	0.0000	Random	0.385	0.903	Transient	Common	Common	Widespread	Widespread	45	110	110
e	<i>Syngnathus typhle</i>	0.0072	0.0000	0.0000	Random	0.412	0.968	Transient	Common	Funct. rare	Widespread	Restricted	23	115	114
e	<i>Taurulus bubalis</i>	0.0058	0.0000	0.0000	Random	0.331	0.774	Transient	Common	Common	Widespread	Widespread	55	71	76
w	<i>Taurulus bubalis</i>	0.0077	0.0000	0.0000	Random	0.337	0.967	Transient	Common	Common	Restricted	Widespread	20	113	113
e	<i>Trachinus draco</i>	0.0072	0.0000	0.0000	Random	0.301	0.968	Transient	Common	Common	Widespread	Restricted	24	121	119
e	<i>Trachipterus arcticus</i>	0.0072	0.0000	0.0000	Recurrent	0.507	0.968	Transient	Common	Funct. rare	Widespread	Restricted	30	136	136
e	<i>Trachurus trachurus</i>	0.0000	0.0003	0.0000	No change	0.387	0.000	Core	Common	Common	Widespread	Widespread	136	12	13
w	<i>Trachurus trachurus</i>	0.0000	0.0046	0.0002	No change	0.381	0.000	Core	Common	Common	Widespread	Widespread	127	6	8
e	<i>Trachyrincus murrayi</i>	0.0072	0.0000	0.0000	Random	0.419	0.968	Transient	Common	Funct. rare	Widespread	Restricted	25	138	138
w	<i>Trigla lyra</i>	0.0074	0.0000	0.0000	Random	0.412	0.933	Transient	Funct. rare	Common	Widespread	Widespread	34	111	112
e	<i>Triglops murrayi</i>	0.0034	0.0000	0.0000	Random	0.342	0.452	Transient	Common	Common	Widespread	Widespread	78	84	85
w	<i>Triglops murrayi</i>	0.0077	0.0000	0.0000	Random	0.352	0.967	Transient	Common	Common	Restricted	Widespread	21	129	129
e	<i>Trisopterus esmarkii</i>	0.0000	0.0091	0.0032	No change	0.353	0.000	Core	Common	Common	Widespread	Widespread	137	2	1
w	<i>Trisopterus esmarkii</i>	0.0000	0.0153	0.0053	No change	0.344	0.000	Core	Common	Common	Widespread	Widespread	128	3	3
e	<i>Trisopterus luscus</i>	0.0034	0.0000	0.0000	Random	0.346	0.452	Transient	Common	Common	Widespread	Widespread	79	87	87
w	<i>Trisopterus luscus</i>	0.0064	0.0000	0.0000	Random	0.335	0.800	Transient	Common	Common	Widespread	Widespread	51	94	94
e	<i>Trisopterus minutus</i>	0.0000	0.0010	0.0000	No change	0.344	0.000	Core	Common	Common	Widespread	Widespread	138	8	9
w	<i>Trisopterus minutus</i>	0.0000	0.0015	0.0000	No change	0.332	0.000	Core	Common	Common	Widespread	Widespread	129	10	10
w	<i>Zenopsis conchifer</i>	0.0077	0.0000	0.0000	Random	0.427	0.967	Transient	Funct. rare	Common	Restricted	Widespread	22	122	122
e	<i>Zeugopterus punctatus</i>	0.0053	0.0000	0.0000	Random	0.340	0.710	Transient	Common	Common	Widespread	Widespread	60	93	92
w	<i>Zeugopterus punctatus</i>	0.0074	0.0000	0.0000	Recurrent	0.344	0.933	Transient	Common	Common	Widespread	Widespread	38	109	107
e	<i>Zeugopterus regius</i>	0.0072	0.0000	0.0000	Random	0.342	0.968	Transient	Common	Common	Widespread	Restricted	26	132	132
e	<i>Zeus faber</i>	0.0012	0.0000	0.0000	Recurrent	0.408	0.161	Core	Common	Funct. rare	Widespread	Widespread	97	50	51
w	<i>Zeus faber</i>	0.0000	0.0000	0.0000	No change	0.396	0.000	Core	Common	Common	Widespread	Widespread	130	40	36
e	<i>Zoarces viviparus</i>	0.0072	0.0000	0.0000	Random	0.334	0.968	Transient	Common	Common	Widespread	Restricted	27	129	129



**Appendix 6.2** Table of species classifications by coast used in this chapter

1. Chao, A. & Ricotta, C. 2019 Quantifying evenness and linking it to diversity, beta diversity, and similarity. *Ecology* **100**, e02852. (DOI:10.1002/ecy.2852).

## Appendix A – Published papers



*Fishing boat off the coast of Elie, 2021*

**REGULAR PAPER**

# Change in the dominance structure of two marine-fish assemblages over three decades

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**Funding information**

This work was funded by the European Research Council (ERCAdG BioTIME 250189 and ERCPoC BioCHANGE 727440).

Marine fish are an irreplaceable resource, but are currently under threat through overfishing and climate change. To date, most of the emphasis has been on single stocks or populations of economic importance. However, commercially valuable species are embedded in assemblages of many species and there is only limited understanding of the extent to which the structure of whole communities has altered in recent years. Most assemblages are dominated by one or a few species, with these highly abundant species underpinning ecosystem services and harvesting decisions.

This paper shows that there have been marked temporal changes in the dominance structure of Scottish marine-fish assemblages over the past three decades, where dominance is measured as the proportional numerical abundance of the most dominant species. We report contrasting patterns in both the identity of the dominant species and shifts in the relative abundance of the dominant in assemblages to the east and west of Scotland, UK. This result highlights the importance of multi-species analyses of harvested stocks and has implications not only for fisheries management but also for consumer choices.

**KEYWORDS**

biodiversity, climate change, dominance, fish diversity, Scottish fisheries

## 1 | INTRODUCTION

The ongoing biodiversity crisis is the consequence of a combination of anthropogenic effects, including over exploitation and climate change (Cheung, 2018; García Molinos *et al.*, 2016; Jackson, 2008). To date, many of the evaluations of marine-fish assemblages, particularly in the context of stock assessment, have focussed on trends in individual species (Boyd *et al.*, 2018; Pershing *et al.*, 2015). Many of these (Baudron *et al.*, 2011; Dutz *et al.*, 2016; Engelhard *et al.*, 2014) report marked changes over the past few years. Recently, however, attention has turned to the dynamics of entire marine assemblages (Greenwood & Maitland, 2009), with investigators increasingly recognizing the need to quantify spatial and temporal change in biodiversity (Iacarella *et al.*, 2018; Jung & Houde, 2003; Magurran *et al.*, 2015; Morley *et al.*, 2017). Shifts in species richness (Daan, 2006; Hiddink & ter Hofstede, 2008; ter Hofstede *et al.*, 2010) and size (Bell *et al.*, 2018) have been reported, but as biodiversity is a multifaceted

concept (Magurran, 2013), there is still much to be learnt about the nature of biodiversity change in assemblages of wild fish.

One frequently used measure of biodiversity is relative species abundance; this quantifies the commonness or rarity of species in comparison with the overall abundance of the assemblage. Species abundance distributions (SAD), which describe the pattern of relative abundance within an assemblage, generally follow the shape of a hallow curve with a few abundant species and many rare ones. The most dominant species typically account for a large fraction of the overall abundance and play an important role in ecosystem function (Davies *et al.*, 2011; Ellingsen *et al.*, 2015; Jones & Magurran, 2018; Wohlge-muth *et al.*, 2016). For this reason, the relative dominance of the most numerically abundant species in an assemblage is an informative measure of community structure and can potentially reveal changes that would otherwise be unseen using metrics such as species richness or total abundance (Supporting Information Figure S1).

Here we draw on time-series data of fish assemblages to the east and west of Scotland to ask how the dominance structure of these

commercially important regions have changed over three decades. This time scale represents the period over which high quality assemblage data are available (ICES, 2014). The study areas being compared in the analysis are geographically close but are exposed to different climatic conditions and exploitation practices; as such, they provide an insight into the extent of recent change in assemblage dominance structure in heavily fished regions of the north-east Atlantic Ocean.

We know that fish assemblages to the west of Scotland are experiencing considerable reorganization as a result of biotic homogenization (Magurran *et al.*, 2015) and that biotic homogenisation and homogenisation of water temperatures are correlated in the west coast assemblages. In contrast, the North Sea to the east of Scotland has exhibited a smaller overall increase in water temperature during the same period (ter Hofstede *et al.*, 2010). Thus, we expect to detect a shift in dominance structure in west-coast fishes over the time frame of interest, with latitudinal heterogeneity in the response. No *a priori* predictions are made for east-coast assemblages, which are included to extend the scope of the analysis and provide a comparison with west coast changes.

## 2 | MATERIALS AND METHODS

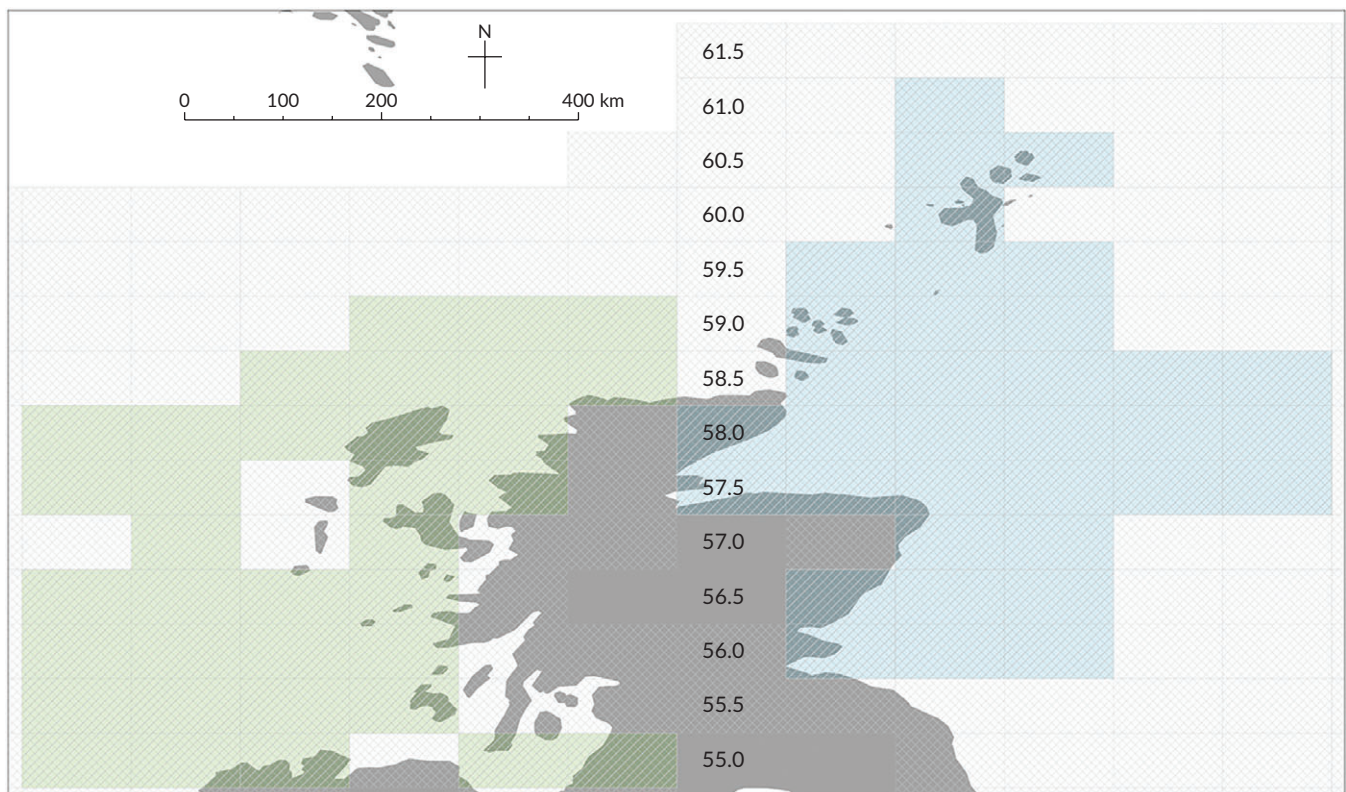
### 2.1 | Materials and data

The Scottish west coast groundfish survey (DATRAS, 2013) takes place annually in January, February and March whilst the North Sea international bottom trawl survey (DATRAS, 2015) is carried out

biannually in January–March (Q1) and July–September (Q3). We used the filter “all species” when selecting the scientific trawl data; this meant that both non-commercial and commercial species were included in the analysis. Catch per unit of effort (CPUE) per length per haul per 30 min was chosen as the measure of abundance as it provided the most comprehensive dataset for both systems. Q1 contains the most consistently sampled areas from both systems and is also the only quarter where all years were sampled. To maintain a fair comparison between the areas only Q1 data are used here with 1985 as the starting point in both cases. Both surveys use an ICES statistical rectangle (rectangles represent a 30' latitude by 1° longitude grid cell) based sampling strategy which is consistent through time.

The *grande ouverture verticale* (GOV) trawl (ICES, 2015) is the gear recommended by the International Council for the Exploration of the Sea (ICES) for all bottom trawl surveys. A comparative study carried out in 2012 (Reid *et al.*, 2012) showed that the results of trawling using this gear performed similarly to that using a standard commercial trawl. In order to ensure consistency between systems our study only uses the data sampled using the GOV gear.

Species and temperature data were sourced from the ICES data portal (ICES, 2014). The species data are taken from two standardised surveys incorporating the ICES divisions VIa (West coast), IVa and IVb (North Sea; <http://www.ices.dk/marine-data/maps/Pages/default.aspx>). The trawl survey gear provides an adequate sample of a wide range of species and sizes; the complete list of fish included in the recorded catch data are given in Supporting Information Table S1. Surveys adhere to strict protocols (ICES, 2015) with all species within



**FIGURE 1** Study area of the green shaded areas show the 35 ICES statistical rectangles used in the survey west of Scotland (■) and the 35 ICES statistical rectangles used from the North Sea survey (□). ■ & □, The ICES rectangles from the wider trawl survey areas. The central column of figures corresponds to the latitudinal bands used in analysis

a haul identified to the lowest taxonomic level possible. Additional information is also recorded, where possible, for length, age, sex and maturity, though these data are not used in our analysis.

Electronic equipment is used to monitor net geometry during all trawl tows; this allows for the appropriate adjustment of warp length according to water depth (ICES, 2015). The depths where hauls are recorded range from 10 to 250 m.

We selected 35 ICES west coast rectangles (Figure 1) that had been most consistently sampled (Magurran *et al.*, 2015) and chose 35 correspondingly well sampled, similarly positioned east coast rectangles for comparison. Each rectangle was assigned to its respective 0.5° latitudinal band. The spatial coverage on the west coast extends from 55.5° to 59.5° N and includes 134 species (128 finfish). The corresponding 35 ICES rectangles (Figure 1) on the east coast extend from 56.5° to 61.5° and include 138 species (129 finfish). For the purposes of this analysis the focus was on finfish but the numerical abundance of the dominant species was computed in relation to the entire assemblage, which also includes a few macroinvertebrates such as the European common squid *Alloteuthis subulata*, as these are the species amongst which resources are partitioned.

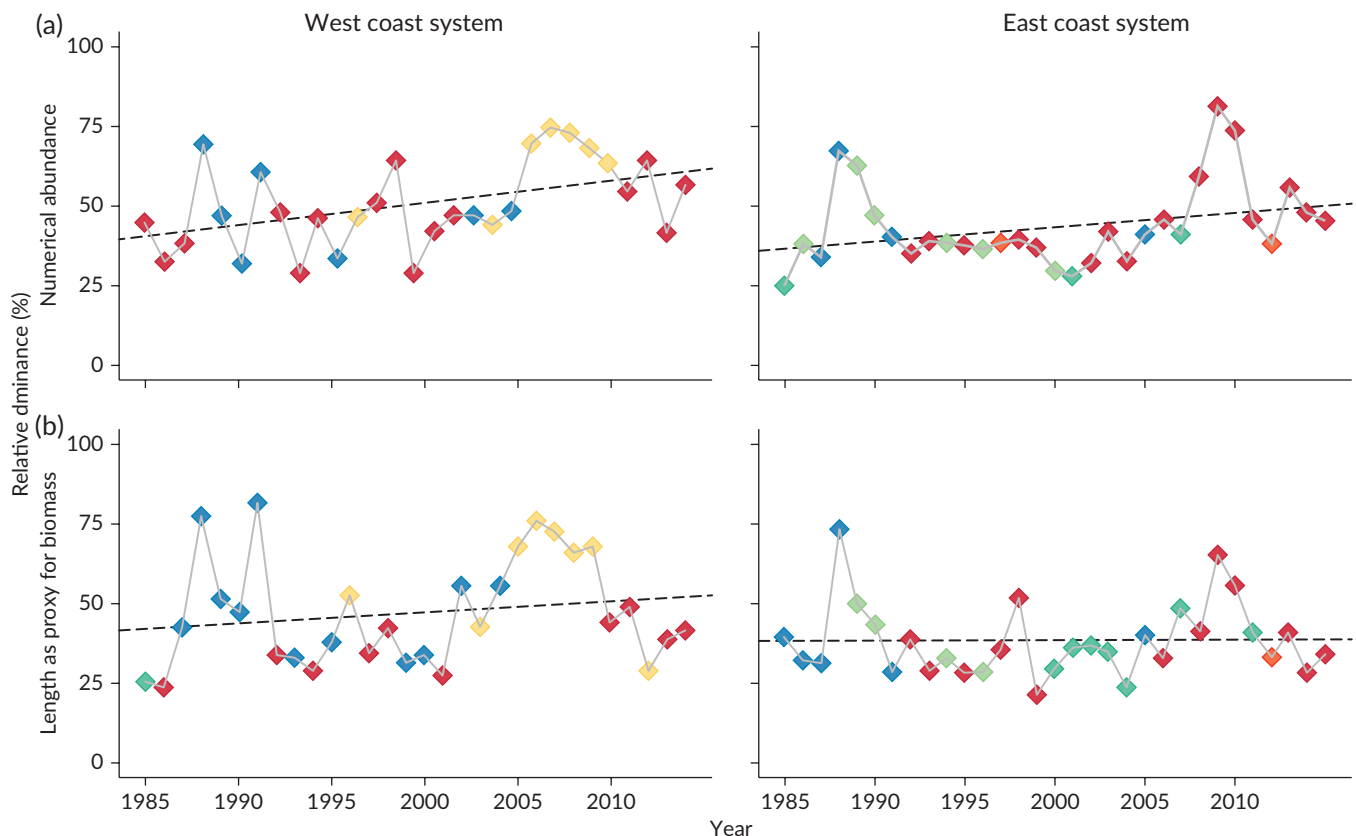
Sea surface ( $\leq 10$  m) temperature data (°C) are collected as part of monitoring and were assigned to the relevant latitudinal band for this analysis (Figure 1).

## 2.2 | Methods

The study data comprises 9 latitudinal bands on the west coast and 11 on the east. Community time series were compiled for each latitudinal band following sample-based rarefaction (Dornelas *et al.*, 2014; Supporting Information Code S1). Because species richness and other diversity metrics are sensitive to sample size, raw (unrarefied) data can lead to bias. Rarefaction (Gotelli & Colwell, 2011) is a statistical resampling methodology that reduces this bias. Here the minimum number of samples per year, per latitudinal band, was resampled to generate a constant number of samples to be used in the analyses. Sample-based rarefaction was used in this study as, in contrast with individual based rarefaction, it retains species identity.

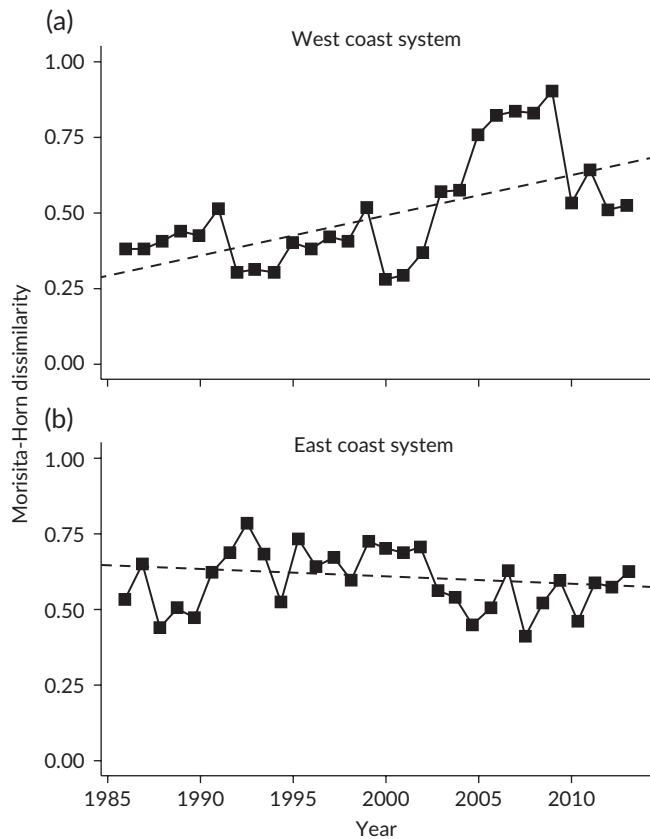
The most numerically abundant species in each latitudinal band and each year, was defined as the dominant species. In the case of a tie (where two or more species were jointly most abundant) the species occurring first in the list of species was chosen. Relative dominance was then calculated as a proportion of the total abundance of species contained within each assemblage. (R code for this function and others can be found in the R markdown document Supporting Information Code S1).

We first quantified the overall annual trend in relative dominance, on each coast, using ordinary least squares (OLS). Next, we computed overall annual change in the composition of the assemblage, in each



**FIGURE 2** Trend in relative dominance of the most dominant species calculated by (a) numerical abundance and (b) length (as a proxy for biomass) across all latitudes by year off the west and east coasts of Scotland. The dominant species identities are similar in both calculation methods and the trends follow similar patterns, although when using length (biomass) the inclines are flatter in both east and west coast systems: west coast system, numerical abundance slope = 0.007,  $P < 0.05$ , biomass slope = 0.003,  $P > 0.05$ ; east coast system, numerical abundance slope = 0.004,  $P > 0.05$ , biomass slope = 0.0001,  $P > 0.05$ . Species: (◆) *Clupea harengus*, (◆) *Melanogrammus aeglefinus*, (◆) *Merlangius merlangus*, (◆) *Scomber scombrus*, (◆) *Sprattus sprattus* and (◆) *Trisopterus esmarkii*





**FIGURE 3** Trend in Morisita-Horn dissimilarity by year (using year 1985 as a baseline). Although the trend is increasing in both systems it is only significant in the west coast system ( $P < 0.001$ ). (a) Upper panel shows West Coast increasing trend. (b) Lower panel shows the East Coast decreasing trend

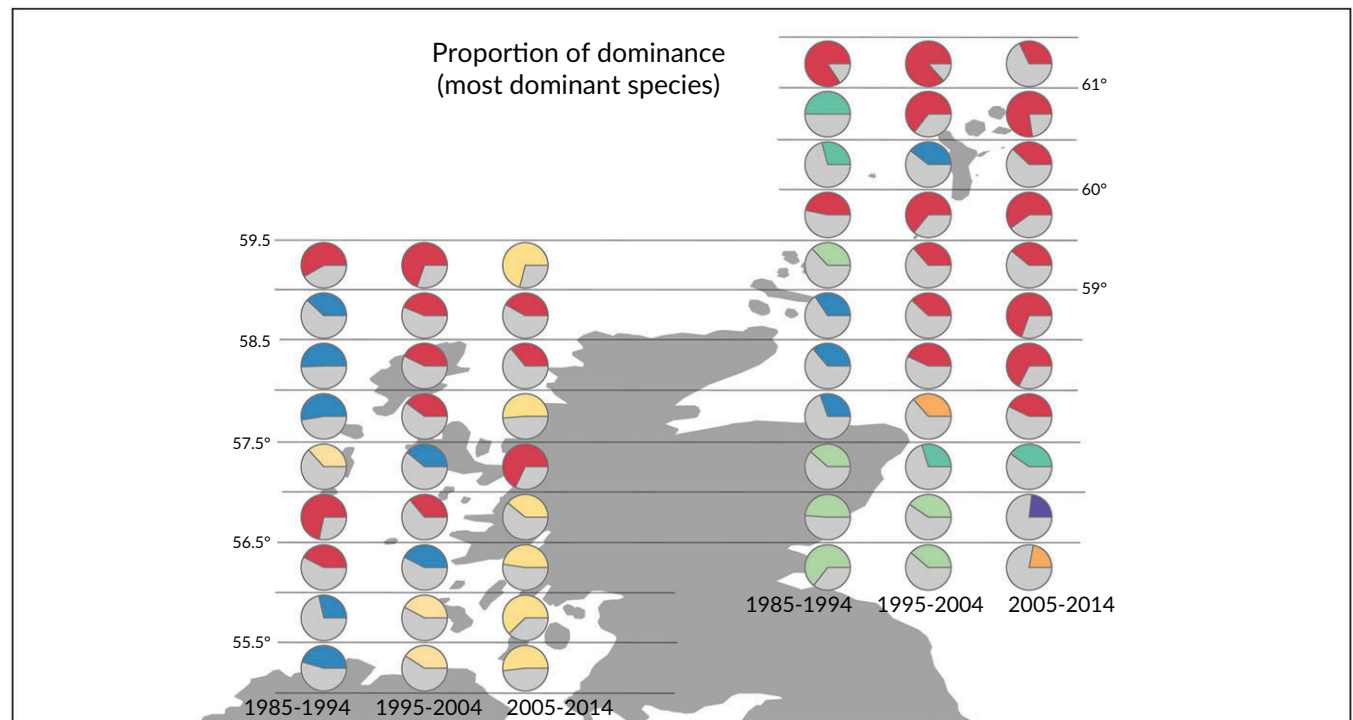
latitudinal band and on each coast, relative to the first year in the time series (1985), using the Morisita-Horn dissimilarity index [vegdist function in the vegan package in R (Oksanen *et al.*, 2017)] and described the trend using an OLS regression. East and west coast trends in mean overall temperature data were treated in the same way. Morisita-Horn was chosen to quantify overall compositional change as it is sensitive to the abundances of the most abundant species (Magurran, 2013). Finally, we used two-way ANOVA, with an interaction term, to test for differences in dominance between coasts:  $\text{model} < \text{aov}(\text{relative dominance} \sim \text{year} * \text{coast})$ .

All analyses used R statistical software ([www.r-project.org](http://www.r-project.org)). Mapping functions were carried out using the ESRI GIS software ArcGIS (ESRI, 2015).

### 3 | RESULTS

The dominance structure of these marine assemblages changed over the 30 year duration of the study (Figure 2). However, although dominance increased in both systems, this increase was significant only for the west coast (OLS regression: west coast  $P < 0.05$ , east coast  $P > 0.05$ ). This result is supported by a two-way ANOVA which revealed significant differences in dominance between years ( $F_{1,56} = 8.493 P < 0.01$ ) and between coasts  $F_{1,56} = 5.175 P < 0.05$ ), but no significant interaction for year x coast ( $F_{1,56} = 0.633, P > 0.05$ ; Supporting Information Tables S2 and S3).

Both systems became increasingly dissimilar (Figure 3) in composition over time (relative to the first year in the time series), with a significant rise in dissimilarity in the west coast, (OLS regression:



**FIGURE 4** Map showing spatio-temporal changes in dominant species in fish assemblages off the west and east coasts of Scotland's (identity and amount). The pie diagrams illustrate changes in the dominance of the most dominant species by 0.5° latitudinal band within 10 year intervals. (●) *Alloteuthis subulata* (squid), (●) *Trisopterus esmarkii* (pout), (●) *Sprattus sprattus* (sprat), (●) *Scomber scombrus* (mackerel), (●) *Merlangius merlangus* (whiting), (●) *Melanogrammus aeglefinus* (haddock) and (●) *Clupea harengus* (herring)

$P < 0.001$ ), but not the east coast (OLS regression:  $P > 0.05$ ). Mean sea surface temperatures from the same locations during Q1 also increased in both systems, by  $1.3^{\circ}\text{C}$  on the west coast and  $0.7^{\circ}\text{C}$  on the east coast. Once again, the trend was significant only for the west coast (OLS regression: west coast  $P < 0.05$ , east coast  $P > 0.05$ ).

Overall differences between the two ecosystems were underlain by within-system differences in relative dominance (Figure 4, Supporting Information Table S3 and Figure S2). Overall dominance varied significantly over time ( $F_{1,256} = 10.65$ ,  $P < 0.001$ ), on the west coast, but there was no effect of latitude, ( $F_{1,256} = 0.1$ ,  $P > 0.05$ ) and no interaction between latitude and time ( $F_{1,256} = 0.6$ ,  $P > 0.05$ ). In contrast, on the east coast there was a significant interaction between latitude and time, ( $F_{1,306} = 4.84$ ,  $P < 0.05$ ) and a significant effect of latitude ( $F_{1,306} = 21.05$ ,  $P < 0.001$ ) but not of time ( $F_{1,306} = 0.04$ ,  $P > 0.05$ ; Supporting Information Table S2).

## 4 | DISCUSSION

The focus here on marine-fish assemblages, rather than fish populations, reveals community wide changes that can be obscured in single species studies. A spatio-temporal approach (Henderson, 2017) in combination with examination of key attributes of community structure, such as the changes in dominance, is an important starting point for understanding the consequences of the melting pot of pressures these systems are currently under (Majewski *et al.*, 2017).

The two coastal systems show distinct differences not only in the proportion of dominance but also in the identity of the most dominant species. Interestingly, it was in the west coast assemblages that we detected the greatest change. Previous work (Magurran *et al.*, 2015) highlighted an increase in biotic homogenisation over the same period and hypothesised that changes in water temperature may have contributed to this pattern. Another recent study (Hansen *et al.*, 2017) found that there were shifts in species dominance expected in freshwater lake systems as a result of warming waters. The observed differences in dominance found between the east and west coasts are therefore potentially linked to the different patterns of change in sea surface temperatures (Simpson *et al.*, 2011; Stuart-Smith *et al.*, 2017; Townhill *et al.*, 2017) since water temperature is a key driver of distribution patterns in marine fishes (Perry *et al.*, 2005). Indeed, the effect of climate change on North Sea circulation and its fish stocks has been discussed elsewhere (Baudron *et al.*, 2013; Hiddink *et al.*, 2014; Turrell, 1992). However, temporal variation in sea surface temperatures (Genner *et al.*, 2004; Henderson *et al.*, 2011; Miller *et al.*, 2011) is unlikely to be the only driver influencing the trends since fishing pressure also leads to marked changes in the structure of marine assemblages (Jackson *et al.*, 2001).

The contrasting outcomes in these two geographic localities illustrate why it is difficult to predict how different systems will respond to environmental and anthropogenic drivers (Poloczanska *et al.*, 2016). Such spatial heterogeneity may be a widespread phenomenon. Contrasting patterns of biodiversity change were also evident in two zones of a bay in Brazil, monitored over three decades, (Araújo *et al.*, 2016).

On the east coast, which exhibits less temporal variation in identity of the most dominant species, the Norway pout *Trisopterus esmarkii* (Nilsson 1855) is the overall dominant for around two thirds of the time series with the exception of the initial decade where haddock *Melanogrammus aeglefinus* (L. 1758) features more prominently. In contrast, on the west coast the identities change from Atlantic herring *Clupea harengus* L. 1758 in the first decade, to *T. esmarkii* in the second and finally Atlantic mackerel *Scomber scombrus* L. 1758 in the third. These species make different contributions to ecosystem function and have different economic values. For example, *S. scombrus* is thought to be a predator of juvenile *T. esmarkii* (ICES, 2005) and while *S. scombrus* catches have high commercial value, *T. esmarkii* is considered useful only as food in the aquaculture industry (ICES, 2005).

Historically, Scotland's economy has enjoyed a significant contribution from the fishing sector and it is important that this tradition be maintained, but only if it can be done in a sustainable manner. A better understanding of fish communities can lead to more efficient management strategies (Cheung *et al.*, 2018; Moriarty *et al.*, 2018). Currently there are new opportunities for the development of broader, constructive approaches to fisheries management (Jacobs *et al.*, 2018) where fish biology plays an important role in informing wild fisheries and their continued sustainability.

Science has a vital part to play in the conservation and management of fish resources (Obregón *et al.*, 2018) but, as this study has demonstrated, greater understanding of how fish assemblages respond to change can be gained if fisheries managers take advantages of the rich toolkit of biodiversity metrics. Even simple measures, such as the dominance index used here, reveal patterns that have hitherto been masked in population based analyses (Perry *et al.*, 2010). As such, they have the potential to shed new light on the causes and consequences of ecosystem restructuring.

## ACKNOWLEDGEMENTS

We are grateful to the two anonymous reviewers whose comments have strengthened our paper considerably.

## Author contributions

F.M. and A.E.M. conceived the project; F.M. undertook the analyses and both authors contributed to the manuscript.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Moyes F, Magurran AE. Change in the dominance structure of two marine-fish assemblages over three decades. *J Fish Biol.* 2019;94:96–102. <https://doi.org/10.1111/jfb.13868>

## Research



**Cite this article:** Moyes F, Trindade-Santos I, Magurran AE. 2023 Temporal change in functional rarity in marine fish assemblages. *Proc. R. Soc. B* **290**: 20222273. <https://doi.org/10.1098/rspb.2022.2273>

Received: 11 November 2022

Accepted: 30 January 2023

**Subject Category:**

Ecology

**Subject Areas:**

ecology, ecosystems

**Keywords:**

marine fish, functional rarity, structural change, biodiversity, species abundance distribution, trait abundance distribution

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Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.6416972>.

# Temporal change in functional rarity in marine fish assemblages

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Recent research has uncovered rapid compositional and structural reorganization of ecological assemblages, with these changes particularly evident in marine ecosystems. However, the extent to which these ongoing changes in taxonomic diversity are a proxy for change in functional diversity is not well understood. Here we focus on trends in rarity to ask how taxonomic rarity and functional rarity covary over time. Our analysis, drawing on 30 years of scientific trawl data, reveals that the direction of temporal shifts in taxonomic rarity in two Scottish marine ecosystems is consistent with a null model of change in assemblage size (i.e. change in numbers of species and/or individuals). In both cases, however, functional rarity increases, as assemblages become larger, rather than showing the expected decrease. These results underline the importance of measuring both taxonomic and functional dimensions of diversity when assessing and interpreting biodiversity change.

## 1. Introduction

Contemporary ecological communities are experiencing biodiversity change that has little precedence in the historical record, with marine systems among those in which this change is particularly marked [1–3]. This biodiversity crisis underlines the importance of measuring biodiversity in robust and ecologically meaningful ways. But because biodiversity is a multifaceted concept [4,5], it also raises questions about the extent to which information on change in one dimension of diversity, such as taxonomic diversity, sheds light on change in other dimensions, such as functional diversity. Growing evidence that ecosystems are being restructured along multiple dimensions of biodiversity [6] underlines the need for improved understanding of the linkages between these dimensions.

Ecological assemblages typically consist of a few common and many rare species, a pattern that is described by a species abundance distribution (SAD). Species that are considered to be taxonomically rare occupy the lowest ranks in this distribution [7,8], with other categorizations of rarity drawing on species occurrence data, and/or features such as habitat specificity (e.g. [9]). A recent macroecological analysis [10] showed that increases in taxonomic rarity are widespread. Such shifts have been attributed to immigration and warming [11–16], and may occur alongside an increase in assemblage size due to greater number of species and/or individuals. Taxonomically rare species could contribute unusual trait combinations to a system [17,18] and play an important role in supporting ecosystem functioning [19,20]. Temporal change in taxonomic rarity thus has the potential to shed light on underpinning changes in functional rarity. However, the biodiversity literature contains many examples of cases where change in one attribute of diversity is uncorrelated or only weakly correlated with another (e.g. [21,22]). Moreover, a taxonomically rare species can have a dominant trait value and vice versa. Therefore, even though metrics of functional rarity can be weighted by taxonomic abundance [23], it does not necessarily follow that trends in taxonomic rarity, and trends in trait (functional)



**Figure 1.** Map showing the latitudinal bands with the central latitude added in text. The west coast system is shaded in green with the east coast in blue (this colour scheme is consistent throughout the paper).

rarity will coincide. To predict whether change in taxonomic rarity and change in functional rarity are correlated, we need to understand how metric responses are shaped by shifts in the underlying SAD.

If an assemblage gains more biomass, or larger numbers of individuals, the number of species in the assemblage is expected to rise, but in a nonlinear way. This is the principle that underlies rarefaction analyses used to make fair comparisons between assemblages [4,24,25]. Owing to the constraints imposed by the uneven distribution of species that characterize SADs [26] other assemblage properties will also change as an assemblage grows (or shrinks). For example, larger assemblages are generally less (taxonomically) even than smaller ones [27]. We therefore expect larger assemblages to exhibit increases in taxonomic rarity. However, trait abundance distributions (TADs) tend to be more even than SADs (e.g. [28]). This higher evenness in TADs [29] suggests that functional rarity may be less responsive to a change in assemblage size than taxonomic rarity. To explore these questions, we construct a null model taking account of both observed species and TADs and in which individuals are progressively drawn at random from a gamma [30] assemblage to construct local assemblages of different size. Departures from this null will shed light on how rare trait combinations are conserved or lost, as assemblages change in size.

Here we focus on two Scottish marine fish assemblages (figure 1), each sampled by scientific trawling over a period of three decades. Although matched by latitude, these assemblages belong to different marine ecosystems: the seas to the

west of Scotland are part of the Celtic-Biscay Shelf ecosystem [31] while those to the east of Scotland are placed in the North Sea ecosystem [32]. These systems share many, but not all, fish species, but have different dominant species, and differ in how species dominance changes over time [33]. They thus provide an interesting test case in which to ask whether shifts in taxonomic rarity are a proxy for change in functional rarity as well as whether these biodiversity changes are consistent across different geographical regions.

## 2. Methods

### (a) Study location

The data used in this work were sourced from the International Council for the Exploration of the Sea (ICES) and are taken from two standardized scientific trawl surveys incorporating the ICES areas VIa (west coast system), IVa and IVb (North Sea) [31,32] (east coast system). Each species record contains a precise geographical location and numerical species abundance represented by CPUE (catch per unit effort), which in this instance refers to the number of individuals of a given species caught per hour using a tow duration of half an hour. Here we use ICES rectangles to form the boundaries of assemblages. These ICES rectangles are freely available for download on the ICES website [34] and represent 30' latitude by 1° longitude in a grid cell. In this work, we chose latitudinal bands which were created by merging the ICES rectangles longitudinally. This produced 11 'bands' on the east and 9 on west coast (see map in figure 1; for further information see electronic supplementary materials).

The west coast system (which is part of the overall Celtic Seas ecoregion) is mostly relatively shallow, particularly in the Irish Sea area where depth is typically less than 100 m, and comprises a variety of habitats [35], including rocky outcrops and sandbanks. The system is largely sheltered from the winds and currents of the North Atlantic and water circulation patterns are influenced by freshwater discharge from rivers such as the Severn and the Shannon as well as the many sea lochs found on the west coast of Scotland [36]. The North Sea system is semi-enclosed and includes the Norwegian Deep in the north-eastern portion where depths can be up to 700 m. Much of the remainder of the ecosystem is relatively shallow with large estuarine areas. The habitats here are largely dominated by sand, mud and some harder grounds around the Orkney and Shetland islands.

## (b) Data handling and analysis

Each latitudinal band produced a 30-year time series. We employed sample-based rarefaction to reduce bias due to sampling effort [8,24] (for further details on the process, see electronic supplementary materials). To do this, we resampled the data based on the minimum number of samples where a sample consisted of all trawl information for a single year within a single latitudinal band. We also filtered records to ensure that no crustaceans or other non-fish were included in our final dataset. This process left us with 116 species in the west coast pool and 121 species in the east coast pool.

We first computed numerical abundance ( $N$ ) and species richness ( $S$ ) at each time step within each latitudinal band to understand how assemblage size is changing. To quantify temporal change in the metrics, we fitted an ordinary least squares (OLS) linear regression model [37]. We also computed the median absolute deviation (MAD), using the `mad` function from the `stats` package in base R [38], to examine the variation in trends within each system.

Next, we assembled information on the fish diversity of each of these latitudinal bands at each time step. To calculate taxonomic rarity, we used the `'funrar'` package in R [39]. The taxonomic rarity of a species within an assemblage is measured by using the inverse of relative abundance. Very rare species have a value close to 1 while common/abundant species will approach 0 (for equation, see electronic supplementary materials). This score is assigned to each species, and therefore, to produce an assemblage level measure, we used the mean score for the species present in a given year. We also calculated Simpson's evenness (taxonomic evenness) [8] and species richness ( $S$ ) in each case.

To compute functional rarity, we selected 11 traits, both continuous and categorical, reflecting the ecological roles of the species. Traits were sourced using the most recent release of FishBase [40] (for further details on trait choice, see electronic supplementary material, table S1 and trait choice). To understand better the shape of these trait distributions we examined the kurtosis and skewness of the continuous traits (see electronic supplementary material, table S3). This was done using the `moments` [41] package in R. We then generated the multidimensional functional space, based on Gower distance, occupied by each assemblage using the R function (`quality_funct_space()`) developed by Maire *et al.* [42]. Functional rarity as used here is weighted by abundance and corresponds to the mean pairwise distance between species within the assemblage (see electronic supplementary material, figure S1 for a pictorial representation). For any species, distance is measured between it and all others in the assemblage, with its functional rarity computed as the mean of these distances (see electronic supplementary materials for equation). As with taxonomic rarity, functional rarity ranges between 0 and 1, with rarer species tending towards 1 and more common species tending towards 0 (for equation see electronic supplementary materials). Additionally, as with taxonomic rarity, this is a species-level metric and we therefore

used the mean rarity values of those species present at each time step within an assemblage [23,43].

Given the potential importance of the distribution of trait values in shaping the response of functional rarity to shifts in assemblage size [28,29], we also calculated the functional evenness of the trait distribution, and the skewness and kurtosis (calculated using the `moments` package in R [41]) of the species-level functional rarity values within each latitudinal band at each time step. Finally, to understand whether functionally rare species recruited to these assemblages are also taxonomically rare, we re-computed the functional rarity metric with no abundance weighting (figure 4g,h).

## (c) Null model

Separate null models (see electronic supplementary material, figure S3) were constructed for the two coastal assemblages. First, a subset of species (58 for the west coast and 55 for the east—these are the typical maximum numbers observed in a latitudinal band) was selected at random from the overall species pool of a given coastal system. A data frame of trait values for these species was created. Next, we re-assigned trait values to each species in this null gamma assemblage by independently randomizing the vector of each trait in the data frame. This shuffling broke any inherent correlation between traits and produced a null gamma assemblage in which each of the species had a randomly allocated set of trait values. Species retained their relative numerical abundance, as expressed in the original dataset. Following this,  $n = 100$  individuals were sampled, at random, from the null gamma assemblage. The same assemblage properties as before, namely total number of species ( $S$ ), mean functional rarity, skewness and kurtosis of functional rarity, functional evenness, mean taxonomic rarity and Simpson's evenness, were computed after each draw. Next, the value of  $n$  was increased in progressive steps (this step was a proportion of the total  $n$  in the chosen assemblage and ranged between 50 and 2000), with assemblage properties again computed at each step, until maximum  $n$  in the subset is reached. The trait array was then re-shuffled before the whole model was re-run. This was repeated 1000 times, with the mean and standard error (95%) of each assemblage property computed on each run. In all cases, we constructed a  $S(N)$  rarefaction plot as a check that the null model was behaving as expected (see electronic supplementary material, figure S4). The whole procedure was then repeated five times, starting with a new draw of either 55 or 58 species from the regional assemblage.

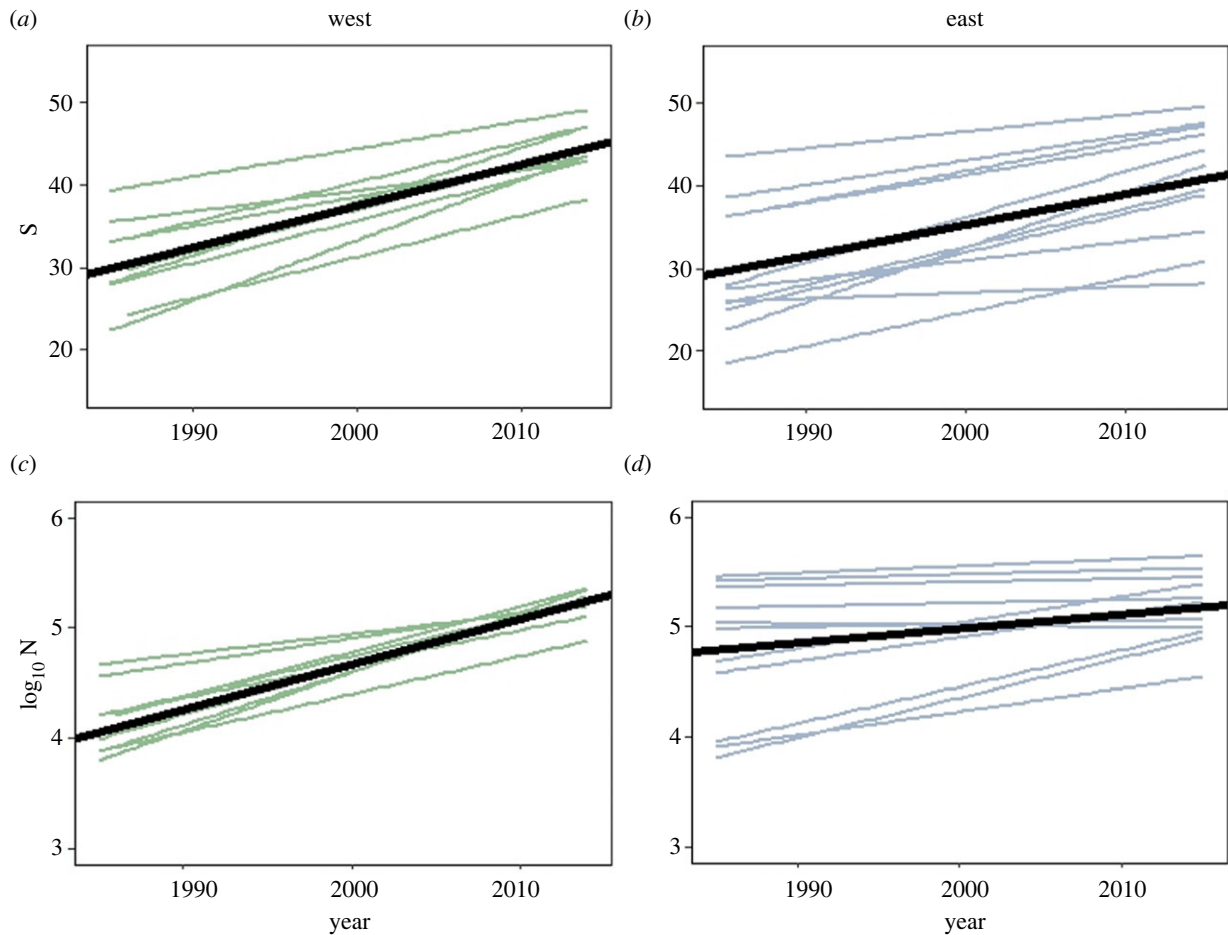
The final output of the model produced a data frame of metrics at each value of  $N$ . We used this to visualize the relationship between metrics in the null. The model performed consistently using a range of initial sample pools (see electronic supplementary material, figure S5), thus providing evidence of the robustness of our results.

## 3. Results

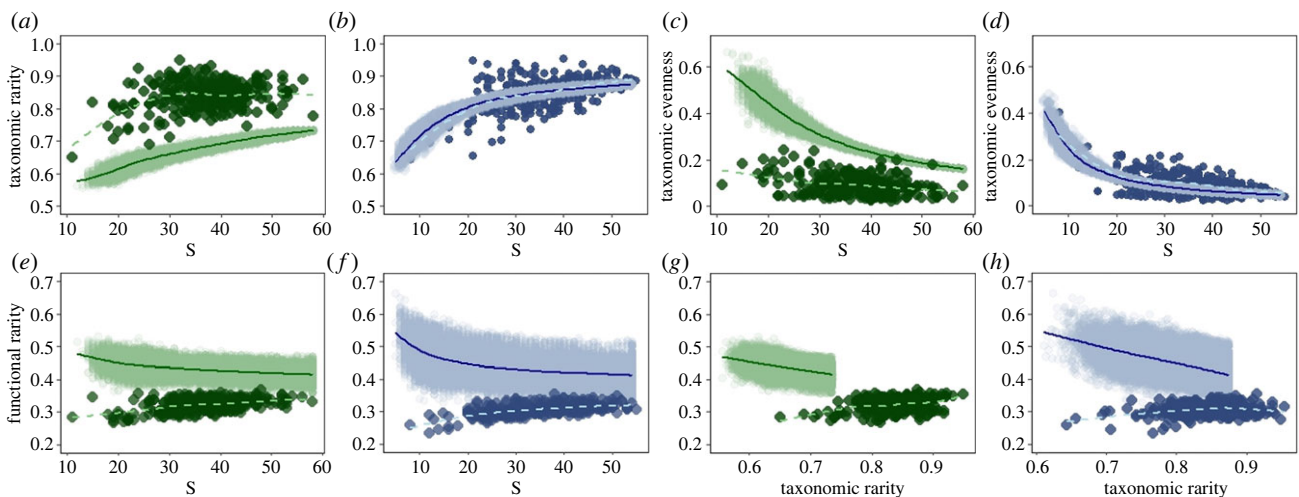
Our analyses revealed that both coastal systems increased in assemblage size ( $S$  and  $N$ ) over the duration of the time series (figure 2). In addition, we observed greater variability in trends in the east coast than the west for all metrics apart from evenness. Results of the MAD were as follows. West coast:  $S = 0.185$  and  $N = 1863$ . East coast:  $S = 0.206$  and  $N = 3375$ .

Our null model showed, as expected, that as the number of individuals in an assemblage increases, so too does the number of species, but in line with expectation on a saturating curve (see electronic supplementary material, figure S4). As assemblage size increases, taxonomic rarity is expected to increase, and evenness to decline, and this is what we





**Figure 2.** Slopes of change for each metric by coastal system (the west coast is shown on the left and coloured in green, with the east coast on the right and coloured blue). The darker line is the common trend (computed as the OLS regression of all the time series) and the lighter lines the individual latitudinal bands. The figure shows the greater heterogeneity of slopes on the east coast as compared to the west (see text for details). The overall slopes (solid black lines) are significant for both metrics in both systems. East:  $S$   $p$ -value  $< 0.0001$ ,  $N$   $p$ -value = 0.0004; west:  $S$   $p$ -value  $< 0.0001$ ,  $N$   $p$ -value  $< 0.0001$ .

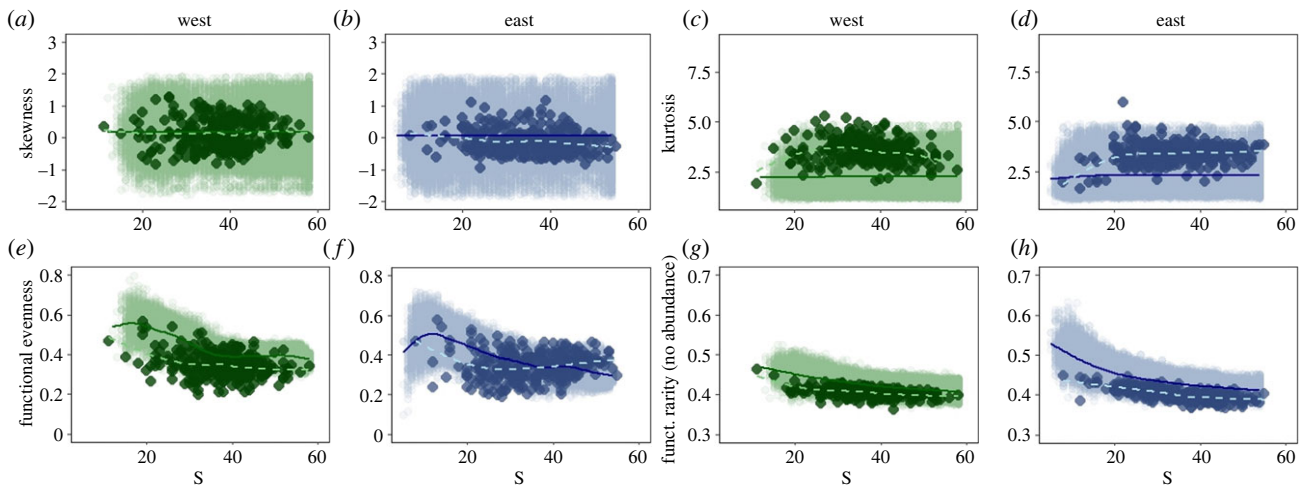


**Figure 3.** Relationship between null and observed. Observed values (yearly results by latitudinal band) are shown as solid points, with the distribution of null results indicated by the shaded area. In both cases trends are indicated using a loess fit, computed using the `stat_smooth(method = 'loess')` option in `ggplot2`. West coast results are shaded green and east coast blue, with the observed loess as a pale dashed line and the null as a darker solid line.

found (figure 3*a–d*). On the east coast levels of taxonomic rarity and evenness were aligned with the null while west coast assemblages had greater taxonomic rarity and less evenness than expected.

In addition, the null model predicted that functional rarity should decline as assemblages grow in size, and as taxonomic

rarity increases (figure 3*e–h*). However, in neither the west coast system nor the east coast system (figure 3) did the observed data show these trends. In both systems, functional rarity showed a weak increase in response to both richness and taxonomic rarity and occurred at lower levels than predicted (figure 3*e–h*). The same patterns were evident when



**Figure 4.** Relationship between null and observed. As with figure 3, observed values are shown as solid points, with the distribution of null results indicated by the shaded area and trends shown using a loess fit. The west coast results are shaded green and east coast blue, with the observed loess as a pale dashed line and the null as a darker solid line.

the null model was re-run with different gamma assemblages indicating that the results are robust against variation in initial composition (see electronic supplementary material, figure S5).

In both west and east systems, values for the skewness of the observed distributions of functional rarity (figure 4*a,b*), plotted in relation to  $S$ , were nested within the null, with average trends close to zero in both cases. There was also overlap between observed and null levels of functional evenness (figure 4*e,f*) and in the kurtosis of functional rarity (figure 4*c,d*). However, in this latter case the distributions of observed functional rarity were moderately leptokurtic (median overall kurtosis: west null = 2.08, observed = 3.5; east null = 2.12, observed = 3.45; see electronic supplementary material, figure S6). Finally, when functional rarity was re-computed ignoring both the species abundance and TADs, the trends in both observed and null were closely matched (figure 4*g,h*).

## 4. Discussion

Assemblages on both coasts are increasing in richness and in numerical abundance. These shifts in assemblage size should lead to increases in taxonomic rarity and decreases in (taxonomic) evenness, and this is what we found. This indicates that the directionality of changes in these taxonomic properties of these species' abundance distributions is consistent with our expectation based on a random draw from the gamma assemblage, albeit with some differences in the magnitude of the response between coasts. All other things being equal, as the null shows, we also expected this observed increase in assemblage size to lead to a decrease in functional rarity [29]. However, we found the opposite with both systems exhibiting a weak positive increase in functional rarity, as they gained more species. Moreover, and in further disagreement with the null, observed functional rarity was broadly maintained as taxonomic rarity increased.

A species' functional rarity value is dependent not only on its own trait combination and abundance but also on the trait combinations and abundance of all other fish in the assemblage [23,39,44]. The shape of this TAD, for example, its degree of

skewness and kurtosis, will determine not just the level of functional rarity, but also shed light on the processes involved in community assembly [28,29]. Our analysis, which took account of the TAD as well as the SAD, detected no disagreement between the observed and null for trends in relation to increases in assemblage size for either functional evenness or the skewness of the functional rarity distribution. On the other hand, distributions of observed functional rarity tended towards leptokurtosis which could help explain why our observed values of functional rarity are lower than the null expectation (figure 3*e,f*). This interpretation is supported by the analysis of functional rarity in which both SAD and TAD were ignored (figure 4*g,h*). Here we uncovered a decline in functional rarity in larger assemblages, as predicted by our initial null. We therefore conclude that the functionally rare species that are entering these local assemblages are less abundant than is predicted from a random draw from the gamma assemblage.

A striking feature of our results is that the observed relationships between functional rarity and richness, and between functional rarity and taxonomic rarity were generally weak with relatively little trend in the metric in response to shifts in assemblage properties. Functional evenness also changed little with assemblage size, particularly in the east coast system (figure 4*f*). Taken together these findings suggest that the functional properties of these marine fish assemblages are conserved as assemblage size changes. Working with within-trait variation, Gross *et al.* [28] reported more even abundance distributions of trait values within dryland plant assemblages than would be expected by chance. Such patterns help maximize local multifunctionality [19,28,29]. In our case, we did not find any marked discrepancy between null and observed functional evenness, but we computed functional evenness across eleven traits rather than within a single trait. It would be interesting to examine the TAD at the individual as well as the species level, but we were unable to do this due to the unavailability of intraspecific trait information.

Our analysis also uncovered interesting differences between the two systems. For example, we observed higher levels of taxonomic rarity relative to the null expectation (figure 3*a,b*), as well as reduced evenness, for given levels of

richness, in the west coast system (figure 3c) as opposed to the east coast system (figure 3d). Since increased taxonomic rarity can be associated with habitat complexity [45–47], this result could reflect the increased structural heterogeneity of the west coast, as well as contrasts in warming trends, and/or recovery from historical fishing pressures [33,48]. Historically, the east coast system (North Sea region) has been more heavily exploited than the west coast system (Celtic Sea area), but, since the beginning of this time series in 1985, fishing pressure has been largely similar in both areas (see electronic supplementary material, figure S7). The differences in taxonomic diversity could also be linked to the increased variability in trends on the west coast (figure 2). Nonetheless, the observed relationship between functional rarity and richness, and the level of functional rarity, were similar in the two coastal systems suggesting that environmental filtering and niche differentiation could be important in shaping the distribution of traits in both cases [29].

To date, investigations of temporal change in marine ecosystems have focused on single populations [49,50]. However, it is becoming clear that multi-species, assemblage-based analyses [51,52], which include information on functional and taxonomic diversity, and potentially also phylogenetic diversity, will be important in tracking biodiversity change in these systems, predicting their resilience in the face of anthropogenic pressures [53], and in shaping conservation decisions and designing fisheries policy [54–56]. As our investigation has shown, different dimensions of biodiversity change are not necessarily correlated. Understanding how this complexity arises, and what its consequences are for the maintenance of ecosystem function, is a substantial future challenge. Null models, as employed here, represent a powerful means of elucidating the processes that underpin assemblage restructuring [56]. For example, it would be interesting to use a null model approach to examine the interactions between environmental filtering and shifts in assemblage size, particularly when the latter is a response to an increase in carrying capacity linked to climate change. Unravelling the mechanistic links between trends in

functional and taxonomic diversity will also be important, in, for instance, discovering the extent to which functional rarity is linked to whether a species is a winner or loser during biodiversity change [33,57].

In conclusion, analyses of the two coastal systems revealed that trends in taxonomic rarity are an inadequate proxy for trends in functional rarity, and that the ongoing increases in assemblage size can have complex, and context-dependent, consequences for assemblage biodiversity. A clearer understanding of the potential drivers of change in functional rarity can assist with more targeted conservation plans and fisheries management, and it is already clear that shifts in community rarity have implications for ecosystem resilience [17,20,58,59]. Our study highlights the importance of taking an integrative and multidimensional approach to protect, maintain and sustain the functional integrity of marine fish assemblages [60–62].

**Data accessibility.** All data are publicly available via the DATRAS portal ([http://datras.ices.dk/Data\\_products/Download/Download\\_Data\\_public.aspx](http://datras.ices.dk/Data_products/Download/Download_Data_public.aspx)). Code is included in the electronic supplementary material [63].

Additional information is also provided in the electronic supplementary material [63].

**Authors' contributions.** F.M.: conceptualization, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; I.T.-S.: conceptualization, formal analysis, visualization, writing—review and editing; A.E.M.: conceptualization, formal analysis, methodology, supervision, validation, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest declaration.** The authors declare no competing interests.

**Funding.** A.E.M. thanks the Leverhulme Trust (RPG-2019–402) for support.

**Acknowledgements.** We are grateful to the reviewers for their insightful comments. I.T.-S. acknowledges CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Coordination for the Improvement of Higher Education Personnel), process number 88881.129579/2016–01 (Finance Code 001) for a PhD scholarship. We also thank the 'Fish lunch' lab group in the Centre for Biological Diversity, University of St Andrews.

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