

Stable isotope analysis of benthic-pelagic coupling in
North East Atlantic fishes

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Abstract

In continental-shelf ecosystems, consumers may be sustained by benthic and/or pelagic pathways, the linkages between them contributing to benthic-pelagic coupling. The relative flux from each pathway can influence the productivity and stability of the food web, yet few studies have investigated this form of benthic-pelagic coupling and its influence on resilience of species at ecosystem scale.

This PhD investigated the extent to which shelf-sea fish species are affiliated with benthic and pelagic pathways across four UK seas (North, Celtic, Irish Sea and English Channel), what influences this and how this relates to fluctuations in fish abundance. Studied drivers of benthic-pelagic coupling included consumer body mass and trophic level, and water depth, temperature and salinity. Factors influencing variability in species' abundances including benthic-pelagic coupling, life history characteristics and variability in fishing pressure, were also examined.

Stable isotope analysis was used to reveal time-integrated species affiliations to the pathways. Isoscapes were created using queen scallops (sedentary bivalve) and predictor variables to correct for baseline spatial variation in sampled fish species' isotopic values. $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ were used to assess the relative contribution of the pathways to fish consumer production. Use of both $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ isotopes as opposed to just $\delta^{13}\text{C}$ reduced uncertainty in modal use estimates.

Across UK seas most species relied to some extent on both pathways, suggesting strong benthic-pelagic coupling, potentially improving community resilience to perturbations. Trophic level most influenced species' affiliations, with an increase in trophic level causing a marked increase in benthic affiliation and a decrease in pelagic affiliation. A positive but weaker relationship between benthic affiliation and mass was also present, whilst the environmental variables had small and inconsistent effects.

A significant positive relationship between variability in species' abundance and benthic-pelagic coupling was found, whilst weaker non-significant relationships existed with the other factors. These results may aid understanding of ecosystem resilience to climatic and anthropogenic perturbations.

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Table of contents

Abstract	ii
Acknowledgements	iii
Table of contents	v
List of figures and tables.....	viii
List of species scientific and common names.....	xv
Chapter 1. Using stable isotope analysis to examine UK marine food webs and their energy pathways	1
1.1 Marine food webs.....	1
1.1.1 What is a food web?	1
1.1.2 What are the characteristics of a marine food web?	3
1.2 Stability and resilience of marine food webs	6
1.3 Effects of the physical environment and human impacts on food webs	8
1.3.1 Climatic changes	8
1.3.2 Fishing.....	9
1.4 Approaches to food web analysis	11
1.4.1 Traditional approaches to studying food webs.....	11
1.4.2 Using stable isotope analysis to study food webs.....	12
1.4.3 Carbon and nitrogen as food web descriptors	14
1.4.4 Isotopic variation	15
1.4.5 Pelagic and benthic pathways	17
1.4.6 Mixing models	18
1.5 The UK environment and marine food webs	19
1.6 Synopsis	22
1.6.1 Synopsis of chapters	22
Chapter 2: Developing isoscapes to underpin the description and analysis of marine food webs	25
2.1 Introduction	25
2.2 Methods	30

2.2.1 Sampling	30
2.2.2 Stable isotope analysis.....	31
2.2.3 Creation of isoscapes	31
2.2.4 Comparison of isoscapes	32
2.2.5 Referring species isotopic values to a common baseline	32
2.3 Results.....	33
2.4 Discussion	39
2.5 Conclusion	42
3. Estimating contributions of pelagic and benthic pathways to consumer production in coupled marine food webs.....	43
3.1 Introduction	43
3.2. Methods.....	45
3.2.1. Sampling	45
3.2.2 Stable isotope analysis.....	45
3.2.3. Source indicator species	47
3.2.4 Mixing models	48
3.2.5 Biomass estimates	50
3.3 Results.....	50
3.4 Discussion	55
3.5 Conclusion.....	60
Chapter 4. Comparative use of benthic and pelagic food web pathways by fishes in three northeast Atlantic shelf seas.....	61
4.1 Introduction	61
4.2. Methods.....	63
4.2.1. Sampling	63
4.2.2 Stable isotope analysis.....	64
4.2.3 Use of $\delta^{13}\text{C}$ vs $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$	65
4.2.4 Source indicator species	66
4.2.5 Covariate variables.....	67

4.2.6 Comparison of isotopic data across UK seas	67
4.3 Results	69
4.4 Discussion	75
4.5 Conclusion	78
Chapter 5. Higher dependence on pelagic food web pathways exacerbates fluctuations in fish populations.....	80
5.1 Introduction	80
5.2 Methods	82
5.2.1 Datasets	82
5.2.2 Acquiring variables: Benthic-pelagic coupling, life history parameters, fishing pressure	83
5.2.3 Data analysis of trawl survey data	84
5.2.4 Data analysis of stock assessment data.....	85
5.3 Results.....	85
5.4 Discussion	88
5.5 Conclusion	91
6. Conclusions.....	93
6.1 Introduction	93
6.2 Main findings and implications for research	93
6.2.1 Stable isotope methodology	93
6.2.2 Ecosystem perspective	95
6.2.3 Anthropogenic pressures	101
6.2.4 Management measures.....	103
6.3 Conclusion	105
Appendices.....	106
Appendix A	106
Appendix B	112
References	128

List of figures and tables

Figure 1, reproduced from Winemiller and Layman, (2006): Schematic illustrations of four models of food web structure A, Christmas tree (structural and interstitial species); B, onion (hierarchy of core and peripheral species); C, spider web (all species affect all others directly or indirectly); and D, internet (network architecture yields disproportionate influence by hub species).....	2
Figure 2: A map displaying the limits and depth gradients of UK Seas	21
Figure 3: The location of scallops sampled in 2010	30
Figure 4: Predicted baseline $\delta^{13}\text{C}$ (left) and $\delta^{15}\text{N}$ (right) isoscapes across UK waters	35
Figure 5: Residuals (observed – predicted $\delta^{13}\text{C}$ values) of $\delta^{13}\text{C}$ values (left) and $\delta^{15}\text{N}$ values (right) interpolated across UK waters with sampling locations displayed in the black outlined circles	36
Figure 6: Differences in $\delta^{13}\text{C}$ (left) and $\delta^{15}\text{N}$ (right) values between jellyfish and scallop derived isoscapes.	37
Figure 7: Prediction error of $\delta^{13}\text{C}$ values from the isoscapes using (a) jellyfish and (b) scallops and $\delta^{15}\text{N}$ values using (c) jellyfish and (d) scallops	38
Figure 8: Mean and standard deviation of $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ for plaice (red), mackerel (blue) and herring (dashed blue) in the North Sea	49
Figure 9: The estimated relative contribution of the pelagic pathway to fish biomass by species in 2006 using both $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ isotopes (SC) or just $\delta^{13}\text{C}$ (C). Species are ranked based on SC estimates. Points show the mode and bars the 50% credible intervals of the posterior distribution	51
Figure 10: The estimated contribution of the pelagic pathway to fish biomass by species from 2002 to 2006 based on $\delta^{13}\text{C}$ analysis. Points show the mode and bars the 50% credible intervals of the posterior distribution	53
Figure 11: Effects of body mass (bottom) and year (top) on contributions of the pelagic pathway to species' biomass from 2002-2006. Positive values indicate increasing reliance on the pelagic pathway with increasing body mass or year. Points show the mode and bars the 50% credible intervals. Modal values of σ ranged from 0.8 to 1.37 across species.	55
Figure 12: Distributions of isotopic values of benthic and pelagic SIS across UK seas	68

Figure 13: Estimated relative contribution of the pelagic pathway to fish biomass by species (CPP) across all seas ordered by CPP of the Celtic Sea (if absent ordered by values in first appearing panel). Points show the mode and bars the 50% credible intervals of the posterior distribution. Colours display the groups to which species are assigned based on location in the water column and morphology. (1 benthic – 7 pelagic, full description in 4.2.5).....70

Figure 14: Estimated effect of depth, mass, salinity, temperature and trophic level on individuals' affiliation to the pelagic pathways across the Celtic, Irish Sea and English Channel. Points show the mode and bars the 50% credible intervals. σ (amount of variation not explained by the parameters) is 0.77,0.78 and 0.58 respectively71

Figure 15: Estimated effect of body mass on CPP across all seas, points show the mode, bars and lines the 50% and 90% credible intervals respectively72

Figure 16: Estimated effect of trophic level on CPP across all seas, points show the mode, bars and lines the 50% and 90% credible intervals respectively73

Figure 17: A comparison of the estimated effect of mass on CPP (x-axis) with the change in species' trophic level with mass (y-axis) across all seas. Points display the mode and bars the 50% credible intervals. For both axes the dashed lines represent the 0 intercepts and the tick marks represent - 2 to 2.....74

Figure 18: Plots of fluctuations in species' abundances against the relative contribution of the pelagic pathway to fish biomass, asymptotic weight, variability in fishing pressure and recruitment based on stock assessment (SA) and trawl survey (TS) data.....87

Figure 19: Total biomass (million tonnes) by year derived from the pelagic and benthic pathway in the North Sea estimated from A. trawl surveys (NS-IBTS) and B. stock assessments (ICES 2017) and biomass derived from species estimated from C. trawl surveys and D. stock assessments98

Figure 20: A. Gross production of each fish guild estimated from the STATLANT landings data (reproduced from Heath, 2005). Total biomass of each fish guild estimated from B. trawl surveys (NS-IBTS) and C. stock assessments (ICES, 2017).....99

Figure 21: A. Proportion of biomass supported by pelagic pathway based on stock assessments and trawl surveys. B. Proportion of biomass supported by fish guilds based on data from Heath, 2005 (upper), stock assessments (middle) and trawl surveys (lower) 100

Figure A.1: Comparisons between estimates of the relative contribution of the pelagic pathway to fish biomass by species in 2006 when using herring (H) greater than 140g or mackerel (M) as pelagic source indicator species. Results are presented for $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ isotopes (SC) or just $\delta^{13}\text{C}$ (C). Points show the mode and narrow bars the 50% credible intervals of the posterior distribution	106
Figure A.2: Effects of body mass (bottom) and year (top) on the use of benthic pathways by North Sea fish species during 2006. Points show the mode and bars the 50% credible intervals. Positive values indicate increasing reliance on the pelagic pathway with increasing body mass or year. Modal values of σ ranged from 0.8 to 1.37 across species.	107
Figure A.3: Estimated effect of depth on CPP across all seas, points show the mode and bars the 50% credible intervals	108
Figure A.4: Estimated effect of salinity on CPP across all seas, points show the mode and bars the 50% credible intervals	109
Figure A.5: Estimated effect of temperature on CPP across all seas, points show the mode and bars the 50% credible intervals	110
Figure B.1: Comparisons between estimates of the relative contribution of the pelagic pathway to fish biomass by species in 2006 when using herring (H) greater than 140g or mackerel (M) as pelagic source indicator species. Results are presented for $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ isotopes (SC) or just $\delta^{13}\text{C}$ (C). Points show the mode and narrow bars the 50% credible intervals of the posterior distribution	112
Figure B.2: The estimated relative contribution of the pelagic pathway to fish biomass by species in 2006 using both $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ isotopes (SC) or just $\delta^{13}\text{C}$ (C). Points show the mode and narrow bars the 50% credible intervals of the posterior distribution	113
Figure B.3: The estimated contribution of the pelagic pathway to fish biomass by species from 2002 to 2006 based on $\delta^{13}\text{C}$ analysis. Points show the mode and narrow bars the 50% credible intervals of the posterior distribution	115
Figure B.4: Effects of body mass (bottom) and year (top) on contributions of the pelagic pathway to species' biomass from 2002-2006. Points show the mode and bars the 50% credible intervals. Modal values of σ ranged from 0.55 to 0.91 across species. Positive values indicate increasing reliance on the pelagic pathway with increasing body mass or year.	116

Figure B.5: Distributions of isotopic values of benthic and pelagic source indicator species (SIS) across UK seas.....	116
Figure B.6: Estimated effect of depth, mass, salinity, temperature and trophic level on individuals' affiliation to the pelagic pathways across the Celtic, Irish Sea and English Channel. Points show the mode and bars the 50% credible intervals. σ (amount of variation not explained by the parameters) is 0.76,0.73 and 0.56 respectively	117
Figure B.7: Estimated relative contribution of the pelagic pathway to fish biomass by species (CPP) across all seas ordered by CPP across the Celtic Sea (if absent ordered by values in first appearing panel). Points show the mode and bars the 50% credible intervals of the posterior distribution. Colours display the functional groups (FG) (1 benthic – 7 pelagic).....	118
Figure B.8: Estimated effect of body mass on CPP across all seas, points show the mode, bars and lines the 50% and 90 % credible intervals respectively	119
Figure B.9: Estimated effect of trophic level on CPP across all seas, points show the mode, bars and lines the 50% and 90 % credible intervals respectively	120
Figure B.10: Estimated effect of depth on CPP across all seas, points show the mode and bars the 50% credible intervals	121
Figure B.11: Estimated effect of salinity on CPP across all seas, points show the mode and bars the 50% credible intervals	122
Figure B.12: Estimated effect of temperature on CPP across all seas, points show the mode and bars the 50% credible intervals	123
Figure B.13: A comparison of the estimated effect of mass on CPP (x-axis) with the change in species trophic level with mass (y-axis) across all seas. Points display the mode and bars the 50% credible intervals. For both axes the dashed lines represent the 0 intercepts and the tick marks represent - 2 to 2.....	124
Figure B.14: Relationships of variability in species' abundance against the relative contribution of the pelagic pathway to fish biomass (CPP), W^∞ , variability in fishing pressure and recruitment based on stock assessment (SA) and trawl survey (TS).....	125
Table 1: A description of active and passive fluxes related to benthic-pelagic coupling and parameters potentially affecting those fluxes.....	5
Table 2: Isotope abundance of hydrogen, carbon, nitrogen, oxygen and sulphur (adapted from Fry, 2006).....	13

Table 3: Examples of $\delta^{13}\text{C}$ values of benthic and pelagic species from various studies	17
Table 4: Synthesis of studies which developed baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes across UK waters	29
Table 5: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baseline values across UK Seas	33
Table 6: A comparison of uncertainties produced in isoscape methods. *assumes regression relationship remains constant in wider study region and this relationship may breakdown beyond tested parameters	41
Table 7: Count of prey items from gut contents analysis which were classified as benthic, pelagic or unknown. Only counts from pelagic and benthic prey items were used to estimate the percentage of benthic prey items eaten.....	48
Table 8: Percentage of pelagic production consumed estimated using gut contents and stable isotope data (modal estimates using C and SC)	51
Table 9: Estimated contribution of pelagic pathways (modal SC and C estimates) to total biomass (tonnes) in the sampling area (estimated contribution to pelagic pathway by mackerel and plaice assumed to be 0.99 and 0.01 respectively)	52
Table 10: Effects of body mass on use of pelagic (p) and benthic (b) pathways in the North Sea during 2006 (mode and 50% credible intervals). Positive values indicate increasing reliance on the relevant pathway	52
Table 11: Correlations, between years, of modal contributions of pelagic pathways to species' biomass.....	54
Table 12: The effect of body mass and year on the contribution of pelagic (p) and benthic (b) pathways to North Sea fish biomass from 2002 to 2006 (mode and 50% credible intervals). Positive values indicate increasing reliance on the relevant pathway	54
Table 13: The minimum, maximum and mean difference of the 50% credible intervals from estimated relative contribution of the pelagic pathway to fish biomass by species (CPP) using $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ (SC) and $\delta^{13}\text{C}$ alone (C).....	65
Table 14: Source indicator species in the Celtic, Irish Sea and English Channel. Mean, minimum, maximum and standard deviation (SD) of $\delta^{13}\text{C}$ values, count of individuals sampled in each of the seas and % of benthic prey recorded in diet data	67
Table 15: Results of ranked correlation between species' mean trophic level and CPP across the seas.....	71

Table 16: The estimated minimum, mean, maximum and range modal effect of depth, salinity, bottom temperature on CPP across the Celtic Sea (Ce), Irish Sea (I) and English Channel (Ch)	75
Table 17: Ranked correlation for the effect of variables between species present in the Celtic, Irish Sea and English Channel	75
Table 18: W_{∞} values (g) for species from the literature and the resultant mean and \log_{10} values.....	83
Table 19: Results of linear models exploring fluctuations of species' abundances against the relative contribution of the pelagic pathway to fish biomass (CPP), W_{∞} , variability in fishing pressure (FP) and recruitment (R) based on trawl survey (TS) and stock assessment (SA) data. Full statistics available in Table A.3.....	88
Table 20: P-values from modelled fluctuations of species' abundances against the relative contribution of the pelagic pathway to fish biomass (CPP). To calculate CPP mean and individual yearly (2002-2006) $\delta^{13}\text{C}$ (C) values were used in addition to $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ combined (SC) in 2006.....	88
Table 21: Coefficients and p-values of models exploring fluctuations of species' abundances against mean $\log_{10} W_{\infty}$ and $\log_{10} W_{\infty}$ values from different studies based on trawl survey data	88
Table A.1: Spearman's ranked correlation for the size of the effect and range of data used across the English Channel, Irish and Celtic Sea	107
Table A.2: Model fit of equation $\ln(\text{logbiomass} \sim 1, \text{random} \sim 1 \text{Species})$ with and without correlation structure corAR1	107
Table A.3: Results from linear models exploring variability of species' abundance against the relative contribution of the pelagic pathway to fish biomass (CPP), W_{∞} , recruitment and variability in fishing pressure based on trawl survey (TS) and stock assessment (SA) data.....	111
Table A.4: Results from ANOVA comparing models using CPP alone and including other variables based on trawl survey (TS) and stock assessment (SA) data	111
Table B.1: Estimated contribution of pelagic pathways (modal SC and C estimates) to total biomass (tonnes) in the sampling area (estimated contribution to pelagic pathway by mackerel and plaice was assumed to be 0.99 and 0.01 respectively).	113

Table B.2: Effects of body mass on use of pelagic (p) and benthic (b) pathways in the North Sea during 2006. Positive values indicate increasing reliance on the relevant pathway	114
Table B.3: Correlations, between years, of modal contributions of pelagic pathways to species' biomass. Based on $\delta^{13}\text{C}$ data that have not been corrected to account for potential trophic fractionation	114
Table B.4: The effect of mass and year on the contribution of pelagic (p) and benthic (b) pathways to North Sea fish biomass from 2002-2006 (mode and 50% credible intervals). Positive values indicate increasing reliance on the relevant pathway with increasing body mass or year.	114
Table B.5: Correlation between the English Channel, Irish and Celtic Sea based on CPP of species present in all three seas. Correlation between the mean modal CPP across all seas and functional groups was 0.45, $p < 0.001$	117
Table B.6: Results of Spearman rank correlation between species trophic level and CPP across UK seas.	117
Table B.7: The estimated minimum, mean, maximum and range modal effect of depth, salinity, bottom temperature on CPP across the Celtic Sea (Ce), Irish Sea (I) and English Channel (Ch).	126
Table B.8: Ranked correlation for the effect of variables between species present in the Celtic, Irish Sea and English Channel	126
Table B.9: Spearman's ranked correlation for the size of the effect and range of data used across the English Channel, Irish and Celtic Sea	126
Table B.10: P-values from modelled fluctuations of species' abundances against the relative contribution of the pelagic pathway to fish biomass (CPP). To calculate CPP mean and individual yearly (2002-2006) $\delta^{13}\text{C}$ (C) values were used in addition to $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ combined (SC) in 2006	126
Table B.11: Results from ANOVA comparing models based on trawl survey (TS) and stock assessment (SA) data.	126
Table B.12: Results of linear models exploring fluctuations of species' abundances against the relative contribution of the pelagic pathway to fish biomass (CPP), W_{∞} , variability in fishing pressure (FP) and recruitment (R) based on trawl survey (TS) and stock assessment (SA) data	127

List of species scientific and common names

Throughout the thesis I will refer to species using their common names for ease. I have listed below the scientific names and common names which refer to each species.

Common name	Scientific name
Anglerfish	<i>Lophius piscatorius</i>
Bass	<i>Dicentrarchus labrax</i>
Black sea bream	<i>Spondyllosoma cantharus</i>
Blue whiting	<i>Micromesistius poutassou</i>
Boarfish	<i>Capros aper</i>
Brill	<i>Scophthalmus rhombus</i>
Bullrout	<i>Myoxocephalus scorpius</i>
Cod	<i>Gadus morhua</i>
Common dragonet	<i>Callionymus lyra</i>
Conger eel	<i>Conger conger</i>
Cuckoo ray	<i>Leucoraja naevus</i>
Dab	<i>Limanda limanda</i>
Greater argentine	<i>Argentina silus</i>
Greater pipefish	<i>Syngnathus acus</i>
Greater weever	<i>Trachinus draco</i>
Grey gurnard	<i>Eutrigla gurnardus</i>
Haddock	<i>Melanogrammus aeglefinus</i>
Hake	<i>Merluccius merluccius</i>
Herring	<i>Clupea harengus</i>
Jellyfish	<i>Cyanea capillata</i>
John dory	<i>Zeus faber</i>
Lemon sole	<i>Microstomus kitt</i>
Lesser spotted dogfish	<i>Scyliorhinus canicula</i>
Lesser weaver	<i>Echiichthys vipera</i>
Ling	<i>Molva molva</i>
Lion's mane jellyfish	<i>Cyanea capillata</i>
Long rough dab	<i>Hippoglossoides platessoides</i>
Mackerel	<i>Scomber scombrus</i>
Megrim	<i>Lepidorhombus whiffiagonis</i>
New Zealand screw shell	<i>Maoricolpus roseus</i>
Norway pout	<i>Trisopterus esmarkii</i>
Nursehound	<i>Scyliorhinus stellaris</i>
Painted ray	<i>Raja microocellata</i>
Pearlside	<i>Maurolicus muelleri</i>
Pilchard	<i>Sardina pilchardus</i>
Plaice	<i>Pleuronectes platessa</i>
Pogge	<i>Agonus cataphractus</i>
Pollack	<i>Pollachius pollachius</i>

Poor cod	<i>Trisopterus minutus</i>
Pout	<i>Trisopterus luscus</i>
Queen scallop	<i>Aequipecten opercularis</i>
Red gurnard	<i>Chelidonichthys cuculus</i>
Saithe	<i>Pollachius virens</i>
Sand sole	<i>Pegusa lascaris</i>
Sandeel	<i>Hyperoplus immaculatus</i>
Sardine	<i>Sardina pilchardus</i>
Scad	<i>Trachurus trachurus</i>
Scaldfish	<i>Arnoglossus laterna</i>
Sea scorpion	<i>Taurulus bubalis</i>
Shark's eye moon snail	<i>Neverita duplicate</i>
Sole	<i>Solea solea</i>
Solenette	<i>Buglossidium luteum</i>
Spotted dragonet	<i>Callionymus maculatus</i>
Spotted ray	<i>Raja montagui</i>
Sprat	<i>Sprattus sprattus</i>
Spurdog	<i>Squalus acanthias</i>
Starry ray	<i>Amblyraja radiata</i>
Starry smoothhound	<i>Mustelus asterias</i>
Streaked gurnard	<i>Trigloporus lastoviza</i>
Thickback sole	<i>Microchirus variegatus</i>
Thornback ray	<i>Raja clavata</i>
Tub gurnard	<i>Chelidonichthys lucerna</i>
Whiting	<i>Merlangius merlangus</i>
Witch	<i>Glyptocephalus cynoglossus</i>

Chapter 1. Using stable isotope analysis to examine UK marine food webs and their energy pathways

1.1 Marine food webs

1.1.1 *What is a food web?*

Tansley in 1935 defined an ecosystem as a biotic assemblage or community and its associated physical environment in a specific place (Pickett & Cadenasso, 2002). The main components of this concept are the biotic and abiotic features and the interactions between them. Food webs are a human construct attempting to simplify and summarise the totality of individual predator: prey interactions within an ecosystem through describing who eats whom. The positions of individuals within the food web are determined by their feeding habits (Pauly & Trites, 1998). Predator: prey interactions within food webs can influence population dynamics through resource availability and mortality from predation as well as affecting ecosystem function and structure through the transfer of energy and matter (Dunne, Williams & Martinez, 2002; de Ruiter, Wolters & Moore, 2005). Food webs therefore can be used to characterise and analyse interrelationships between ecosystem functioning, community structure and stability as well as aiding understanding in how these might be affected by environmental disturbance and change (DeAngelis, 1992; de Ruiter, Wolters & Moore, 2005).

Because food webs are immensely complex and difficult to describe completely, they are summarised using models, with the development of a food web model requiring four key facets. Firstly, the scale of the food web needs to be established. Any food web is embedded within a larger system and therefore the temporal and spatial boundaries are arbitrary (Moore & Hunt, 1988; Holt, 1997). Different parts of a food web can be investigated such as sink food webs, which focuses on the network of links to a predator (Cohen, 1978) or source webs which concentrates on taxa with a low position in the web. Secondly, the resolution of the food web model needs to be ascertained. For example, individuals, functional groups, species populations or trophic levels reflecting the length of food chains supporting them, body size or taxa (Winemiller & Layman, 2006). Thirdly, how food web links are estimated needs to be resolved as the strength of interactions affects stability and system dynamics (Paine, 1980; McCann, Hastings & Strong, 1998) as well as food web structure. For example, different interaction strengths between trophic links can lead to various food web structures (Figure 1). The focus of the food web will also affect the portrayal of

its structure. For example, energetic webs are used to understand pathways of energy flow through a system whilst functional webs concentrate on dynamically important linkages which regulate other organisms' abundance (Zanden *et al.*, 2016). Lastly, drivers of spatial and temporal variation need to be determined. Species' life history and environmental variations can influence species interactions and interaction strength, food web structure and population dynamics (Winemiller & Layman, 2006).

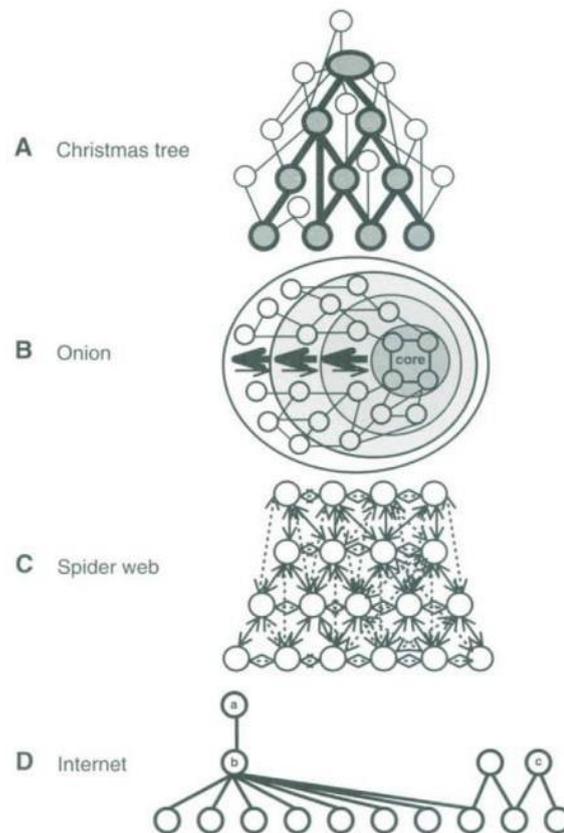


Figure 1, reproduced from Winemiller and Layman, (2006): Schematic illustrations of four models of food web structure **A**, Christmas tree (structural and interstitial species); **B**, onion (hierarchy of core and peripheral species); **C**, spider web (all species affect all others directly or indirectly); and **D**, internet (network architecture yields disproportionate influence by hub species)

There are several conceptual ideas which have been developed to describe the general properties of complex food web structure. For example, Elton described ecological pyramids in 1927, with a 'pyramid of numbers' suggesting that smaller organisms which are low in the food chain will be more abundant than larger organisms higher in the food chain and the pyramid should be bottom heavy, although this is not always the case (Trebilco *et al.*, 2013). This is due to the conservation of energy, increasing entropy and inefficient energy transfer from predator to prey and the pyramid has since been re-expressed in terms of

production, biomass and trophic level (Trebilco *et al.*, 2013). Size spectra is an alternative way to understand community structure, with the slope of size spectra describing the rate at which biomass or abundance changes with increasing body size and are remarkably consistent in aquatic ecosystems at approximately zero and -1 for biomass and abundance spectra respectively (Sheldon *et al.*, 1972; Dickie, Kerr & Boudreau, 1987; Boudreau & Dickie, 1992).

Another long-held debate is whether food webs are structured in compartments or modules, which are subgroups of species with strong trophic interactions with little interaction between subgroups (Paine, 1980; Pimm, Lawton & Cohen, 1991; Cohen, 1978). Consumers are thought to have strong interactions if in their absence marked changes ensue (MacArthur, 1972), whilst the removal of species with weak interactions will yield no or slight change. The relative strength of interaction is affected by the consumer's density, prey size and predator food preference, particularly when prey is competitively superior (Paine, 1980). The modularity of food webs is thought to be important because it may increase the stability of the food web (May, 1972, 1973; Pimm & Lawton, 1980). However very few unequivocal examples have been found in reality (Rezende *et al.*, 2009).

Metrics describing food web properties have also been developed such as species richness and number of species interactions or links. However, their use in describing wider properties is contended, such as whether or not increasing species richness causes connectivity to decline or whether higher connectivity decreases, increases or has alternating effects on overall stability (Link, 2002).

1.1.2 What are the characteristics of a marine food web?

Marine ecosystems are inherently different from terrestrial ecosystems, with the dominance of small primary producers and many studied food webs exhibiting many weak species interactions often based more strongly on size than species identity. This may be due to the specific characteristics of marine food webs such as the openness of the system, large ontogenetic changes in size across life histories, the high abundance of generalists and high degree of omnivory (Link, 2002). Broad diets, the ability for species to quickly change to more abundant prey items, often at different trophic levels as well as switching trophic levels throughout their lifetimes produces a weakly connected system, with few species directly or highly dependent on other species (Garrison & Link, 2000; Blanchard *et al.*, 2011; Link, 2002). . Marine food webs also tend to have long average food chain lengths spanning 4

trophic levels, where food chain length is the number of trophic levels between the top predator and primary producers (Schoener, 1989; Vander Zanden & Fetzer, 2007).

Most marine food webs are strongly size-structured with size-based predation being predominantly responsible for the transfer of energy (Barnes *et al.*, 2010). Predators tend to feed on smaller prey and can be one to three orders of magnitude larger than their prey, although there are notable exceptions (Cohen *et al.*, 1993a; Woodward *et al.*, 2005). Most predators consume smaller prey because these are more productive and easier to catch and process and because changes in prey size choice are constrained by the evolved morphology of predator and prey (Scharf, Juanes & Rountree, 2000a). Larger predators tend to feed at higher trophic levels and are less abundant and productive due to the inefficient energy transfer from prey to predators (Jennings, Warr & Mackinson, 2002). The rate at which this available energy declines with increasing mass depends on the trophic transfer efficiency (TE) and mean predator-prey mass ratio (PPMR), where TE is the proportion of prey production converted to predator production (Jennings & Mackinson, 2003). This inefficient energy transfer also results in an ecological pyramid with greater biomass at low trophic levels and less biomass at higher trophic levels (Trebilco *et al.*, 2013).

Small unicellular algae called phytoplankton are the principal primary producers supporting marine food webs and are key in maintaining stability (Steele, 1974). This production can be passed to consumers through a pelagic or benthic pathway. Pelagic generally refers to the activity in the water column whilst benthic refers to the activity near or on the seafloor and there are no well-defined boundaries between benthic and pelagic, especially in shallower water, although this may become more pronounced with depth and separation by a permanently stratified water column. Linkages between these pathways is called benthic-pelagic coupling, which can be defined as the exchange of energy and nutrients between benthic and pelagic systems and can occur between individuals at all stages and trophic levels. For example, nutrients which become resuspended during storm events stimulate phytoplankton and bacterial production, which in turn stimulates consumers at higher trophic levels (Fanning, Carder & Betzer, 1982; Wainright, 1987). Pelagic organisms not consumed ultimately sink to the seabed, feeding on the benthic community. Pelagic and benthic grazers can also feed on large resuspended particles (Arfi & Bouvy, 1995). Many marine organisms also have both pelagic and benthic lifestages.

For example, benthic species can have planktonic larvae, potentially spending hours to months in the water column depending on the species. Pelagic organisms can also have a benthic resting phase, lasting from weeks to years (Marcus & Marcus, 1998). The amount of production reaching the benthic community is affected by many factors including: physical mixing, pelagic grazing rates, water column depth, proximity to nutrient sources, temperature, primary production, euphotic depth, and the composition of nekton and zooplankton communities (Maxwell & Jennings, 2006; Woodland & Secor, 2013). Benthic-pelagic coupling can have active fluxes related to biological processes or passive fluxes related to physical processes which can be affected by several parameters, as summarised in Table 1. The relative flux of production to each of the two pathways determines the biological structure and production of marine food webs and can influence standing biomass, species composition, taxonomic and functional diversity and productivity of the pelagic and demersal communities (Sommer, 1989; Valiela, 2015).

Description of flux	Type	Parameters affecting flux
Consumption of benthic fauna by pelagic predators or pelagic fauna by benthic predators (e.g. suspension feeding)	Active	Depth, mixing and stratification, community composition, salinity, life cycle of species, prey composition and biomass
Migrations of benthic fauna or pelagic fauna (e.g. diel migrating zooplankton or benthic fish defecating)	Active	Depth, mixing and stratification, community composition, life cycle of species
Flux of detritus from pelagic to benthic system (e.g. marine snow, carcasses)	Passive	Affected by amount of pelagic material in the environment such as phytoplankton blooms and environmental conditions such as mixing and stratification
Recycling of detritus from benthic to pelagic system through bioturbation	Active	Presence of meiofauna & macrofauna can increase fluxes. Changing environmental conditions can affect community composition & capacity
Resuspension of benthic fauna and detritus into pelagic system	Passive	Depth, mixing and stratification, fishing e.g. bottom trawling
Macrophyte inorganic nutrient uptake	Active	Changing environmental conditions can affect community composition (e.g. decline in salinity reduces macroalgae and uptake of pelagic nutrients, increasing phytoplankton production)
Molecular diffusion	Passive	Direction of fluxes related to oxygen conditions, affected by stratification, temperature & mixing
Sedimentation of benthic material	Passive	Regulated by nutrient conditions and climate. Amount of sedimentation affected by amount of pelagic material and sediment resuspension
Allochthonous organic material input	Passive	Distance to shore and major rivers/estuaries, river flow and runoff, precipitation

Table 1: A description of active and passive fluxes related to benthic-pelagic coupling and parameters potentially affecting those fluxes

1.2 Stability and resilience of marine food webs

One key goal of ecological research is to identify and understand mechanisms which influence the stability and resilience of ecosystems, where resilience is measured by the return speed to a stable system after perturbation (Ings *et al.*, 2009; Rooney *et al.*, 2006; Blanchard *et al.*, 2011). Early views on defining stability in food webs suggested organisms had relatively static interactions and were presumed to fluctuate near equilibrium (Zanden *et al.*, 2016). In 1973 May posited a stability criterion, $i(SC)^{1/2}$, where in the food web i is the average interaction strength, S is the number of species and C is connectance, suggesting food webs near equilibrium will tend towards stability (Rooney & McCann, 2012). Currently it is thought that food webs are much more dynamic in regards to organism interactions and the consequence of these interactions, with shifts in interactions potentially leading to rapid changes in ecosystems (Zanden *et al.*, 2016).

There are contradictory views on mechanisms influencing stability, for example whether increased species richness and complexity beget stability, with recent studies suggesting weak interactions in the food web can dampen oscillations from strong interactions (MacArthur, 1955; May, 1973; Rooney & McCann, 2012). This may be due to existence of modules or compartments in the form of slow and fast energy pathways, referring to turnover rates or production: biomass ratios. The existence of these pathways have been suggested by soil ecologists and empirical analysis in aquatic food webs suggest they may also be present in marine food webs, with the fast and slow pathways related to the pelagic and benthic pathways respectively (Rooney *et al.*, 2006). Theoretical explorations corroborated with empirical observations suggest system dynamics can be stabilised by the presence of fast and slow channels and top predators to couple the channels (Ives & Hughes, 2002; Post, Conners & Goldberg, 2000; Rooney *et al.*, 2006). However, few studies have investigated benthic and pelagic pathways and their impact on the stability of an ecosystem (Blanchard *et al.*, 2011).

Empirical analysis suggests the energy pathways exhibit different characteristics, with the pelagic pathway being a fast pathway comprising smaller, faster growing populations with higher biomass turnover rates and strong interactions compared to the benthic pathway which is a slow pathway and comprised of weak interactions (Rooney *et al.*, 2006; Rooney & McCann, 2012). For example, the high production of the pelagic pathway can support the high metabolic demand of consumers such as

juvenile fish and invertebrates (Woodland & Secor, 2013). Mobile predators which are not subject to the same foraging constraints can switch between prey types as a response to changing densities in the channels, integrating pelagic and benthic food sources and stabilising the pathways with rapid predatory switching behaviour (Woodland & Secor, 2013; Rooney *et al.*, 2006). This benthic-pelagic coupling can provide food webs with stability through the slower pathway and efficiency through the fast pathway (Rooney & McCann, 2012).

When the systems are perturbed, theoretically, the pelagic pathway responds quickly, allowing predator populations to rapidly recover. The lagged response of the benthic pathway allows prey populations in both channels to behave in an asynchronous fashion with each other, producing a less variable resource base for predators and a rapid yet stable recovery from a perturbation (Rooney & McCann, 2012; Rooney *et al.*, 2006). Blanchard *et al.* (2011) suggested that theoretical food-web configurations where predators have strong benthic-pelagic coupling, feeding from both pathways with the majority of food coming from the pelagic pathway, resulted in the fastest return to steady-state. However, they also found a fast return to equilibrium when predators fed predominately in the benthic pathway and a non-linear relationship existed between resilience and degree of predator coupling, with the precise relationship dependent on the component of the ecosystem most affected and the type of perturbation (Blanchard *et al.*, 2011).

Blanchard *et al.* (2011) concluded that the resilience of size structured food webs to perturbations can depend on the strength of benthic-pelagic coupling, with communities with little benthic-pelagic coupling potentially being more vulnerable than strongly coupled systems. The strength of benthic-pelagic coupling can be affected by several factors. For example, coupling can be stronger in shallower waters, due to a decrease in depth facilitating vertical migrations of benthic and pelagic organisms (Kopp *et al.*, 2015). Benthic communities may also receive energy directly from the pelagic pathway where filter feeders graze phytoplankton directly as most organisms can access both benthic and pelagic carbon sources, irrespective of their water column position preference (Kopp *et al.*, 2015). Species located high in the food web can also increase the strength of coupling because they are omnivorous, are more mobile and have a large foraging area (Kopp *et al.*, 2015). Perturbations from human impacts can also affect the strength of benthic-pelagic coupling. For example, removing top predators which couple the systems could

increase the vulnerability of the systems and their component populations (Blanchard *et al.*, 2011). However, the resilience of a system is complex and requires more knowledge of feedback mechanisms operating within the pathways, external constraints on the system and behaviours of organisms which can affect the structure of the food web (Blanchard *et al.*, 2011).

1.3 Effects of the physical environment and human impacts on food webs

1.3.1 Climatic changes

Climate forcing varies on many time-scales from years to decades as well as longer term underlying change. Seasonal changes occur due to the production cycle of zooplankton, where the greatest variation is found in smaller animals and declines with increasing body size, reflecting the increases in metabolic rates and turnover times (Jennings *et al.*, 2008b). Climate also varies naturally over decades, such as the North Atlantic Oscillation (NAO) which refers to the redistribution of atmospheric mass between the subtropical Atlantic and Arctic and can produce large changes in North Atlantic wind direction and speed, the intensity and number of storms, heat and moisture transport and weather patterns (Alheit *et al.*, 2012). When the NAO is positive, as it was between the late 1980s and 1995, this can result in, amongst other things, warmer seas, shifting zooplankton and fish species from a boreal community to a warm temperate community (Alheit *et al.*, 2012). However, this signal is interrelated with the Atlantic multidecadal oscillation (AMO) and also to climate change and their combined impact on marine ecosystems is poorly understood.

Long term climatic warming can alter the strength of benthic-pelagic coupling and the food web structure. For example, warming can cause increased vertical stratification and reduce nutrient supply, potentially altering the balance between the pelagic and benthic pathways (Barange *et al.*, 2011). Warming has also led to smaller average body sizes across species and within populations (Simpson, Blanchard & Genner, 2013; Baudron, Needle & Marshall, 2011). This is due to larger individuals requiring greater long-term energy requirements which warmer environments can fail to provide. Smaller body sizes may cause increased turnover times, potentially affecting the rate of energy fluxes between the pathways. Warming has also already begun to alter the distribution and abundance of species and will continue to do so as the temperature continues to increase. Changes in the abundance of species could affect the ecosystem structure whilst deepening of species could affect the strength of benthic-pelagic coupling. Boreal species are also expected to shift their distribution

polewards, whilst Lusitanian species will increase in abundance although the rate and direction of shift will vary among regions and species (Cheung *et al.*, 2012).

Long term changes have been predicted and observed in UK shelf seas' climate which can affect the structure and function of marine food webs (Cheung *et al.*, 2012). For example, sea surface temperature (SST) of UK and North Atlantic coastal waters has already warmed by 0.2-0.6°C per decade over the past 30 years, faster than the global average, with predicted global SST estimated to rise a further 1.5-2.6°C by 2100 (Dulvy *et al.*, 2008; Simpson *et al.*, 2011). This warming is estimated to reduce the average body weight of individuals by 14-24% by 2050 (Simpson, Blanchard & Genner, 2013). Warming has also altered the distribution and abundance of species. For example, in the North Sea two thirds of fish species have shifted mean latitude or depth, with some demersal fish assemblages deepening at a rate of around 3.6m per decade (Dulvy *et al.*, 2008). Such changes have already been observed, with landings of commercial Lusitanian species increasing by 250% over the past 30 years whilst boreal species landings have halved (Simpson, Blanchard & Genner, 2013).

1.3.2 Fishing

Food from aquatic environments provides a significant contribution to human health and nutrition. Maintaining a safe, sufficient and nutritious supply which is also economical, environmental and socially sustainable in the long term is an ongoing and substantial challenge for society (Jennings *et al.*, 2016). Global demand for food from aquatic environments is increasing, with annual catch of shellfish and fish from marine fisheries on a global scale amounting to more than 100 million tonnes (Gislason, 2001), with demand expected to rise faster than population growth. Approximately seventy-five percent of the world's landings are caught where primary production is high on the continental shelf or in coastal and estuarine environments, and in intensively fished areas like the North Sea, approximately one third of fish biomass is removed each year (Gislason, 2001). Therefore wild-capture fisheries are a critical component of aquatic food, but production is close to maximum for sustainable ecosystem productivity and is unlikely to sustainably increase in the future and could potentially decline if poorly managed (Garcia & Rosenberg, 2010).

Quantification of the direct and indirect impacts of fishing on ecosystems is difficult. For example, marine ecosystems are subject to large fluctuations, both natural and anthropogenic, such as climatic changes, eutrophication and gas and oil extraction

which can make it challenging to isolate which changes to the ecosystem occurred due to fishing (Callaway *et al.*, 2007). There is also a scarcity of data from unexploited ecosystems as most data collection began after the onset of fishing (Gislason, 2001). This can cause an underestimation of the extent of changes because analyses based on ecosystems which are already impacted by fishing will only observe further changes that are occurring (Jennings & Blanchard, 2004). For example, commercial landings data are affected by this 'shifting baseline' as records have only been maintained for a relatively short period of time (Christensen & Richardson, 2008). Furthermore, using landings data as ecosystem indicators can be problematic; landings may not reflect real changes in the ecosystem as they are also influenced by changes in technology, the market economy and human behaviour (Caddy *et al.*, 1998).

Fishing can perturb marine ecosystem structure and functioning. For example, fishing tends to selectively remove the largest individuals first and as fishing mortality increases, the mean size of individuals' decreases as large, slow-growing species decline more rapidly than smaller, faster-growing counterparts (Pinnegar *et al.*, 2002). Large species also typically feed at higher trophic levels and so fishing can result in a decline in the mean trophic level of exploited fish communities (Jennings *et al.*, 2002). This occurred in the Celtic sea, with trophic level (TL) of landings decreasing by 0.03-0.04 TL per year, and to the lesser extent throughout the entire northeast Atlantic at 0.02 TL per year (Pinnegar *et al.*, 2002). This loss of species high in the food web which integrate the pathways can reduce the active fluxes of benthic-pelagic coupling and potentially reduce stability in the pathways (Kopp *et al.*, 2015).

A decline in the biomass of an entire community can also occur as large species are removed (Guénette & Gascuel, 2012). For example, Jennings and Blanchard, (2004) estimated that the biomass of large to the largest fishes in the North Sea is approximately 98.3% lower than in the absence of fisheries exploitation. This reduced biomass can cause turnover time to increase, leading to greater instability in production and biomass, increasing populations' sensitivity to environmental changes (Jennings & Blanchard, 2004).

Alternative types of fishing may also affect the pelagic and benthic system in different ways. For example, overfishing of forage and planktivorous fish or bottom trawling for

benthic species may synchronize the pelagic and benthic pathways, thus removing their heterogeneity (Rooney *et al.*, 2006).

To allow the continued contribution of wild-capture fisheries to human nutrition thorough and careful management is needed to: i.) reduce overfishing and rebuild overexploited populations ii.) reduce the environmental impacts of fishing iii.) adapt management to the effects of climate change (Garcia & Rosenberg, 2010). This will require knowledge of: i.) the present characteristics and state of the fisheries ii.) ecosystem resilience to external and internal drivers iii.) constraints which may limit the effectiveness of governance (Garcia & Rosenberg, 2010). Both management and predictions of fishery futures under climate change require some understanding of processes affecting the dynamics and production of fish populations. While understanding and measurement of processes such as recruitment have long been a focus of fisheries science, much less is known about other underlying causes of variability in fish populations, especially those linked to food web processes such as dependence on different food web pathways. Understanding the effects of food web processes may better inform future projections of population dynamics and help assess the risk of populations falling below defined biomass thresholds even if fishing mortality is controlled.

1.4 Approaches to food web analysis

1.4.1 Traditional approaches to studying food webs

The study of food webs aims to understand the frequency and strength of trophic interactions among organisms. This requires knowledge of species feeding habits, which can be used to build models of the network of these interactions. Models can be used to characterise food webs in terms of the number and strength of links and importance of different organisms, they can also be used to explore manipulations to the systems, such as changing the strength of interactions or organisms present. Modelling can be conducted on several scales, with the simplest model examining the diet of one species and the most complex evaluating an entire ecosystem. For example, Ecopath with Ecosim uses mass balanced models to describe the energy flows within an ecosystem, species interactions and ecosystem effects of fishing and environmental changes (Heymans *et al.*, 2016; Pauly, Christensen & Walters, 2000). However, in order to compile and run the model, information must be known first about the consumer and detritus groups' production, respiration, egestion, natural and fishing mortality (Heymans *et al.*, 2016).

Traditionally, food webs have been studied using a number of methods: direct food observations, scat and stomach contents analysis (Burns *et al.*, 1998; Deb, 1997; Hyslop, 1980; Michener & Kaufman, 2007; Pauly & Trites, 1998; Pauly, Christensen & Walters, 2000). However, for fish species, direct observations of feeding are impossible for those which feed nocturnally or which are roving, where feeding grounds are unknown and scat collection is also impractical (Burns *et al.*, 1998).

Gut contents analysis (GCA) is the examination of an individual's stomach contents to find out what has been eaten. These findings are subsequently generalised to represent the diet composition of a species (Deb, 1997). GCA can be qualitative, where the prey items of a species are listed, or it can be quantitative where either the number, volume or weight of individuals is recorded and expressed as a proportion of total individuals in all food categories (Hyslop, 1980). GCA is valuable for establishing new food links or to determine the strength or frequency of species interactions (Deb, 1997). Identification of individuals found in gut contents can also be established through DNA sequencing although this requires species sequences to be held in the database and can also be a costly process (Smith *et al.*, 2005).

However, there are several issues with GCA. GCA only reveals the most recent diet which might not be representative of the overall diet, particularly if the species relies on seasonal prey items or is opportunistic (Burns *et al.*, 1998). Developmental stages of organisms, predator gut vacuity, seasonality, assimilation of food items, variety of prey and number of samples collected can also all influence the interpretation of GCA (Deb, 1997). Furthermore, rate of digestion can mean that prey can be too far digested to permit identification or the taxonomic resolution is reduced and soft-bodied prey can also be significantly underestimated as what remains in the gut is not absorbed and so interpretation of the assimilated diet can be biased (Burns *et al.*, 1998). It may also be difficult to gain quality results for rare or small species. This can all lead to species being incorrectly assigned within a food web.

1.4.2 Using stable isotope analysis to study food webs

For decades ecologists have been using stable isotope analysis (SIA) to elucidate dietary information about animals and plants (Gannes, O'Brien & Del Rio, 1997; Jardine & Cunjak, 2005). Animal ecologists use SIA for myriad applications from reconstructing diets, ecosystem and population ecology, tracing movements and assessing physiological condition (Martínez Del Rio *et al.*, 2009; Gannes, O'Brien & Del Rio, 1997).

Isotopes are forms of the same element that differ in the number of neutrons in the nucleus (Fry, 2006). Stable isotopes are those isotopes which do not undergo radioactive decay over time and account for less than ten percent of all known isotopes. Stable isotopes consist of ‘heavier’ and ‘lighter’ isotopes, depending on the number of extra neutrons in the nucleus, with isotopes gaining mass with the addition of neutrons. The most common stable isotopes used in ecology are hydrogen (^1H , ^2H), carbon (^{12}C , ^{13}C), nitrogen (^{14}N , ^{15}N), oxygen (^{16}O , ^{17}O , ^{18}O) and sulphur (^{32}S , ^{33}S , ^{34}S , ^{36}S). The abundance of stable isotopes differs, with the lightest stable isotopes accounting for more than 95% of all isotopes for the above mentioned elements as shown in Table 2.

Element	Isotope Abundance			
	Low Mass		High Mass	
Hydrogen	^1H	99.984	^2H	0.016
Carbon	^{12}C	98.89	^{13}C	1.11
Nitrogen	^{14}N	99.64	^{15}N	0.36
Oxygen	^{16}O	99.76	^{18}O	0.20
Sulphur	^{32}S	95.02	^{34}S	4.21

Table 2: Isotope abundance of hydrogen, carbon, nitrogen, oxygen and sulphur (adapted from Fry, 2006)

Different processes change the ratio between the heavy and light isotopes which can lead ecologists to make inferences about animal behaviour such as long-term diet preferences. Samples of tissues are ground to a fine powder to achieve homogeneity. These are then converted into a gas and the ratio of heavy to light isotopes is recorded by Isotope Ratio Mass Spectrometry (IRMS). This ratio is compared to a standard reference material, to give the ‘isotopic signature’ of the sample which is expressed using the delta notation (δ). This is calculated by:

$$\delta X = \left[\left(\frac{R_{\text{SAMPLE}}}{R_{\text{STANDARD}}} \right) - 1 \right] * 1000$$

Where X is the heavier isotope, R_{SAMPLE} is the corresponding ratio in the sample, R_{STANDARD} is a reference ratio of an internationally accepted standard gas (Jardine & Cunjak, 2005) and the δ has units of per mil (‰). Most δ values range from -100 to 50 ‰ and samples with higher δ values are relatively enriched in the heavy isotope, whilst samples with lower δ values are relatively enriched in the light isotope (Fry, 2006).

1.4.3 Carbon and nitrogen as food web descriptors

Foods that animals eat often displays characteristic isotopic signatures and so, to some extent isotopically, 'you are what you eat' (Gannes, O'Brien & Del Rio, 1997; Caut, Angulo & Courchamp, 2009). In dietary analysis carbon and nitrogen are the two main elements used (Dalerum & Angerbjörn, 2005). The benefit of using SIA for dietary analysis arises from the ability to analyse differences between the carbon and nitrogen isotopic ratios of an animal and its diet, which is known as fractionation, trophic enrichment or the discrimination factor (Caut, Angulo & Courchamp, 2009; Martínez Del Rio *et al.*, 2009). This can provide information on nutrient sources, energy flows and trophic relationships within a food web (O'Reilly *et al.*, 2002).

Isotopic fractionation is caused by enzymatic discrimination where enzymes responsible for amino acid transamination and deamination preferentially remove 'lighter' amine groups (e.g. ^{12}C and ^{14}N containing), leading to an enrichment of the heavier isotope in the consumer tissues (Mintenbeck *et al.*, 2008; Gannes, O'Brien & Del Rio, 1997). For $\delta^{15}\text{N}$ ($^{15}\text{N}:^{14}\text{N}$) consumers are enriched during each assimilation step typically between 1.3‰ to 5.3‰, with average enrichment often treated as 3.4‰ (Adams & Sterner, 2000; Minagawa & Wada, 1984). Therefore animals higher up the food chain typically have higher $\delta^{15}\text{N}$ values than those lower in the food chain and so $\delta^{15}\text{N}$ can be used as an indicator of an individual's trophic position within a particular food web (Mintenbeck *et al.*, 2008). For example, assuming that a fixed $\delta^{15}\text{N}$ value of 3.4‰ can be used across all components of the food web, the relative species trophic position can be estimated, and the food web structure can begin to be constructed or one of the main descriptors of food web structure can be derived. However, this assumption of constant isotope fractionation across trophic levels has been challenged, with a narrowing of consumer fractionation with increasing $\delta^{15}\text{N}$ suggested instead (Hussey *et al.*, 2014). This decline in fractionation for consumers at higher trophic levels is not causally linked to dietary $\delta^{15}\text{N}$ but may be due to diet quality (Fry, 2006). Consumers with diets which have amino acid compositions dissimilar from their own and with lower protein content may have greater fractionation than expected and therefore fractionation may be lower at higher trophic levels due to the dominance of piscivory and protein content of diet (McMahon *et al.*, 2015; Jennings & van der Molen, 2015). Generally, variation in $\delta^{15}\text{N}$ fractionation may also be due to changes in ^{15}N retention can vary according to species, quality of

food, growth rate of the consumer, method of excretion and nutritional stress (Michener & Kaufman, 2007; Trueman, McGill & Guyard, 2005).

$\delta^{13}\text{C}$ ($^{13}\text{C}:^{12}\text{C}$) is enriched by only 0.5-1‰ per trophic transfer and as it changes little through the food web can be used as a tracer of primary carbon sources (Mintenbeck et al., 2008; Jacob et al., 2005). However in practice, for marine fish, fractionation may be higher, with values of 1-2 ‰ more appropriate (Sweeting et al., 2007b). Fractionation can also vary with $\delta^{13}\text{C}$ due to body size, species identity, food quality, feeding rate, changes in physiology, nutritional status, growth rate and metabolism (Olive et al., 2003; Post, 2002; McConnaughey & McRoy, 1979; Lorrain et al., 2002; Sweeting et al., 2007b). $\delta^{13}\text{C}$ can be particularly useful where there are large differences in isotopic values, for example between C3 and C4 plants, terrestrial and marine systems and pelagic and benthic systems (Michener & Kaufman, 2007; France, 1995).

1.4.4 Isotopic variation

Isotopic variation not only occurs due to feeding habits but also due to several different factors including variability in: fractionation, baseline isotopic values, tissue types and turnover time, lipid content and diet quality. If these factors are not adequately addressed major biases can occur in analysis.

Fractionation of both nitrogen and carbon isotopes varies due to several factors such as growth rate, species identity and food quality. Considerable variation also exists amongst ecosystems over time and space at the base of the food web, which is propagated up the food web. Without suitable temporal and spatial baseline estimates of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ it is impossible to determine whether isotopic variation in an organism is due to a change in the carbon flow or food web structure, or just a variation in the baseline (Post, 2002).

Different types of tissues have varying diet-tissue fractionation and turnover times which can cause isotopic variation (Martínez Del Rio et al., 2009; Olive et al., 2003; Pinnegar & Polunin, 1999). The rate at which tissue turnover occurs is related to the metabolic rate of the tissue and so tissues with fast metabolic rate will have fast turnover (Dalerum & Angerbjörn, 2005). For example, some tissues, such as plasma and liver have high turnover rates of a couple of days and so their isotopic composition will reflect the recent dietary inputs, whilst other tissues such as muscle have slower turnover rates and so will reflect the average dietary inputs over a few

months (Hobson & Wassenaar, 1999). This means that if there is a change in the isotopic composition of the diet of a consumer, this does not manifest in the slower turnover tissues immediately and is lagged over a period of time until equilibrium is reached (Hobson & Clark, 1992). Thus the isotopic composition of the consumer could reflect neither the previous or current diet, but the influence of both (Sweeting, Jennings & Polunin, 2005). Some tissues such as scales and shells are inert and so reflect the dietary inputs which were incorporated whilst they were being formed (Martínez Del Rio *et al.*, 2009).

Diet quality can also affect isotopic variance. For example, when an animal is starving, enrichment of ^{15}N still progressively occurs over the course of starvation because starving animals 'live on their own meat' and so the excreted 'lighter' nitrogen is not replaced by dietary protein (Gannes, O'Brien & Del Rio, 1997; Olive *et al.*, 2003). Also, parasites isotope ecology is not as expected; they are not enriched in ^{15}N with respect to their host organism but are consistently and significantly depleted (Olive *et al.*, 2003; Pinnegar, Campbell & Polunin, 2001).

Variation in lipid content can have a significant effect on $\delta^{13}\text{C}$ values of organisms, biasing food web interpretation (Smyntek *et al.*, 2007). Lipids are approximately 6-8% depleted in ^{13}C relative to protein and can result in $\delta^{13}\text{C}$ values being 3-4‰ more negative than when normalised (Sweeting, Polunin & Jennings, 2006; Post *et al.*, 2007). This depletion occurs due to a kinetic-isotope effect occurring during lipid biosynthesis mainly during the conversion of pyruvate into acetyl-CoA during the pyruvate dehydrogenase reaction (Sweeting, Polunin & Jennings, 2006; Mintenbeck *et al.*, 2008). As most lipid classes contain no nitrogen and are mainly composed of carbon, atomic C:N ratios are a good proxy for lipid content, as increases in C:N values closely track increases in lipid content (Post *et al.*, 2007; Tarroux *et al.*, 2010). The C:N ratios are calculated as $(\%C/12)/(\%N/14)$ (Barnes *et al.*, 2008). Lipid correction can occur either through lipid extraction and separation analysis or using arithmetic correction techniques, such as using C:N ratios, to predict lipid-extracted $\delta^{13}\text{C}$ (Sweeting, Polunin & Jennings, 2006). However, it is not necessary to correct for lipid content when the C:N ratio is less than 3.5 for aquatic animals as the $\delta^{13}\text{C}$ values will exhibit no difference between the non-extracted and lipid extracted values (Post *et al.*, 2007; Tarroux *et al.*, 2010).

SIA is a useful tool to analyse marine food webs to the extent that it integrates realised feeding relationships. Collection of tissue samples is normally straightforward and a large number can typically be collected. Different animal tissues can also be collected to reflect differing time-scales of diet assimilation from a few days to the lifetime of the individual (Hobson & Wassenaar, 1999). Stable isotopes can also record food source information and trophic position and so can capture complex interactions whilst also tracking mass or energy flow through ecological communities (Post, 2002).

1.4.5 Pelagic and benthic pathways

Since stable isotope analysis can trace material that has been through pelagic or sediment cycles it can collectively measure both active and passive fluxes related to benthic-pelagic coupling. In marine systems $\delta^{13}\text{C}$ can be used to differentiate between pelagic and benthic pathways (Kopp *et al.*, 2015; Le Loc'h, Hily & Grall, 2008; France, 1995). Species feeding on phytoplankton and other particulate organic matter (POM) are depleted in ^{13}C in comparison to benthic deposit feeders (Table 3). Microbial recycling and degradation occurring in the bottom nepheloid layer may enrich $\delta^{13}\text{C}$ in benthic systems (Le Loc'h, Hily & Grall, 2008). In pelagic systems increased water turbulence supplies cells with fresh carbon at higher rates, promoting $\delta^{13}\text{C}$ depletion (France, 1995).

Study	Benthic species and $\delta^{13}\text{C}$ value	Pelagic species and $\delta^{13}\text{C}$ value
Woodland & Secor, 2013	Shark's eye moon snail $-15.35 \pm 0.38\%$	Copepods $-21.68 \pm 0.56\%$
Kopp <i>et al.</i> , 2015	Queen scallops $-17.4 \pm 0.5\%$	Copepods $-21.1 \pm 0.9\%$
France, 1995	Benthic algae $-17 \pm 4\%$	Planktonic algae $-22 \pm 3\%$
Davenport & Bax, 2002	Bivalve <i>Glycymeris striatularis</i> -18% or New Zealand screw shell -18.1%	Zooplankton -21.3%
Jennings <i>et al.</i> , 1997	Algae -14.9% to -16.5% or Posidonia -14.8% to -16.8% across sites	Zooplankton -19.3% to -19.8% across sites
Le Loc'h, Hily & Grall, 2008	Bivalve <i>Nucula sulcata</i> -16.03 ± 0.19	Zooplankton $-20.4 \pm 0.82\%$

Table 3: Examples of $\delta^{13}\text{C}$ values of benthic and pelagic species from various studies

Sulphur isotopes ($\delta^{34}\text{S}$) are less widely used in food web analysis, potentially due to the relatively high cost of analysis (Barnes & Jennings, 2007). However, sulphur can also be useful to differentiate between sources as the isotopic signatures of consumers remain within $\sim 4\%$ of their sulphur sources (Connolly *et al.*, 2004). Also the variation of $\delta^{34}\text{S}$ among types of production sources is much larger than $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, with both organic and inorganic sulphur from the environment contributes towards the total sulphur pool and isotope ratio of a consumer (Barnes & Jennings, 2007). Only a small level of fractionation of $\delta^{34}\text{S}$ ($0-1\%$) occurs across trophic levels

because the only two amino acids (methionine and cysteine) which contain sulphur are both essential to animals and so little or no fractionation occurs when incorporating S-containing amino acids into animal tissues, although more fractionation can occur when organic sulphur is oxidised and during other metabolic processes (Barnes & Jennings, 2007)

Both sulphur in seawater and sediments participate in the biological sulphur cycle, which in part is characterized by sulphur oxidizing and reducing bacteria. The main isotope fractionation that occurs is the bacterial reduction of seawater sulphate to H₂S in shallow sediments and anaerobic bottom waters. The reduced sulphur in marine sediments results in ³⁴S depletion relative to seawater sulphate (Thode, 1991). In the open ocean marine sulphate has a remarkably consistent mean δ³⁴S value of 21‰, likely a consequence of the biogeochemical cycling of sulphur (Barros *et al.*, 2010). Pelagic producers predominately deriving sulphur from seawater sulphates such as microalgae and phytoplankton tend to have δ³⁴S of ca. 19-21‰ whilst benthic producers utilising sedimentary sulphides can be depleted in ³⁴S by as much as 30‰ relative to marine sulphates (Barros *et al.*, 2010; Connolly *et al.*, 2004; Thode, 1991). This should allow differentiation between pelagic and benthic pathways due to the little fractionation. For example, in five reef-associated fish it was found that two pelagic fish had significantly higher δ³⁴S values than three benthic feeders (Thomas & Cahoon, 1993).

1.4.6 Mixing models

Mixing models can be used to estimate the contribution of benthic and pelagic pathways to consumer tissue. Briefly, these are used to estimate the fractional contribution of the benthic or pelagic isotopic source to a tissue from the isotopic composition of the benthic and pelagic sources and the consumer tissues (Martínez Del Rio *et al.*, 2009). Several types of mixing model have been developed, but Bayesian approaches are increasingly adopted. They offer advantages (Bond & Diamond, 2011) over frequentist approaches for several reasons. First, the number of potential sources can exceed the number of isotope systems, allowing the identification of unique solutions of source proportions (Galván, Sweeting & Polunin, 2012). Second, they can incorporate external prior information, corresponding to a *priori* knowledge known about the consumer diet which can be vague or informative depending on the amount of information known. This can further narrow the precision of the estimated dietary proportions (Parnell *et al.*, 2010). Third, they can account for

variation in discrimination factors and separate trophic discrimination factors (TDF) and their variation can be characterised and allocated for each source (Bond & Diamond, 2011). Uncertainty in systems and sources of variation not associated with isotopic uncertainty such as unidentified minor dietary sources or physiological differences can also be included (Parnell *et al.*, 2010). In the Bayesian mixing models developed by Parnell *et al.*, (2010) model fitting is conducted using Markov chain Monte Carlo (MCMC) methods which generate simulations of plausible values based on the data and prior information and posterior distributions are produced which represent true probability densities for the relevant parameters (Parnell *et al.*, 2010).

1.5 The UK environment and marine food webs

The structure of marine food webs is heavily affected by the surrounding oceanography, climate and human impacts. The marine environment encircling the UK is ideal for examining benthic-pelagic coupling and ecosystem structures as it contains shallow shelf seas, where benthic-pelagic coupling may be strong, as well as a shelf edge which is predominantly pelagic, and therefore is a good opportunity for examining contrasts. Furthermore, few existing measures have established benthic-pelagic coupling in UK seas despite it being a potentially important process in determining the resilience of an ecosystem.

Marine food webs are directly influenced by production sources (1.12), the variety and productivity of which are affected by the surrounding oceanography (Grebmeier & Barry, 1991). Depth, wind and currents can affect primary production. In shallow waters, wind-induced mixing and bottom currents can interact to create turbulent mixing through the water column to the seafloor, re-suspending nutrients which allows these areas to be continuously productive. In deep waters, carbon and remineralised nutrients on the seabed are too deep to be readily mixed back to the surface (Denny, 2008). Stratified waters will also reduce the amount of mixing occurring between the two layers of water, preventing the resuspension of nutrients.

The UK is surrounded by four regional seas: Irish Sea, Celtic Sea, English Channel and North Sea (Figure 2). The Irish Sea comprises the area extending in the south from Carnsore Point to St. David's Head to the North Channel between Larne and Corsewall Point (Bowden, 1980). Water flows northwards on the west side, with part of it flowing out of the North Channel whilst the remaining part passes eastward to the south of the Isle of Man (Bowden, 1980). A southerly counter flow also exists

close to the Irish coast (Bowden, 1980). The majority of the Irish Sea is continuously mixed due to strong tidal currents although a deep basin region in the west becomes stratified during summer (Huthnance, 2010). The Celtic Sea is a relatively shallow but very extensive embayment and is separated by the Irish Sea to the north and the English Channel in the east; it stretches from Land's End to Ushant, whilst the western limit is at the 200m contour at the edge of the continental slope (Pingree, 1980). Flow travels north towards the Bristol Channel and then flows westward across St. Georges Channel, with a component entering the Irish Sea (Pingree, 1980). Vertically mixing occurs in winter (November – April), but strong thermal stratification occurs during summer (Huthnance, 2010). The eastern entrance to the English Channel is at Dover Strait whilst the Celtic Sea is to the west and circulation is anticlockwise in the summer and clockwise in the winter (Pingree, 1980). The English Channel is generally well mixed although in the Western Channel a tidal mixing front occurs where the well-mixed regime meets stratified waters in the Celtic Sea (Huthnance, 2010). The North Sea is bounded by countries to the west, south and east and the northern limits begin at the edge of the continental shelf. The northern and southern North Sea are distinct due to the northern North Sea having a mean depth greater deeper than the southern North Sea which has a maximum depth of 50m (Callaway *et al.*, 2002). This promotes different circulation patterns, with the southern North Sea being permanently vertically mixed due to tidal currents whilst the northern North Sea has thermally stratified waters which flow anticlockwise and another inflow is from the Atlantic Ocean (Callaway *et al.*, 2002).

Changes in climate also greatly affect the structure of UK marine food webs (1.3.1). Increasing temperatures will alter food webs as species track their preferred thermal conditions and distributions will continue to shift for the next five decades (Simpson, Blanchard & Genner, 2013; Pinnegar *et al.*, 2013). Warming can also affect the strength of benthic-pelagic coupling through reduced nutrient supplies and increased vertical stratification (Barange *et al.*, 2011). However, few studies have investigated the impact this might have on the structure of food webs and food chain length.

UK marine food webs are also heavily influenced by fishing (1.3.2). Commercial fishing is an important socio-economic activity in coastal regions across the UK (Cheung *et al.*, 2012; Heath *et al.*, 2012). In 2011, fish and shellfish landings were around 600,000 tonnes resulting in sales of £828.2 million (Heath *et al.*, 2012). Landings can be broadly assigned to four main guilds: pelagic piscivores (average

1.01 million tonnes per year; 59 species including Atlantic mackerel and horse mackerel); planktivores (average 5.96 million tonnes per year, 61 species including Atlantic herring and sardines); demersal piscivores (average 2.84 million tonnes per year, 118 species including cod, saithe and whiting); and benthivores (average 0.35 million tonnes per year, 103 species including plaice, sole and gurnards) (Heath *et al.*, 2012). Invertebrates such as scallops, langoustine and lobster are also important species which are landed (Cheung *et al.*, 2012). The UK seas are intensively fished, modifying substantially the abundances and sizes of fish and their prey fields (Simpson, Blanchard & Genner, 2013).

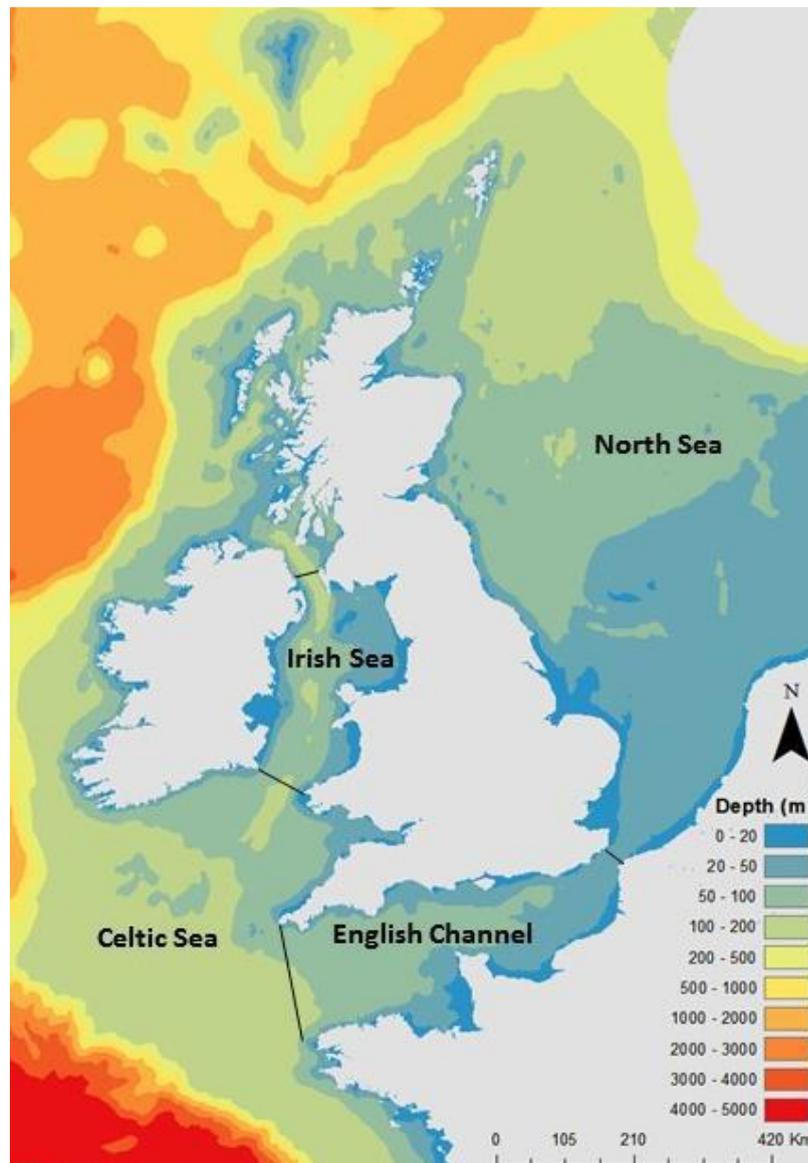


Figure 2: A map displaying the limits and depth gradients of UK Seas

1.6 Synopsis

A vital component in marine ecosystems is benthic-pelagic coupling. However, few studies have examined benthic-pelagic coupling and its influence on aspects of ecosystem stability.

This PhD focused on gaining more comprehensive knowledge on benthic-pelagic coupling by establishing the extent to which shelf sea fish species are affiliated to the benthic and pelagic pathways across four UK seas (North Sea, Celtic Sea, Irish Sea and English Channel). Variables which might affect benthic-pelagic coupling such as consumer body mass and trophic level, sea depth, water temperature and salinity were investigated. Furthermore, factors potentially causing variation in species' abundance such as benthic-pelagic coupling, life history characteristics and variability in fishing pressure were examined. This may aid understanding in how ecosystems might respond to climatic and anthropogenic changes.

Stable isotope analysis was the main tool used to elucidate information about the extent to which species are affiliated to the benthic and pelagic pathways. This provides information on realised feeding activity, integrated over several months or more. $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ were used as they can differentiate between the benthic and pelagic pathway and have small fractionation across trophic levels. Baseline isoscapes were also created to account for spatial baseline isotopic variation and to correct sampled consumers' isotopic values.

The marine environment surrounding the UK was ideal for investigating benthic-pelagic coupling. It contains varied oceanography, is affected by climatic changes and is intensively fished. Furthermore, few existing measures have established benthic-pelagic coupling in UK seas despite it being an important process in determining the resilience of an ecosystem.

1.6.1 Synopsis of chapters

Chapter 2: Developing isoscapes to underpin the description and analysis of marine food webs

Spatial variation of isotopic composition exists in a wide range of environmental materials. This variation can be modelled using isoscapes, which are maps describing isotopic variation across wide geographic areas. The development of isoscapes is necessary to account for spatial baseline isotopic variation, otherwise

consumer isotopic data could be misinterpreted. This chapter aimed to develop baseline isoscapes to correct for sampled species' isotopic values. Specific objectives were:

- i.) Development of baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes across UK waters using queen scallop samples and environmental variables
- ii.) Comparison of North Sea baseline scallop isoscapes with published baseline jellyfish isoscapes
- iii.) Correction of fish species' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across UK waters using scallop isoscapes

Chapter 3: Contribution of pelagic and benthic pathways to North Sea food webs

Understanding how marine food webs are structured is imperative when assessing how ecosystems might respond to extensive changes such as fishing or climate change. In marine ecosystems, benthic-pelagic coupling is a crucial component affecting the structure of food webs. This chapter aimed to establish a systematic approach for estimating the extent to which 15 shelf fish species in the North Sea are affiliated with the pelagic and/or benthic pathway using stable isotopic analysis.

Specific objectives were:

- i.) Comparison of the resolution of contributions to the pathways determined by one isotope ($\delta^{13}\text{C}$), two isotopes ($\delta^{13}\text{C}$ and $\delta^{34}\text{S}$) and gut contents analysis
- ii.) Estimation of the proportion of total fish community biomass supported by the benthic and pelagic pathways
- iii.) Assessment of inter-annual and size-related variation in the contributions of benthic and pelagic pathways to biomass

Chapter 4: Comparative use of benthic and pelagic food web pathways by fishes in three northeast Atlantic shelf seas

The strength of benthic-pelagic coupling can affect the stability and resilience of marine ecosystems. However, this can vary widely due to organismal behaviour which might be influenced by the animals' body size and trophic level as well as environmental parameters such as sea depth, water temperature and salinity which can be influenced by mixing. This chapter aimed to gain more comprehensive

knowledge on how the strength of benthic-pelagic coupling might differ through establishing whether the use of benthic and pelagic food web pathways varies systematically among species, and in food webs in different UK seas using stable isotope analysis. Specific objectives were:

- i.) Assessment of how the affiliation to benthic and pelagic pathways for fish species differs across UK seas
- ii.) Assessment of how trophic level, consumer body mass, salinity, depth and bottom temperature might be related to species' affiliation to benthic and pelagic pathways

Chapter 5: Higher dependence on pelagic food web pathways exacerbates fluctuations in fish populations

Understanding why ecosystems fluctuate and what might affect stability of ecosystems is a central issue in the conservation and management of natural resources. The structure and variability of food webs are fundamental to the stability of ecosystems. In the sea, this stability might be influenced by benthic-pelagic coupling, species' life history characteristics and human activity such as fishery exploitation. This chapter aimed to understand the potential causes of variation in abundance of up to 15 shelf sea fish in the North Sea over a quarter century. Specific objectives were how the assessment of variability in species abundance relates to:

- i.) Benthic-pelagic coupling
- ii.) Life history characteristics
- iii.) Variability in fishing pressure

Chapter 6: Conclusions

This chapter describes the implications of the research presented in this thesis. Three key areas are investigated: an assessment of the ways in which food web structure has changed over time in UK seas; an examination of how anthropogenic pressures such as climate change and fishing might affect benthic-pelagic coupling and the functioning of the ecosystem; and a commentary on suitable management measures to maintain benthic and pelagic pathways to promote resilience.

Chapter 2: Developing isoscapes to underpin the description and analysis of marine food webs

2.1 Introduction

Natural spatial variability exists in the isotopic composition of a wide range of environmental materials such as water, carbon and nitrogen (Bowen, 2010). Isotopic composition of these environmental materials varies due to changing environmental conditions, such as biological, geological, hydrological and climatological conditions across landscapes. This can now be modelled across many systems (Bowen, 2010). This led to the term 'isoscapes' (isotopic landscapes) being coined in 2005, defined as maps which describe isotopic variation across broad geographic areas (West *et al.*, 2010). Isoscapes can be constructed using reference samples at known geographic locations and predictions of isotopic composition can also be made at unmonitored sites using common predictor environmental variables (Bowen, 2010; MacKenzie *et al.*, 2014).

The majority of existing isoscapes have been developed for oxygen and hydrogen isotopes in terrestrial systems. This is due to the variation of oxygen and hydrogen isotopes in water across landscapes caused by isotope effects associated with condensation, evaporation, precipitation. For example, $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in meteoric precipitation vary spatially (Rozanski, Araguas-Araguas & Gonfiantini, 1993). This variation is predominately caused because ^2H and ^{18}O are preferentially removed from moisture in air masses as precipitation, leaving subsequent precipitation and residual vapour depleted in these isotopes (Bowen, 2010). As patterns of precipitation are determined by atmospheric circulation and the water cycle, models can be used to map isotope distributions (e.g. Sturm *et al.*, 2005).

However, in marine systems oxygen and hydrogen isotopes rarely provide sufficient spatial resolution, with a small magnitude of spatial variation in ocean surface-water isotopic composition (< 20%) compared with meteoric freshwaters (Bowen, 2010). Carbon and nitrogen isotopes are a suitable alternative for marine isoscapes because they vary spatially at a broad range of scales due to physiological variations in isotope fractionation and geographic variations in isotopic composition (MacKenzie *et al.*, 2014).

Spatial variation in $\delta^{13}\text{C}$ values of primary producers is influenced by isotopic fractionation in particulate organic matter (POM) during assimilation by phytoplankton

(MacKenzie *et al.*, 2014). The degree of carbon isotopic fractionation that occurs during photosynthesis is related positively by the rate of dissolved CO₂ uptake (Laws *et al.*, 1995a), negatively by phytoplankton growth rate (Burkhardt, Riebesell & Zondervan, 1999b) and cell size (Popp *et al.*, 1998) and is also influenced by community composition, with higher fractionation observed in cells with greater surface area to volume ratios (Popp *et al.*, 1998; Falkowski, 1991). Patterns in phytoplankton $\delta^{13}\text{C}$ also strongly reflect temperature gradients particularly at high latitudes, with $\delta^{13}\text{C}$ increasing with higher sea surface temperatures, due to temperature co-varying with the direct drivers of isotopic fractionation such as CO₂ concentration and solubility (Magozzi *et al.*, 2017; Rau, Takahashi & Des Marais, 1989; Barnes, Jennings & Barry, 2009).

Spatial variations in nitrogen isotopes are more complex than carbon and a several factors can influence organic base $\delta^{15}\text{N}$ such as the differential utilization of nitrogen sources (e.g. N₂, ammonium and nitrate) in time and space (Dugdale & Goering, 1967; Dore *et al.*, 2002) and the incomplete consumption of nitrogenous nutrients (Altabet & Francois, 2001). At smaller spatial scales anthropogenic sources of nitrogen can also generate an enriched $\delta^{15}\text{N}$ coastal signal in POM (McMahon, Hamady & Thorrold, 2013).

This study uses the development of isoscapes to inform understanding of variation in the isotopic composition of individuals across large spatial areas in order to perform dietary analysis. When conducting dietary analysis, carbon and nitrogen are the two main elements used (Dalerum & Angerbjörn, 2005) and spatial and temporal variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in primary producers exist at the base of the food web (MacKenzie *et al.*, 2014), and is propagated through it. Since isotopic differences among species and body sizes are expected as a result of changes in the origins and transformations of their food, baseline variations that are not accounted for could distort the interpretation of species- and size-specific isotopic data (Barnes and Jennings, 2009; Lorrain *et al.*, 2015). Any spatial variation in the baseline is therefore used to adjust the isotopic values of species- or size-classes before their isotopic values are used to make inferences about food web structure (Kopp *et al.*, 2015). Another method used to avoid misinterpretation caused due to local spatial and temporal variation in bulk isotopic signatures is the use of compound specific stable isotope analysis of amino acids (CSIA-AA). As 'source' amino acids fractionate little, they can be used to reflect the base of the food web (Kurle & McWhorter, 2017).

However, this technique is expensive and very time intensive thus limiting possibilities for replication in time and space.

There are several different techniques used in the development of isoscapes. Geostatistical methods allow isotopic values to be predicted at un-monitored sites based on the premise of spatial autocorrelation from known reference samples (Bowen, 2010). This assumes or infers from the data that values at spatially nearby locations will be more similar than those at locations further apart. However, this approach does not allow for prediction beyond monitoring stations as well as the quantification of prediction error and if reference samples are unevenly distributed the isoscape models can be strongly influenced by single data points.

Interpolation with regression-based predictors can partly rectify these issues as environmental correlates such as salinity, depth and temperature can be used to aid predictions of isotopic compositions in areas with no reference samples. However, this assumes that the regression relationship between the reference samples and the correlates in the sampled area are constant throughout the wider study region (Trueman, MacKenzie & St John Glew, 2017). Further uncertainty from the isoscape can be related to error from the regression model and increased spatial distance between reference samples and estimating this uncertainty is difficult and has not been accomplished for marine isoscapes (Bowen & Ravenaugh, 2003). Using an approach which couples regression and geostatistics capitalises on both techniques' strengths. For example, Bowen and Wilkinson, (2002) introduced a hybrid model which used a regression model to define large-scale patterns and geostatistics for finer-scale variation.

Empirical techniques use statistical models to derive mechanistic relationships between parameters and isotopic values which are extrapolated to predict isotopic variation at un-monitored sites. Uncertainty estimates can also be quantified, allowing confidence of predicted values to be reported (Bowen, 2010). However, these methods do not account for spatial autocorrelation which might exist and they require a good understanding of the causes of isotopic spatial variation.

Simulation methods utilise coupled ocean physics-biogeochemistry models to provide the framework for predicting isotopic variation using mechanistic relationships (Magozzi *et al.*, 2017). This does not require the collection of reference isotopic samples but sufficient spatial resolution of ocean models and the knowledge

of the mechanistic relationships is needed. Currently stable isotopes have only been incorporated into global ocean models.

If an isoscape is created using reference samples, baseline values across the study area need to be measured and as the isoscape is temporally unstable the choice of a reference organism will reflect that. For example, the stable isotope composition of primary producers such as phytoplankton may be informative when local and short-term seasonal isotopic baseline measurements are needed, because phytoplankton have short life spans and fast tissue turnover times (Jennings and Warr, 2003; Lorrain *et al.*, 2015). However, for studies across greater timescales a primary consumer which has slow tissue turnover is ideal as it integrates mean isotopic values in its diet and therefore is less prone to reflect short-term fluctuations of a primary producer's isotopic values.

Sessile invertebrates such as suspension feeding bivalve molluscs are an example of a more suitable baseline candidate because they have slower tissue turnover times and longer life histories (Cabana & Rasmussen, 1996). They also feed on a combination of material that supports benthic production including phytoplankton and so might provide an isoscape baseline for both pelagic and benthic species, and as they have a restricted diet their among individuality variation is reduced (Jennings and Warr, 2003). They also provide a clear spatial reference as they have minimal mobility (MacKenzie *et al.*, 2014). In order to further reduce between individual variance it is desirable to try to account for size and species differences and to use one species that is abundant and widely distributed (Jennings and Warr, 2003). One such species in UK waters is the queen scallop, however, sampling is restricted to areas with suitable habitat requirements and so can be uneven, creating uncertainty in the isoscape generated. Common predictor environmental variables can be used to improve isoscape accuracy (Bowen, 2010).

A dispersed pelagic primary consumer can be used as an alternative baseline organism. Jellyfish (and in particular Scyphomedusae) are widely dispersed across the upper pelagic layers and they can be sampled widely across UK waters (MacKenzie *et al.*, 2014). They grow rapidly and have short life spans and so their tissues reflect their assimilated diet during the growth season. Lion's mane jellyfish, a species sampled in UK waters, grows to reach sexual maturity within 2-5 months of the release of ephyra from the polyp and dies after reproduction (MacKenzie *et al.*, 2014). It has a generalist diet and feeds opportunistically on a large range of pelagic

organisms, which can increase isotopic variation between individuals. It is not sedentary and so an exact spatial location of feeding is unknown although it is relatively passive compared to some other pelagic zooplankton, moving mainly with prevailing currents (MacKenzie *et al.*, 2014).

Currently several baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes have been developed across UK waters (Jennings & Warr, 2003a; Barnes, Jennings & Barry, 2009; MacKenzie *et al.*, 2014; Trueman, MacKenzie & St John Glew, 2017). These used interpolation or interpolation with regression-based predictors, with reference organisms of queen scallops or lion's mane jellyfish and various environmental correlates (Table 4). The majority of the isoscapes focused on the North Sea, with no isoscape available for baseline $\delta^{13}\text{C}$ in west Celtic, Irish Sea and English Channel.

Study	Isotope	Area sampled	Method	Reference organism	Correlates used in regression models
Jennings & Warr, 2003	$\delta^{15}\text{N}$	North, Celtic, Irish Sea and English Channel	Interpolation with regression-based predictors	Queen scallops (sampled in 2001)	Day of sampling, shell height, depth, surface temperature, bottom temperature and summer salinity
Barnes et al, 2009	$\delta^{13}\text{C}$	North, Celtic Sea, English Channel			Annual mean bottom temperature
Mackenzie et al, 2014	$\delta^{13}\text{C}$ & $\delta^{15}\text{N}$	North Sea	Interpolation & interpolation with regression-based predictors	Lion's mane jellyfish (sampled in 2011)	Mean bottom temperature for $\delta^{15}\text{N}$; sea surface temperature, bottom temperature and water depth for $\delta^{13}\text{C}$
Jennings and van der Molen, 2015	$\delta^{15}\text{N}$	North, Celtic, Irish Sea and English Channel	Interpolation with regression-based predictors	Queen scallops (sampled in 2010)	Annual mean bottom temperature, annual mean bottom salinity, and minimum salinity with an interaction between bottom temperature and salinity
Trueman et al, 2017	$\delta^{13}\text{C}$ & $\delta^{15}\text{N}$	North Sea	Interpolation	Lion's mane jellyfish (sampled in 2015)	-

Table 4: Synthesis of studies which developed baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes across UK waters

The main aim of this chapter was to develop baseline isoscapes to refer sampled fish species isotopic values to a common baseline. Baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes across UK waters were developed using queen scallop samples and environmental variables. To assess the consistency of different isoscapes the North Sea baseline scallop isoscapes were compared with published lion's mane jellyfish isoscapes. As

this research was intended to support comparisons of isotopes in fishes of different species and size-classes, fish species' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across UK waters were referred to a common baseline.

2.2 Methods

2.2.1 Sampling

Queen scallop $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data were taken from a database described in Jennings & van der Molen, (2015). Samples were collected from July to November 2010 from 85 sampling sites across the North, Irish, Celtic Seas and English Channel (Figure 3) using four and eight metre beam trawls and Grand Ouverture Verticale trawls. The surveys were conducted by R.V "Tridens", R.V "Corystes" and R.V "Endeavour" using bottom trawls. At each site several scallops were collected, individual shell heights were measured to the nearest mm and individuals with a shell height of 50-60mm were preferentially retained where available. Scallops were immediately frozen to -30°C .

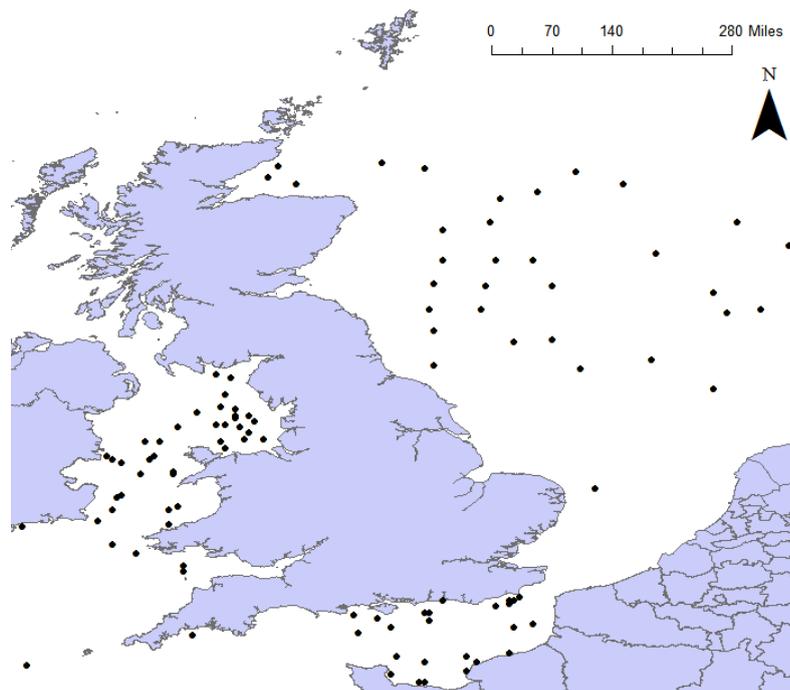


Figure 3: The location of scallops sampled in 2010

Environmental and other variables used in the analysis included: annual bottom temperature, annual salinity, depth, longitude, latitude and distance to shore.

Distance to shore was that to the UK shoreline and France. These variables were chosen based on previous studies and potential relationships between the variables and isotopic variation. Annual bottom temperature, annual salinity and depth were modelled using the Cefas north-west European shelf seas 3D setup for the General

Estuarine Transport Model (GETM; Burchard & Bolding, 2002; www.getm.eu), which covers an area from 46.4°N to 63°N and 17.25°W to 13°E with a resolution of 0.05° latitude and 0.02° longitude from 1995 to 2010. Monthly mean salinity and temperature values were extracted for the year 2010 from the near-bottom and surface model layer and these were averaged across the year to give an annual measurement. More details about how the model was created can be found in Jennings & van der Molen, (2015).

2.2.2 Stable isotope analysis

Scallops were thawed in the laboratory and a sample of 1-2g of adductor muscle tissue was removed. This was then refrozen, freeze dried and ground using a pestle and mortar to a fine homogenous powder (particles <60um). The powder was transferred to a glass vial and each sample was thoroughly mixed before 1.0mg of the sample was weighed and placed into a tin capsule for stable isotope analysis. All equipment was cleaned after processing each sample.

The Europa Scientific 20-20 IRMS with a Europa Scientific Roboprep-CN preparation module by Iso-Analytical Ltd was used to determine the nitrogen and carbon isotopic composition of the samples. Every four to six samples the system was calibrated to compensate for drift with time using two samples of reference material (a standard mix of ammonium sulphate and beet sugar). The experimental precision for carbon and nitrogen was <0.20. Scallop $\delta^{13}\text{C}$ were not lipid normalised.

2.2.3 Creation of isoscapes

Environmental variables were used to predict $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to create baseline isoscapes. To identify variables that best explained the spatial variation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, the data were split into training and prediction sets, linear models were fitted and the resultant predictions were compared with true observations (Barnes, Jennings & Barry, 2009).

Data was randomly divided into 60% 'training' and 40% 'prediction' data sets. The effect of each variable as a predictor was tested individually as well as a second and third variable. To evaluate the performance of the training set models, the prediction data set was used and the summary statistic $D = \text{mean} (X(p) - \hat{X}(p))$ was calculated as a prediction error (Barnes, Jennings & Barry, 2009), where $X(p)$ is the predicted value of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ from the training set and \hat{X} is the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ value from the predicting set. The mean value of D was calculated from 1000 runs which were

based on random choices of the training and prediction data sets to ensure results were unbiased by any particular choice of sets.

The best prediction model was selected based on that which reduced the percentage prediction error (D) the most. These models were used to estimate baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across UK seas from 49.39 to 69.51 latitude and -8.89 to 5.59 longitude. Data were excluded where temperature was less than 5°C or greater than 14°C. All analyses were performed in the statistical environment R Studio (Version 0.99.486; R Development-Core-Team, 2007).

Prediction error of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were calculated by subtracting the predicted isotopic values from observed isotopic values at the scallop sampling locations, which were interpolated across UK waters using the tool ‘Spline with barriers’ from ArcGIS (Version 10.2.1; ESRI, 2011) (MacKenzie *et al.*, 2014).

2.2.4 Comparison of isoscapes

An alternative isoscape for the North Sea was produced using lion’s mane jellyfish by kriging between sample sites (Trueman, MacKenzie, & St John Glew, 2017). To compare isoscape values, the scallop isoscapes were corrected due to differences in trophic level (TL), trophic fractionation and biochemical composition of tissues between scallops and jellyfish. This was calculated using the equation: Final isotope value = Scallop isotope values + ((Fractionation * TL difference) + Tissue offset) and values below (Trueman, MacKenzie, & St John Glew, 2017). Differences in isotopic values between the isoscapes were calculated by randomly choosing 8619 points within the isoscapes, the maximum number of points allowed to be randomly selected given the spatial resolution of the isoscapes, and subtracting scallop isotopic values from jellyfish isotopic values. These were then interpolated across the North Sea using the tool ‘Spline with barriers’ from ArcGIS (Version 10.2.1; ESRI, 2011).

Variable	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Fractionation	1	3.4
TL difference	1	1
Tissue offset	-0.8	1

2.2.5 Referring species isotopic values to a common baseline

The baseline scallop $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes were used to refer individual fish species $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic values to a common baseline across UK waters for

each sea area. The baseline values associated with each individual's sampling site were subtracted from the individual's isotopic value. Values for whole sea areas (North, Celtic, Irish Sea and English Channel) were rescaled by adding the mean predicted baseline value for each sea area (Table 5) to individuals' isotopic values to produce comparable results to other studies (Kopp *et al.*, 2015).

Sea	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
North	4.74	-17.53
Celtic	7.67	-18.18
Irish	9.46	-17.85
Channel	8.51	-18.02

Table 5: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baseline values across UK Seas

2.3 Results

Isoscape $\delta^{13}\text{C}$ values were estimated using (Equation 1 with the percentage prediction error reduced to 0.62‰. $\delta^{15}\text{N}$ values were estimated using (Equation 2 with percentage prediction error reduced to 0.76‰. The $\delta^{13}\text{C}$ isoscape indicated lower values in offshore waters and higher values closer to British coastline whilst the $\delta^{15}\text{N}$ isoscape suggested there were high values close to the British coastline and lower values in offshore waters, particularly in the north (Figure 4).

(Equation 1) $\delta^{13}\text{C} = -14.82 + (\text{bottom temperature} * -0.27) + \text{distance to shore} * -0.01$

(Equation 2) $\delta^{15}\text{N} = -488.86 + (\text{bottom temperature} * -41.13) + (\text{salinity} * 12.24) + (1.19 * \text{bottom temperature} * \text{salinity})$

Prediction error between the isoscape and sampled scallop isotopic values ranged from -2.28 to 2.15‰ for $\delta^{13}\text{C}$, with mean prediction error of $-0.02 \pm 0.72\%$, whilst $\delta^{15}\text{N}$ prediction error ranged from -2.22 to 2.12 ‰, with mean prediction error of $0.13 \pm 1.05\%$ (Figure 5). For $\delta^{13}\text{C}$ prediction error seemed greatest in the southwest North Sea and Celtic Sea, both where there are few sampling points. For $\delta^{15}\text{N}$ prediction error was also greatest in the southwest North Sea as well as the Irish Sea and to a lesser extent in the English Channel.

Differences between scallop and jellyfish isoscapes ranged from -1.26 to 3.86‰ for $\delta^{13}\text{C}$ whilst differences in $\delta^{15}\text{N}$ ranged from -10.06 to 2.96‰ (Figure 6). The mean $\delta^{13}\text{C}$ difference was $1.01 \pm 0.94\%$ suggesting the jellyfish isoscape tended to predict slightly higher $\delta^{13}\text{C}$ values than those of the scallop isoscape, whilst a mean $\delta^{15}\text{N}$ difference of $-0.57 \pm 0.94\%$ suggests the reverse occurred for $\delta^{15}\text{N}$. Larger

differences for $\delta^{13}\text{C}$ seemed to cluster together whilst for $\delta^{15}\text{N}$ the largest differences occurred along the UK coastline where the scallop isoscape predicted much higher $\delta^{15}\text{N}$ values than the jellyfish isoscape. Prediction error across the jellyfish and scallop isoscapes was low at and between sampling locations and high where few or no sampling sites were located (Figure 7).

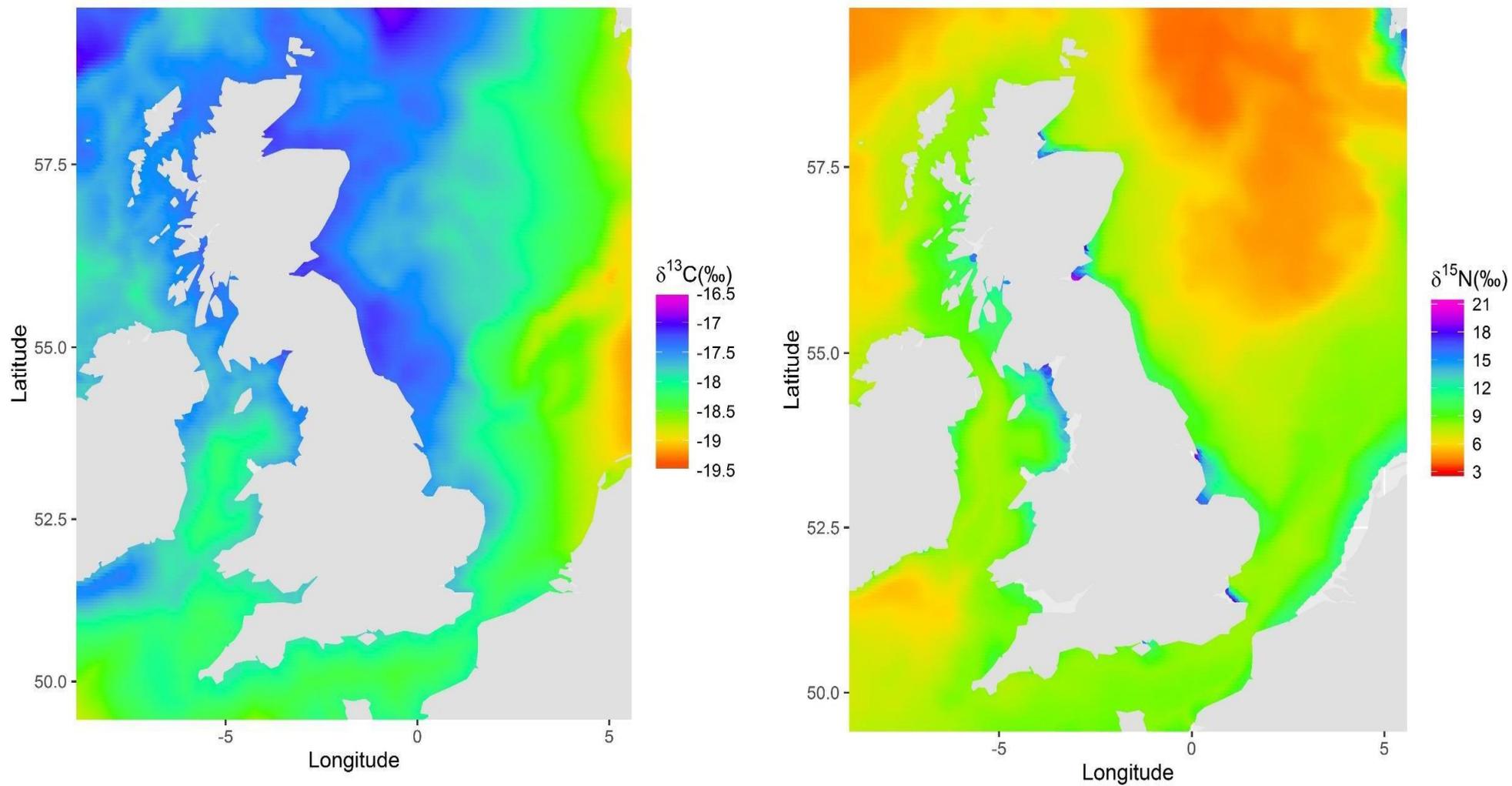


Figure 4: Predicted baseline $\delta^{13}\text{C}$ (left) and $\delta^{15}\text{N}$ (right) isoscapes across UK waters

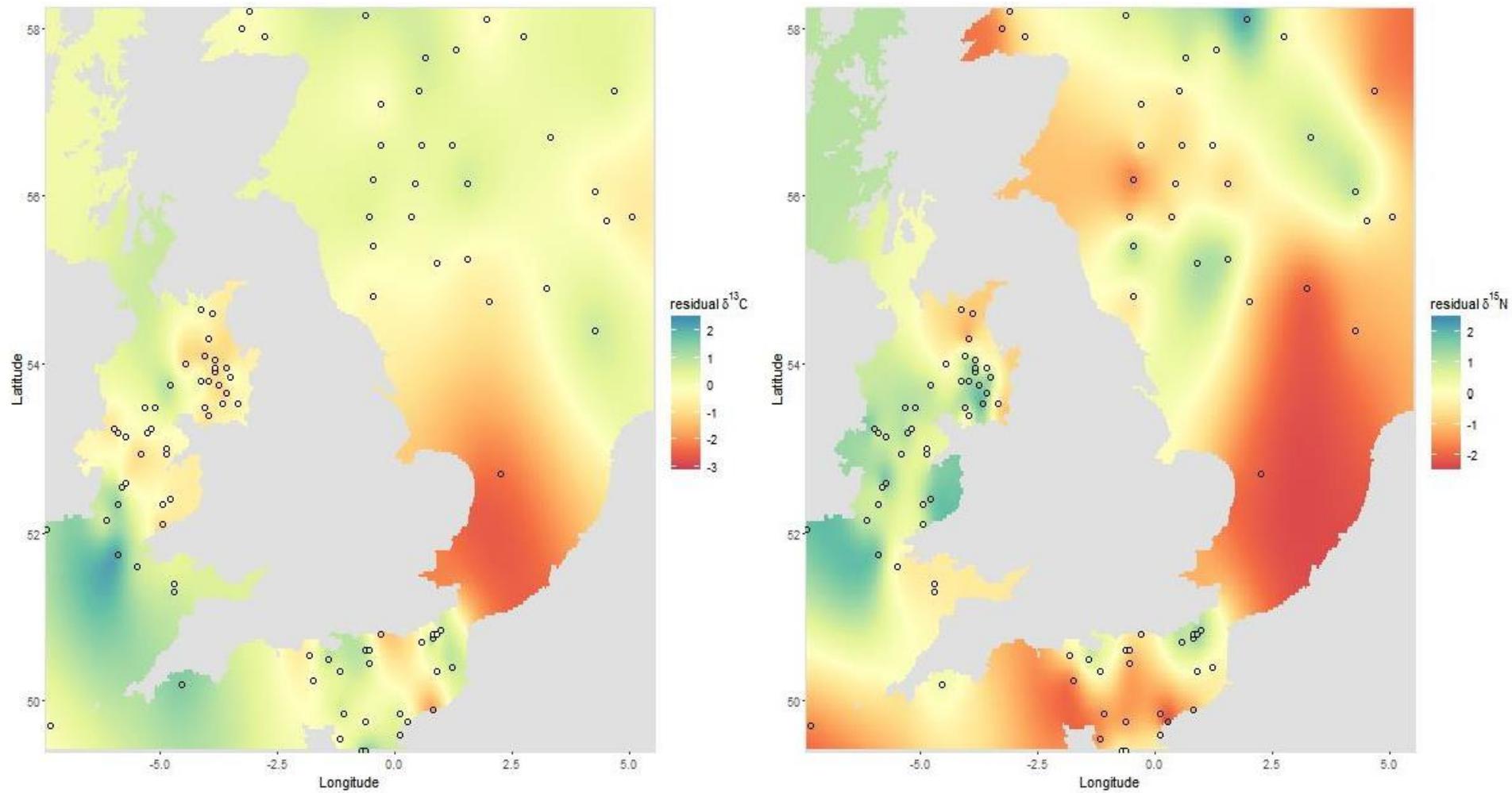


Figure 5: Residuals (observed – predicted $\delta^{13}\text{C}$ values) of $\delta^{13}\text{C}$ values (left) and $\delta^{15}\text{N}$ values (right) interpolated across UK waters with sampling locations displayed in the black outlined circles

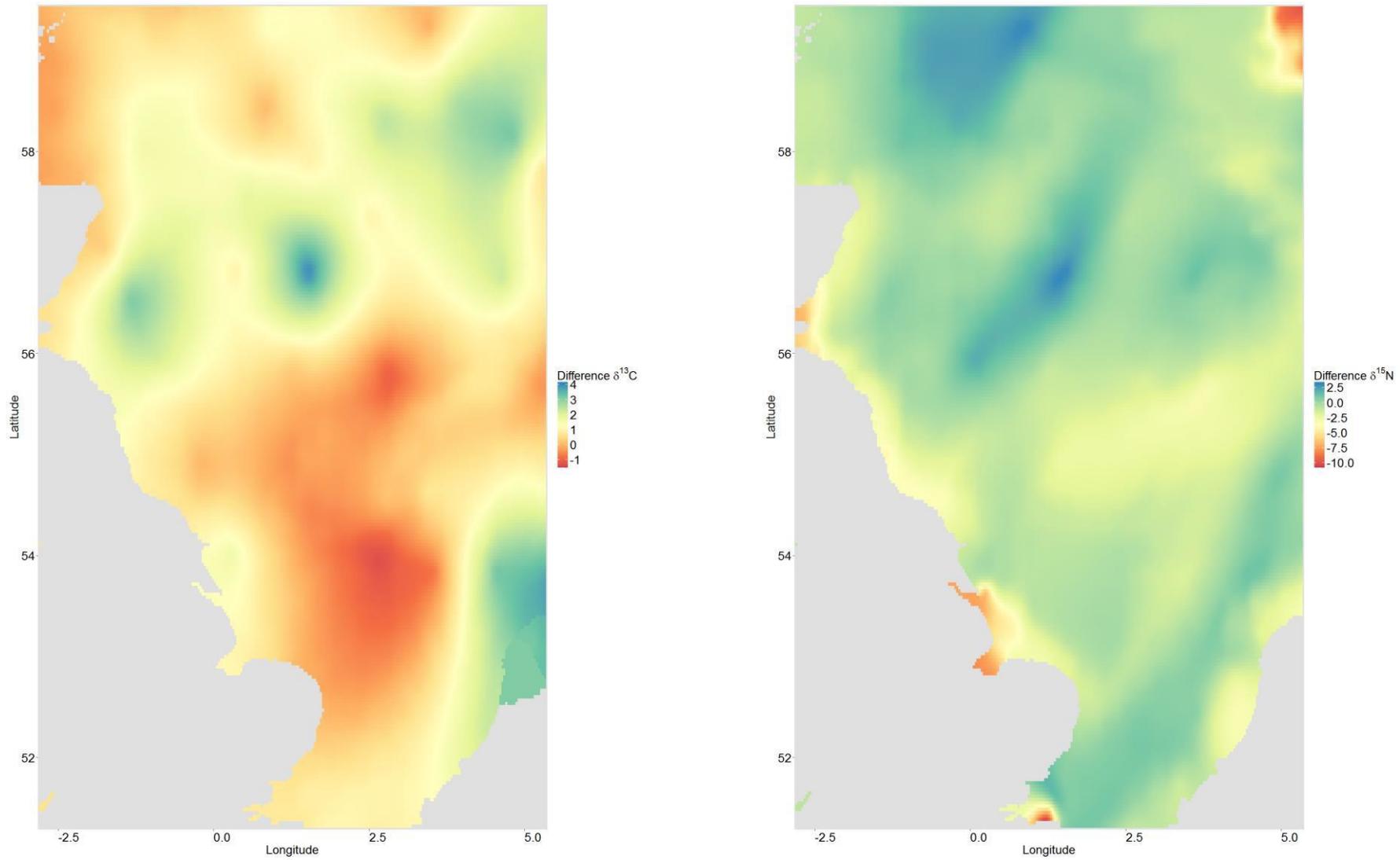


Figure 6: Differences in $\delta^{13}\text{C}$ (left) and $\delta^{15}\text{N}$ (right) values between jellyfish and scallop derived isoscapes.

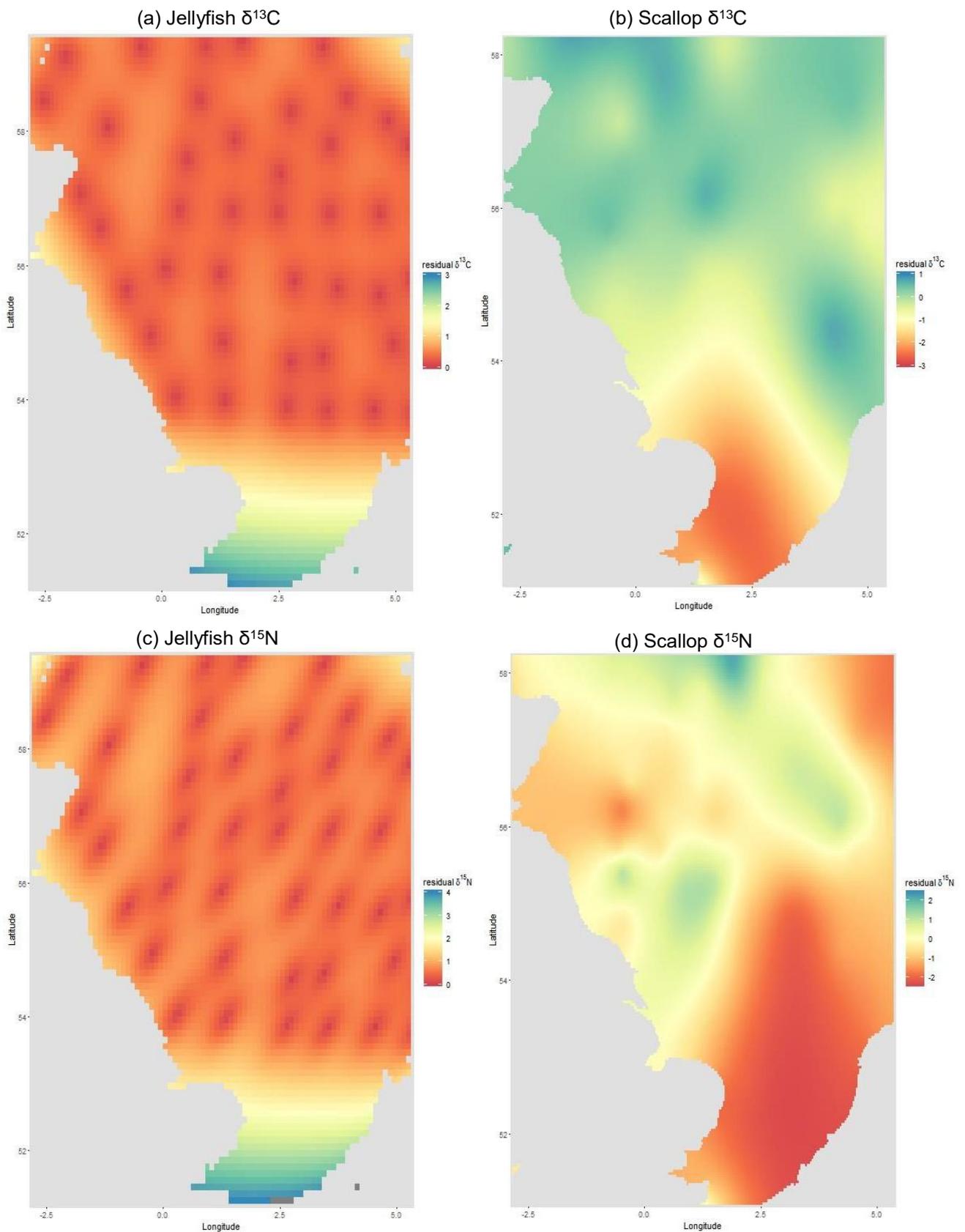


Figure 7: Prediction error of $\delta^{13}\text{C}$ values from the isoscapes using (a) jellyfish and (b) scallops and $\delta^{15}\text{N}$ values using (c) jellyfish and (d) scallops

2.4 Discussion

Baseline isoscapes were developed using queen scallop $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and environmental variables across UK waters. Prediction error across the scallop isoscapes was relatively small, suggesting the isoscapes are suitable to use for referring sampled individuals' isotopic values to a common baseline. The isoscapes created using scallops and jellyfish in the central and northern North Sea were consistent with each other suggesting both species can be used as baseline indicators (MacKenzie *et al.*, 2014; Trueman, MacKenzie & St John Glew, 2017).

Environmental variables such as annual bottom temperature, annual salinity and distance to shore were used to predict isotopic values. However, mechanistic understanding of drivers of spatial variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at this spatial resolution is not fully understood, although developing such understanding was not the purpose of the present study. Temperature was the strongest predictor variable in explaining variation in the isotopic values although this is not likely to be a causal effect; since temperature influences on fractionation of diet to consumers is considered to be small (Barnes, Jennings & Barry, 2009; MacKenzie *et al.*, 2014). Indirectly, temperature may influence the isotopic composition of nutrient sources which are assimilated by primary producers and or the fractionation within primary producers (MacKenzie *et al.*, 2014).

Temperature is likely to be a strong predictor for $\delta^{13}\text{C}$; at large ocean basin scales it co-varies positively with carbon isotopic particulate organic matter (POM) due to interactions between dissolved CO_2 contents, cell size and growth rates (Laws *et al.*, 1995b; Popp *et al.*, 1998; Burkhardt, Riebesell & Zondervan, 1999a). Distance to shore is also likely to predict $\delta^{13}\text{C}$ values; there is generally a decline with $\delta^{13}\text{C}$ values further from shore due to the progressive loss of terrestrially-derived carbon, which is also more isotopically negative, through biological processing and sedimentation (MacKenzie *et al.*, 2014; Miller, Brodeur & Rau, 2008). However, the reverse trend may also be seen, potentially reflecting a high proportion of *Spartina spp* or macroalgae in particulate organic carbon coastal sources or increased growth rates of phytoplankton due to warmer waters (MacKenzie *et al.*, 2014).

Bottom temperature may help predict $\delta^{15}\text{N}$ due to a complex interaction among hydrodynamics, bottom temperature and $\delta^{15}\text{N}_{\text{NO}_3}$ values (MacKenzie *et al.*, 2014). Salinity is also a predictor of $\delta^{15}\text{N}$ due to the correlation between salinity and the

presence of nitrate and ammonia in riverine nutrient inputs as riverine ammonia is more ^{15}N enriched than ammonia excreted by zooplankton (Jennings & van der Molen, 2015). Differences in mixing of the water column and stratification may also contribute to changes in $\delta^{15}\text{N}$ as these affect the resuspension, mobilisation and regeneration of nutrients in sediments, providing an important nitrate source for primary production (Jennings & van der Molen, 2015; MacKenzie *et al.*, 2014). For example, the southern North Sea is much shallower (typically 30m depth) with well-mixed waters compared to the northern North Sea (depth generally exceeds 80m) which is seasonably stratified (Holligan *et al.*, 1989). This results in isotopically enriched $\delta^{15}\text{N}$ values in the south from riverine input and re-suspended material whilst the low $\delta^{15}\text{N}$ values in the north suggests little nitrate is assimilated to the northern basin, also correlating with a decline in bottom temperatures with the increased water depth (MacKenzie *et al.*, 2014).

Developing a baseline isoscape using queen scallops makes several assumptions. Firstly, it assumed differences in scallop isotopic values reflect differences in phytoplankton isotopic values rather than variance in scallop feeding strategies. This is a plausible assumption because scallops feed unselectively on small particles and phytoplankton and since scallop muscle has a long turnover time it is likely they integrate annual average production of phytoplankton (Jennings & Warr, 2003a; Trueman, MacKenzie & St John Glew, 2017). This long turnover time also validates the use of annual environmental variables, as opposed to using seasonal variables. Secondly, as sampling was uneven due to the habitat requirements of scallops it was assumed that the model can be used to predict isotopic values in areas not sampled. Environmental variables were used to aid prediction although the relationships are unlikely to be casual and are not synonymous with ecological explanations (Jennings & Warr, 2003a). Therefore, prediction was limited to the extent of the area which was sampled and prediction error is likely to increase in locations which are not sampled and have different environmental conditions such as low salinity inshore waters. When sampled species' isotopic values were referred to a common baseline they were taken at the individual sampling locations which can differ from feeding sites, potentially resulting in an incorrect correction particularly if the individual is very mobile (Jennings & Warr, 2003a).

Differences between the scallop and jellyfish isoscapes seem to be clustered spatially, for example in coastal regions for $\delta^{15}\text{N}$, potentially due to the different

methodology used to create the isoscapes. The jellyfish isoscape was developed using interpolation from a regular sampled grid whilst the scallop isoscape used interpolation with regression-based predictors as the reference samples were not evenly distributed. Using interpolation results in low prediction error within the area sampled, albeit with error rapidly increasing outside this area whilst including regression-based predictors results in increased error when prediction power was poor or fewer samples were taken in areas with different environmental conditions.

The two isoscape development methods also produce different uncertainties (summarised in Table 6), the scale of which might affect the application of isoscapes. For example, if interpolation with regression-based predictors is used and the environmental correlates are data-poor or the regression relationships between isotopic variation and the correlates are inadequately understood uncertainty in the isoscape will be substantial, potentially resulting in poor spatial resolution for the application of the isoscape. Isoscapes can be used for a multitude of applications such as tracking migrating animals, removing spatial variation of higher trophic level consumers, geolocation for archaeology and forensic investigations (West *et al.*, 2010). If high spatial resolution is needed, for example to geolocate the origin of animal, then interpolation may be more beneficial if there are sufficient gridded reference samples. Interpolation with regression-based predictors may be suitable if larger scale trends across a substantial area is needed, for example when referring sampled species to a common baseline, provided the uncertainties with environmental correlates are not too substantial. Future studies may aim to produce isoscapes using the prediction-led or simulation method at a higher spatial resolution, which could also incorporate temporal variability.

Uncertainty	Interpolation	Interpolation with regression-based predictors
Isotopic measurement (e.g. machine error)	✓	✓
Between-individual variance	✓	✓
Increased uncertainty beyond sampling sites	✓	Less so*
Error from regression model	x	✓
Increased uncertainty with low number of/ uneven sampling points	✓	Less so*
Increased uncertainty at fine spatial resolution	Less so	✓
Environmental correlates	x	✓

Table 6: A comparison of uncertainties produced in isoscape methods. *assumes regression relationship remains constant in wider study region and this relationship may breakdown beyond tested parameters

2.5 Conclusion

This study aimed to develop $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baseline isoscapes and to refer sampled species' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to a common baseline. This is necessary because not accounting for spatial baseline variation can cause consumer isotopic data to be misinterpreted.

A sessile invertebrate, queen scallop, was used as a baseline species and environmental variables assisted in predicting $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Prediction error across the isoscapes were relatively small in the majority of the central and northern North Sea and comparison to baseline isoscapes created for the North Sea using lion's mane jellyfish were consistent, suggesting the scallop isoscapes were suitable to correct sampled individuals' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Further study into the causes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ spatial variation and environmental drivers may lead to greater accuracy in the development of baseline isoscapes.

3. Estimating contributions of pelagic and benthic pathways to consumer production in coupled marine food webs

3.1 Introduction

Marine consumers may feed from food chains supported directly by primary production or on those supported by detritus (Moore *et al.*, 2004). Phytoplankton primary production is mostly consumed in the water column, although in shallow tidally mixed regions both seabed fauna and zooplankton can be major phytoplankton consumers (Norén, Haamer & Lindahl, 1999). In shallow shelf seas, a large proportion of the detritus produced in the water column will accumulate on the seabed and is consumed by seabed (benthic) fauna (Kiørboe *et al.*, 1994; Carstensen, Conley & Müller-Karulis, 2003; Noji, Noji & Barthel, 1993; Steele & Collie, 2005). In deeper areas more detritus is broken down by microbial activity in the water column and flux to the seabed is relatively low (Suess, 1980; Marsay *et al.*, 2015). Detritus-based production cycles are typically dampened and attenuated in relation to cycles in primary production.

Differences in the production dynamics of pelagic and benthic detrital pathways influence the distribution, reproductive cycles, growth rates, stability and productivity of the consumers they support (Burrell, 1988; Levinton & Kelaher, 2004; Hargrave, 1973; Graf, 1992; Marcus & Marcus, 1998). Food web models suggest that the presence of pathways supported by primary production and detritus, dubbed “fast” and “slow” respectively, help to stabilise food webs (McCann, Rasmussen & Umbanhowar, 2005). Further, stronger coupling between these pathways may increase food web resilience to human and environmental perturbations (Blanchard *et al.*, 2011). Various factors may also influence species’ affiliation to the pathways such as inter-annual and consumer-size related variation. For example, changes in planktonic productivity can alter the strength of benthic-pelagic coupling (Woodland & Secor, 2013). Furthermore, small-bodied species and juvenile life stages might depend more on the pelagic pathway due to limited gape size and higher turnover rates (Woodland & Secor, 2013). Larger individuals with fewer prey size constraints may switch between available prey types, resulting in an increase in trophic reliance on both pathways (Scharf, Juanes & Rountree, 2000a; Woodland & Secor, 2013).

Diet and stable isotope-based methods have been used to measure the extent to which consumers feed on prey from pelagic or benthic environments (Kopp *et al.*, 2015; Woodland & Secor, 2013). Diet data alone will not discriminate benthic

production directly supported by phytoplankton from benthic production recycled through seabed pathways, although diet data can be used as inputs to food web models to achieve this if the diet composition of all interacting consumers is well resolved (Polunin & Pinnegar, 2002). Stable isotope analysis (SIA) of consumer tissue has the potential to discriminate benthic production directly supported by phytoplankton from benthic production recycled through seabed pathways, with the advantage that stable isotope signatures of larger consumers reflect the composition of assimilated diet over several months (Fry, 2006; Michener & Kaufman, 2007).

Several previous studies of marine pelagic-benthic coupling have shown that consumer $\delta^{13}\text{C}$ can be linked to use of benthic and pelagic pathways (e.g. Davenport & Bax 2002; Kopp et al. 2015; Giraldo et al. 2017; Woodland & Secor 2013). Species feeding in the pelagic pathway tend to have relatively low $\delta^{13}\text{C}$ values compared to species feeding on benthic material (e.g. Kopp et al. 2015; Le Loc'h et al. 2008) owing to differences in the $\delta^{13}\text{C}$ values of primary producers, detritus and associated bacteria remineralising carbon (e.g. Bouillon & Boschker 2006; France 1995; Middelburg 2014;). Diet-tissue fractionation of ^{13}C is often assumed to be small ($<1\text{‰}$), but in practice, for marine fish, fractionation may be higher, with values of 1-2 ‰ more appropriate (Sweeting *et al.*, 2007a)

Sulphur stable isotopes are also expected to provide effective discrimination of marine pelagic and benthic pathways but are only rarely used for this purpose, potentially due to the relatively high cost as S analysis must be conducted separately from C analysis (Barnes & Jennings, 2007; Connolly *et al.*, 2004; Michener & Kaufman, 2007). Producers predominately deriving sulphur from seawater sulphates such as microalgae and phytoplankton tend to have $\delta^{34}\text{S}$ of ca. 19-21‰ whilst producers utilising sedimentary sulphides will have lower $\delta^{34}\text{S}$ values (Thode, 1991) by as much as 30‰ relative to marine sulphates, the latter being reduced in anaerobic sediments (Barros *et al.*, 2010; Connolly *et al.*, 2004; Thode, 1991). Sulphur also has the advantage that there is little or no diet-tissue fractionation in $\delta^{34}\text{S}$ between a fish consumer and diet (0-1‰, $\delta^{34}\text{S}$ Barnes & Jennings 2007) so errors in assumptions about diet-tissue fractionation will be smaller and they will have a relatively small influence on the estimated contributions of different sources in mixing models (e.g. Parnell *et al.*, 2010), although fractionation may vary more across the entire food chain when differing metabolic pathways are present.

The main aim of this chapter was to establish a systematic approach for estimating the contributions of benthic and pelagic pathways to individuals, species and a community. Methods were developed using C and S stable isotope data to estimate the relative contributions of predominantly pelagic food chains supported by phytoplankton consumers (dubbed “pelagic pathways”) and benthic food chains supported by detrital pathways (“benthic pathways”) to the biomass of 15 species of shelf sea fish in the North Sea. The relative contributions of benthic and pelagic pathways as determined from combined ^{13}C and ^{34}S SIA with those determined using only the cheaper ^{13}C SIA were compared. Finally, inter-annual and consumer size-related variation in the contributions of benthic and pelagic pathways to biomass were assessed and the proportion of total fish community biomass supported by these pathways were estimated.

3.2. Methods

3.2.1. Sampling

The following data and is taken from Jennings & Cogan, (2015). Fish were caught in an area from 57.5° N - 61.5° N to 1° W - 4° E (mean depth 155 m) in August and/or September from 2002 to 2006 during the North Sea English Bottom Trawl Survey, using a Grande Ouverture Verticale bottom-fished otter trawl net with a 20mm cod-end liner which was towed at approximately four knots for thirty minutes. Fifteen fish species which had the highest rank biomass in the North Sea English Bottom Trawl survey during 2000 and 2001 in the sampling area were caught each year, with an aim to collect up to four individuals from different length classes which spanned the range of total body lengths caught in 2000 and 2001. The location of all samples caught were recorded as the middle of the sampling area of 59.5° N, 2° E.

Individuals' total body mass was recorded to the nearest 0.1g wet after blotting to remove surface water, or to 1g for larger fishes (typically > 1kg). One to five cm³ of white muscle tissue from the dorsal musculature of each individual was dissected and immediately frozen to -20°C.

3.2.2 Stable isotope analysis

In the laboratory the frozen stored samples were freeze dried and ground to a homogeneous fine powder using a pestle and mortar. After processing each sample, all equipment was cleaned. Individual samples were transferred to glass vials prior to weighing into tin capsules for SIA.

The carbon stable isotope composition of samples was determined with a Europa Scientific 20-20 IRMS with a Europa Scientific Roboprep-CN preparation module operated by Iso-Analytical Ltd (Crewe, UK). In the preparation module two reference samples of Iso-Analytical Standards IA-R014 (powdered bovine liver), IA-R005 (beet sugar) and IA-R045 and IA-R046 (ammonium sulphate) were placed between every four to six one mg samples of dried fish tissue. The carbon isotope composition of tissue samples was expressed in conventional delta notation ($\delta^{13}\text{C}$), relative to the abundance of ^{13}C in Pee Dee Belemnite. Twenty percent of samples were processed in duplicate for quality control. Standard deviation for samples within batches for a duplicated pair tended to be slightly higher than for replicates of reference material (but $<0.25\%$) and the 95th percentile of the overall distribution of absolute differences in each duplicated pair was 0.21% . Experimental precision for all batches of samples was $< 0.1\%$.

The C:N dry mass ratios of the samples were also determined in the same analysis; when sample C:N ratios were higher than 3.5 (see Jennings & Cogan, (2015) for C:N values), the $\delta^{13}\text{C}$ values were lipid corrected (Post *et al.*, 2007). Lipid correction used the following equation from Sweeting *et al.*, (2006),

$$\delta_{protein} = \frac{(\delta_{sample} * C:N_{sample}) + (7 * (C:N_{sample} - 3.663))}{C:N_{sample}} \text{ which was refined using}$$

experimental data from European sea bass tissues and produces estimates of $\delta^{13}\text{C}$ comparable with those based on chemical lipid extraction for fish tissue (Sweeting *et al.*, 2006).

For ^{34}S analysis, tin capsules containing 2 mg dried fish tissue or reference material plus 4 mg vanadium pentoxide were processed with an automatic sampler coupled to a Europa Scientific 20–20 isotope ratio mass spectrometer operated by Iso-Analytical Limited (Crewe, UK). The reference material used was IA-R036 (Iso-Analytical working standard barium sulphate, $\delta^{34}\text{S}_{\text{V-CDT}} +20.74\%$) calibrated and traceable to NBS-127 (barium sulphate, $\delta^{34}\text{S}_{\text{V-CDT}} +20.3\%$). Two capsules containing organic standards, with a composition closer to fish tissue than the inorganic standards, were run after every five tissue samples. The organic standards were IA-R036 and IA-R027 (Iso-Analytical working standard whale baleen, $\delta^{34}\text{S}_{\text{V-CDT}} +16.3\%$). Analytical precision was good (standard deviation of organic standards $< 0.25\%$). All results are presented in conventional per mil notation ($\%$) in relation to the primary ^{34}S isotope standard V-CDT (troilite of the Canyon Diablo meteorite).

$\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ isotopic values of fish consumers were also adjusted to a 'common' trophic level (TL) to account for small trophic level differences which might influence the isotopic values of individuals, independent of any contribution of benthic and pelagic pathways. Median TL estimates (Jennings & van der Molen 2015) were adjusted for trophic fractionation as follows: $\delta^{13}\text{C}_{\text{corrected}} = \delta^{13}\text{C}_{\text{actual}} + (-1.74(\text{TL}_{\text{actual}} - 4.5))$ and $\delta^{34}\text{S}_{\text{corrected}} = \delta^{34}\text{S}_{\text{actual}} + (-0.45(\text{TL}_{\text{actual}} - 4.5))$ where $\text{TL}_{\text{actual}} - 4.5$ generates an arbitrary common baseline TL that is close to the mean for all sampled individuals and the multipliers represent the mean trophic fractionation of each isotope in teleost fish as reported in Barnes et al. (2007) and Sweeting et al. (2007) respectively. Further analyses were run both with TL corrected and uncorrected isotopic values (TL uncorrected results in Appendix B).

3.2.3. Source indicator species

Two source indicator species (SISs) were selected, to characterise the isotopic composition associated with high dependence on the pelagic or high dependence on the benthic pathway respectively. The affiliation of the remaining 13 species in the community to these pathways was expressed in relation to the dependence of the SIS. Each SIS was initially identified using a combination of diet and stable isotope data. Diet data were obtained from the Integrated Database and Portal for Fish Stomach Records (DAPSTOM, Pinnegar 2014). All available diet records for the Irish, Celtic, North Sea and English Channel, were used to classify the prey of each fish species in the size-ranges sampled in this study. The prey of each fish species were classified as 'benthic', 'pelagic' or 'unknown' based on position in the water column (Table 7). Benthic prey were assumed to be all species or groups living on or in the seabed which were more likely to consume material cycled through benthic pathways. Pelagic prey were assumed to be all species or groups living anywhere else in the water column, which were more likely to be supported by food chains based on living phytoplankton. 'Unknown' prey included prey items which were unidentifiable (e.g. partially digested), non-living items (e.g. rock or sand) or items for which the ecology is not sufficiently understood. Mackerel had consumed the highest proportion of pelagic items by number, while plaice and lemon sole had consumed the highest proportion of benthic items (Table 7). Calculations were based on prey number because prey mass data were not available. Plaice and lemon sole had consumed 99.1 and 99.2% benthic prey respectively, but given that the mean $\delta^{13}\text{C}$ values of plaice was less negative than the mean for lemon sole (-16.9‰ vs -17.9‰),

and that this difference would have held even after accounting for the small differences in trophic level between these species (Jennings & van der Molen, 2015), we took plaice as the SIS. To test the sensitivities of SIS and to assess if results may be affected by the migratory movements of mackerel outside the North Sea, supplementary analyses were conducted using North Sea herring *Clupea harengus* as a SIS for pelagic production (Figure A.1).

A comparison between stable isotope data and diet data was also made using diet data from DAPSTOM based on the North Sea IVa and IVb ICES division rectangles at all available dates. Classification of prey items was also conducted as above.

Species	Benthic	Pelagic	Unknown	% benthic
Mackerel	492	1735	423	22.1
Herring	89	732	277	10.8
Norway pout	56	121	45	31.6
Saithe	671	392	53	63.1
Dab	2297	35	115	98.5
Grey gurnard	3245	180	1281	94.7
Haddock	8840	233	1585	97.4
Long rough dab	154	19	22	89
Scad	33	107	9	23.6
Lemon sole	370	3	10	99.2
Starry ray	117	1	26	99.2
Whiting	10000	2784	3015	78.2
Anglerfish	422	55	213	88.5
Cod	23289	1022	2011	95.8
Plaice	7118	62	264	99.1

Table 7: Count of prey items from gut contents analysis which were classified as benthic, pelagic or unknown. Only counts from pelagic and benthic prey items were used to estimate the percentage of benthic prey items eaten

3.4.4 Mixing models

Two end-member Bayesian mixing models were used to estimate the contribution of the pelagic and benthic pathways to fish biomass. Both models were based on simmr (Parnell, 2016), one using $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ as inputs and one using only $\delta^{13}\text{C}$.

The model equations were the following equations 1-4 from Parnell et al. (2013):

$$Y_i \sim N(p_i^T(s_i + c_i), \Sigma), i = 1, \dots, N, \quad (1)$$

$$Y_{ik}^s \sim N(\mu_k^s, \Sigma_k^s), i = 1, \dots, N_k^s, k = 1, \dots, K, \quad (2)$$

$$Y_{ik}^c \sim N(\mu_k^c, \Sigma_k^c), i = 1, \dots, N_k^c, k = 1, \dots, K. \quad (3)$$

$$\phi_i = \text{ilr}(p_i) = V^T \log \left[\frac{p_{i1}}{g(p_i)}, \dots, \frac{p_{iK}}{g(p_i)} \right] \text{ with } g(p_i) = \left(\prod_{k=1}^K p_{ik} \right)^{1/K} \quad (4)$$

The source values s_{jk} are assumed to be normally distributed based on the mean and standard deviation of the stable isotopic composition of the two SISs (Figure 8). A prior is given for the dietary proportions of each individual i on source k (denoted p_{ik}) based on the centralised log-ratio normal distribution. The residual standard deviation (denoted σ_{ij} for isotope j) was given a uniform prior distribution from 0-100. Trophic fractionation factors or concentration dependencies were not included. The model did not include uncertainty and errors from machine measurements, trophic correction, lipid correction for $\delta^{13}\text{C}$ and spatial isotopic variation of consumers.

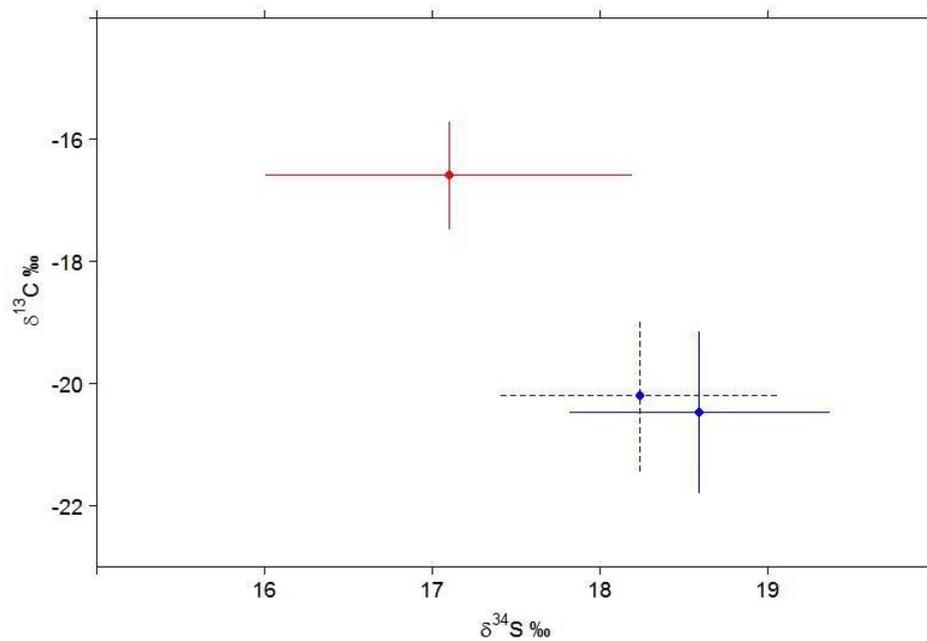


Figure 8: Mean and standard deviation of $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ for plaice (red), mackerel (blue) and herring (dashed blue) in the North Sea

Individuals were grouped by species and 100,000 iterations were run to generate a posterior probability density based on estimated contributions of the pelagic pathway to biomass. The mixing model using $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ data was run for the 2006 data and the model using just $\delta^{13}\text{C}$ was run for every year from 2002 to 2006. Output comprised estimates of modal and 50% credible intervals of the posterior distribution.

To examine the effects of body size (mass) within species and year on the contribution of the pelagic pathway, the two end-member Bayesian mixing model described above was adapted to include covariates. The model was developed in R using packages R2jags (Su & Yajima, 2015) and plyr (Wickham, 2011). The model was run grouping all species together to examine the overall effect of mass and year. Species were also separated to examine the effect of mass and year on individual

species. One million iterations were run for all individuals and 100,000 iterations for individual species. Output comprised estimates of modal and 50% credible intervals of the contribution of the pelagic pathway in centralised log-ratio transformed space, a value for convergence of the model for all parameters (\hat{R}) and an estimate for the amount of variation not explained by the parameters (σ). We only present results for models where the \hat{R} value was close to 1, indicating model convergence has occurred.

3.3.5 Biomass estimates

Biomass estimates were based on numbers-at-length recorded in the International Bottom Trawl Survey in the area 0°-4°E and 56°-62°N in 2006. Catch numbers by species and length per hour of trawling were converted to mean numerical density per ICES statistical rectangle using information on haul meta-data, gear dimensions and gear efficiency (Walker *et al.*, 2017). For each species, mean numerical density by length was converted to total numbers-at-length for the whole study area by multiplying the numerical density in each rectangle by the area of the rectangle and summing over all rectangles. Estimates of biomass by species and length were then obtained by converting individual lengths (L , cm) to individual weights (W , g) using the relationship $W=aL^b$, with parameters a and b from Silva *et al.* (2013), and multiplying individual weights by numbers-at-length.

3.3 Results

Estimates of the relative contributions of pelagic and benthic pathways to fish biomass in 2006, as generated with combined $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ (SC) analysis, were more precise than those generated with $\delta^{13}\text{C}$ (C) alone (Figure 9). However, the rank order relative contribution of pelagic pathways, based on relative modal importance of the pelagic pathway, was almost identical (Figure 9), with a Spearman rank correlation between modes of the credible intervals of 0.96, and 0.90 and 0.93 correlations for the lower and upper bounds of the 50% credible interval.

Contributions of the pathways are described as relative because they are expressed in relation to the assumed pelagic contributions of mackerel and plaice, which were taken as 0.99 and 0.01 in the absence of data or a mechanism to define absolute estimates.

Comparison of the importance of the pelagic pathway determined with SIA (based on average modal C and SC estimates) and the percentage of pelagic organisms in the

diets of species analysed using gut contents, revealed weak correlation (0.12 C and 0.2 SC ;Table 8).

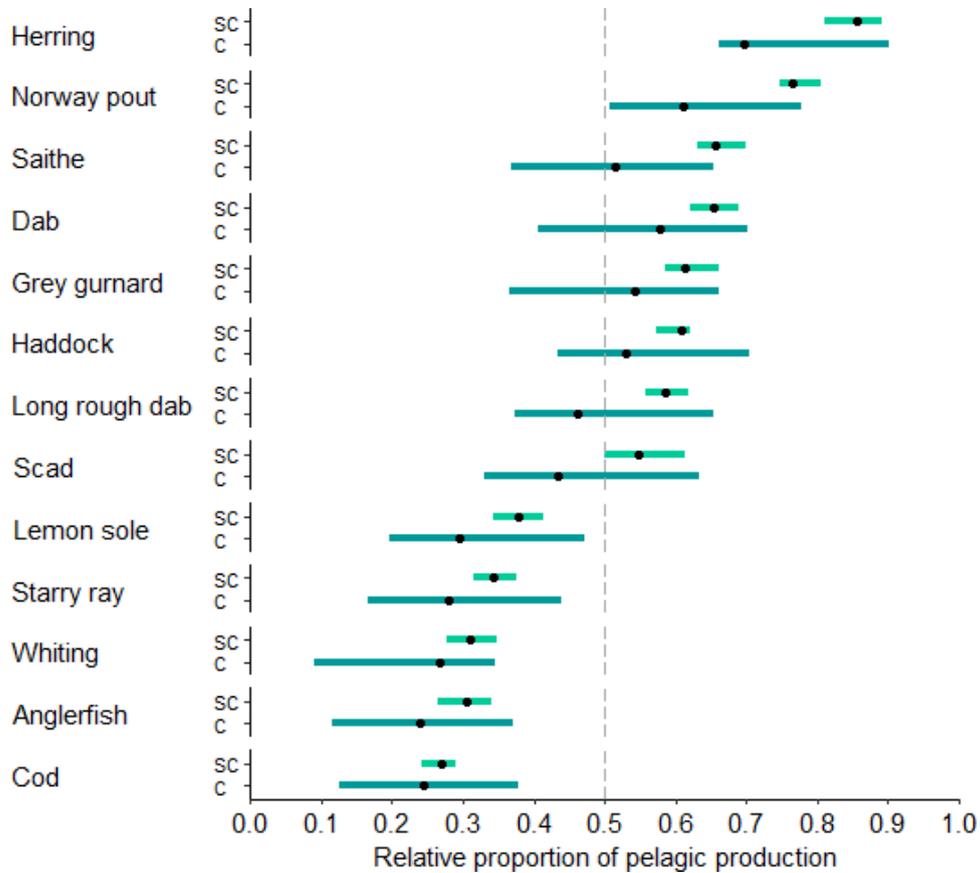


Figure 9: The estimated relative contribution of the pelagic pathway to fish biomass by species in 2006 using both $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ isotopes (SC) or just $\delta^{13}\text{C}$ (C). Species are ranked based on SC estimates. Points show the mode and bars the 50% credible intervals of the posterior distribution.

Species	Gut contents	C	SC
Herring	89.2	69.6	85.7
Norway pout	68.4	61.1	76.4
Saithe	36.9	51.5	65.6
Dab	0.6	57.9	65.4
Grey gurnard	2.5	54.4	61.3
Haddock	2.6	53.0	60.7
Long rough dab	11	46.1	58.5
Scad	92.9	43.3	54.6
Lemon sole	0	29.5	37.7
Starry ray	0.8	28.1	34.3
Whiting	75.6	26.7	31.1
Anglerfish	5.3	23.9	30.5
Cod	8.1	24.5	26.9

Table 8: Percentage of pelagic production consumed estimated using gut contents and stable isotope data (modal estimates using C and SC)

The overall relative contributions of pelagic pathways to fish biomass in 2006, based on the modal values from the SC and C models and the estimates of fish biomass, were 71% and 59% respectively (Table 9). This result implies that 29 or 41% of biomass was sustained by energy that had cycled through benthic detrital pathways. Herring and saithe, the most abundant species in the community, had 86% and 66% pelagic affiliations respectively (Figure 9, SC estimates).

Species	Species' biomass (t)	Biomass "pelagic" (t) $\delta^{34}\text{S}$ & $\delta^{13}\text{C}$	Biomass "pelagic" (t) $\delta^{13}\text{C}$
Mackerel	324104	320863	320863
Herring	643212	551282	447761
Norway pout	144739	110586	88489
Saithe	1460296	958157	752536
Dab	62670	40964	36284
Grey gurnard	99286	60872	53974
Haddock	261692	158852	138752
Long rough dab	30328	17732	13971
Scad	2508	1371	1087
Lemon sole	6830	2575	2014
Starry ray	4892	1679	1373
Whiting	90294	28094	24080
Anglerfish	26976	8218	6435
Cod	26554	7151	6513
Plaice	7317	73	73
(Totals)	(3191700)	(2268470)	(189420)

Table 9: Estimated contribution of pelagic pathways (modal SC and C estimates) to total biomass (tonnes) in the sampling area (estimated contribution to pelagic pathway by mackerel and plaice assumed to be 0.99 and 0.01 respectively).

In 2006, based on both SC and C, there was a marked decrease in pelagic affiliation and an increase in benthic affiliation with body mass for the community as a whole. The larger value of σ for C demonstrated that more variation was unexplained when S data were not included in the analyses (Table 10).

	$\delta^{13}\text{C}$ & $\delta^{34}\text{S}$			$\delta^{13}\text{C}$		
	25%	Mode	75%	25%	Mode	75%
Body mass[p]	-1.21	-0.68	-0.17	-1.11	-0.59	-0.07
Body mass[b]	0.17	0.69	1.20	0.15	0.67	1.18
σ	0.90	0.92	0.93	1.11	1.14	1.17

Table 10: Effects of body mass on use of pelagic (p) and benthic (b) pathways in the North Sea during 2006 (mode and 50% credible intervals). Positive values indicate increasing reliance on the relevant pathway.

Interannual changes in the relative contribution of pelagic pathways to species' biomass, as determined with $\delta^{13}\text{C}$ data, were modest (Figure 10), and correlations

between years for the modal contributions of pelagic pathways were always >0.57 (Table 11). The Bayesian model with a 'year' covariate reinforced this result, showing only weak year effects (Table 12). The weak year effect detected was negative (mode, -0.04), implying a fall in the relative proportion of biomass supported by pelagic pathways from 2002 to 2006.

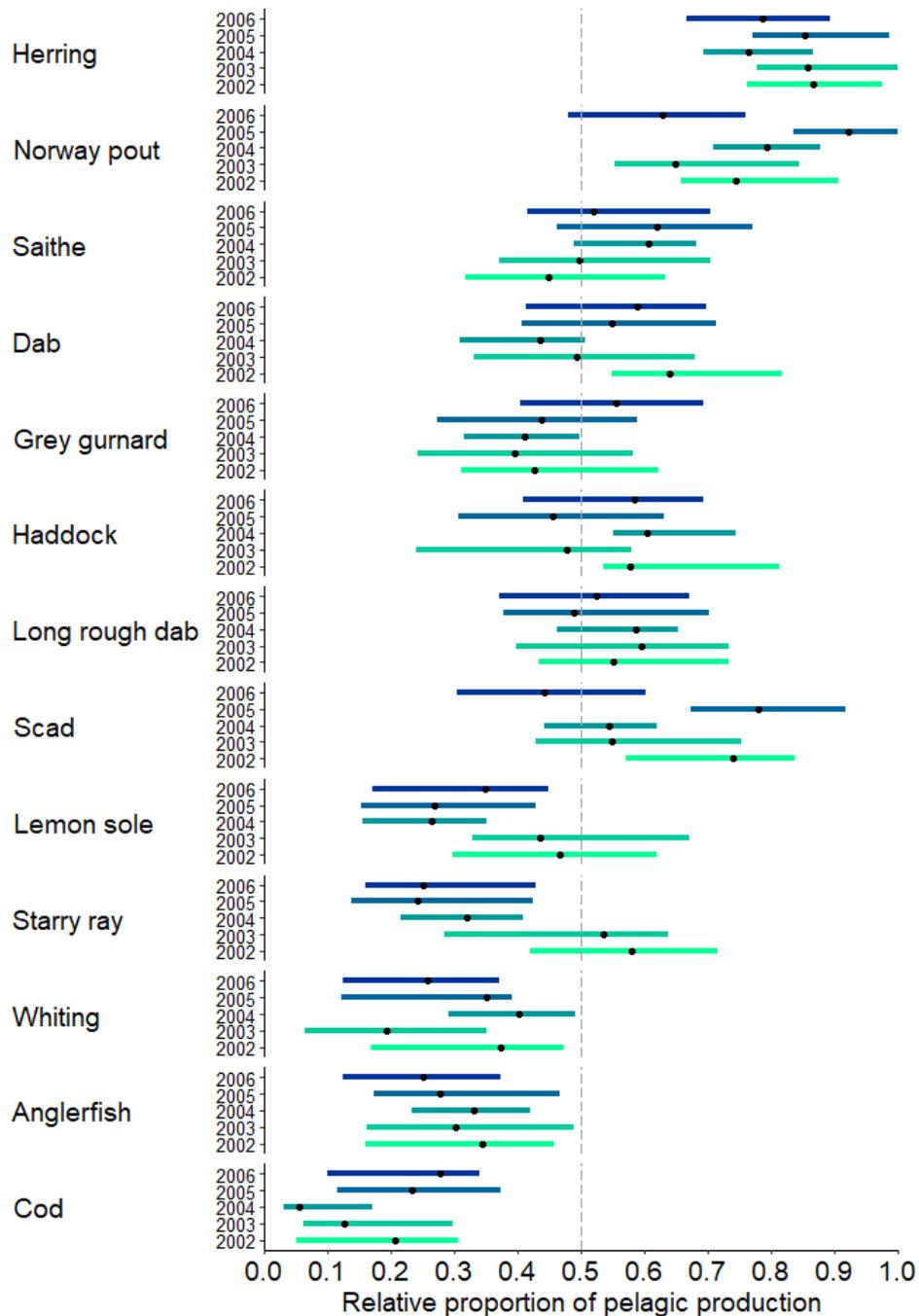


Figure 10: The estimated contribution of the pelagic pathway to fish biomass by species from 2002 to 2006 based on $\delta^{13}\text{C}$ analysis. Points show the mode and bars the 50% credible intervals of the posterior distribution.

Year	2002	2003	2004	2005	2006
2002	-	0.88	0.65	0.73	0.63
2003		-	0.74	0.76	0.57
2004			-	0.93	0.79
2005				-	0.78
2006					-

Table 11: Correlations, between years, of modal contributions of pelagic pathways to species' biomass.

	25%	Mode	75%
Body mass [p]	-3.49	-2.93	-2.37
Body mass [b]	2.38	2.93	3.48
Year [p]	-0.50	-0.04	0.45
Year [b]	-0.42	0.05	0.54
σ	1.30	1.32	1.33

Table 12: The effect of body mass and year on the contribution of pelagic (p) and benthic (b) pathways to North Sea fish biomass from 2002 to 2006 (mode and 50% credible intervals). Positive values indicate increasing reliance on the relevant pathway.

The effect of body mass on the use of the pelagic pathway by the whole fish community was negative and much stronger than the effect of year (Table 12). The high σ indicates that much of the variation in relative use of the pelagic pathway is unexplained by year or mass.

The effects of year and body mass on the contribution of the pelagic pathway (Figure 11) or benthic pathway (Figure A.2) to individual species' biomass from 2002-2006 were species dependent. The negative relationship between mass and relative use of the pelagic pathway was especially strong for whiting, dab, starry ray and lemon sole. Conversely, body mass was positively related to the relative use of the pelagic pathway for herring and grey gurnard.

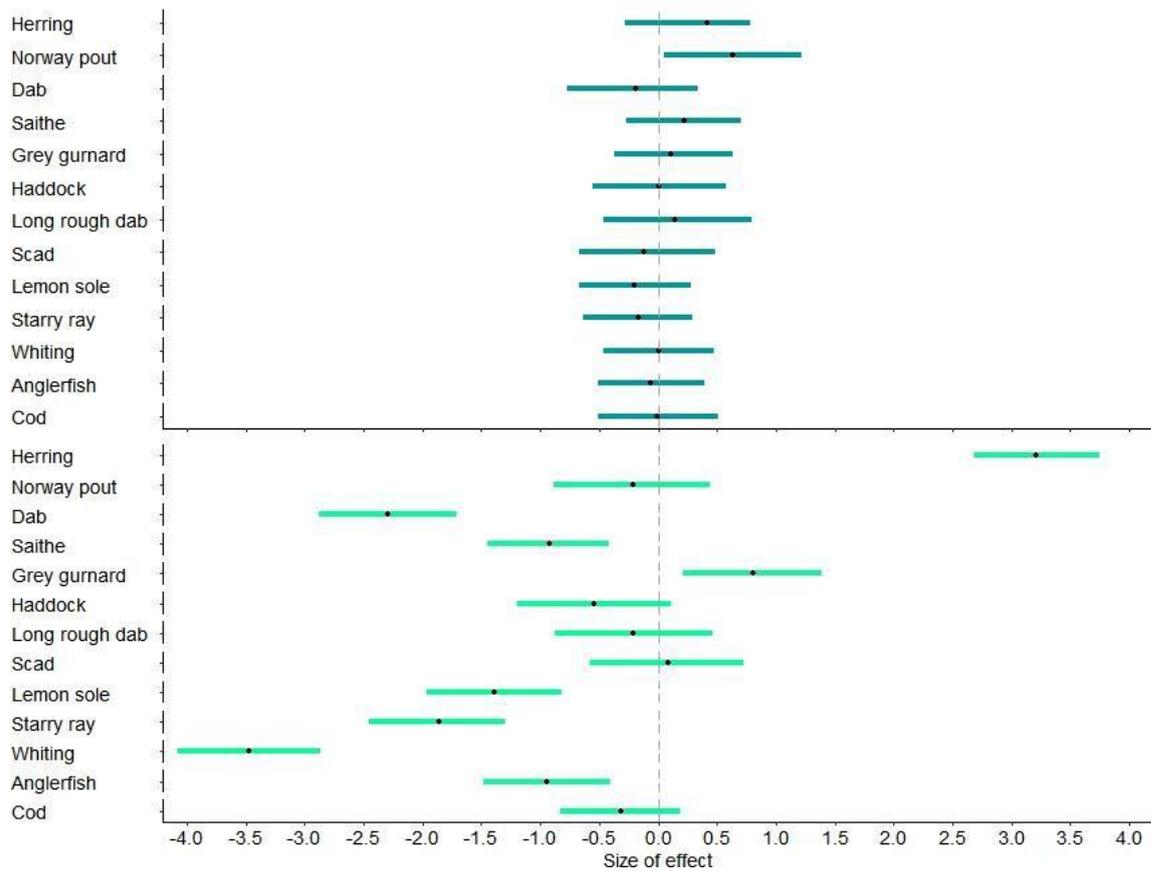


Figure 11: Effects of body mass (bottom) and year (top) on contributions of the pelagic pathway to species' biomass from 2002-2006. Positive values indicate increasing reliance on the pelagic pathway with increasing body mass or year. Points show the mode and bars the 50% credible intervals. Modal values of σ ranged from 0.8 to 1.37 across species.

3.4 Discussion

When attempting to understand the significance of pelagic and benthic food web pathways, our method provides an important complement to diet studies. This is because it characterises the extent to which production is channelled through pelagic or benthic systems as opposed to focusing on the habitat choice of prey or where those prey are consumed. Thus, our results show that even those species feeding on the seabed rely significantly on pelagic production, probably because a proportion of their bottom-living prey are feeding directly on phytoplankton (Jumars, Dorgan, & Lindsay, 2015; Lehane & Davenport, 2002; Vedel, 1998). Diel vertical migration of zooplankton may also play a significant role in the channelling of pelagic production to benthic consumers (Ringelberg, 2010). Conventional diet studies describing the extent to which consumers feed on prey found in pelagic or benthic environments may not indicate the extent to which consumers are supported by food chains supplied by phytoplankton grazing or benthic detrital chains. This is because some

benthic fauna gain a substantial proportion of their energy from grazing pelagic phytoplankton or zooplankton in shallow shelf seas (Jumars, Dorgan, & Lindsay, 2015; Lehane & Davenport, 2002; Vedel, 1998) and because invertebrates and fish accessible to predators feeding in the water column may feed extensively on benthic detritus and food chains supported by benthic detritus (Jumars, 2007; Marcus & Marcus, 1998; Mauchline, 1980). Nekto-benthic organisms, for example, are well recognised as important prey of pelagic fishes such as herring (Casini, Cardinale, & Arrhenius, 2004) as well as bottom-dwelling fishes (Mauchline, 1982).

Results implied that the use of the pelagic feeding pathway by herring increased with body mass. This was counter to the trend for other species. Previous studies of the trophic role of herring based on nitrogen stable isotope analysis have implied that trophic level consistently decreases with body mass, falling by almost one trophic level as mass increases from 30g to 300g (Jennings, D'Oliveira, & Warr, 2007). There are at least two potential drivers of the apparent increase in use of the pelagic pathway and decrease in trophic level. First, interactions between the spatial distributions of base $\delta^{13}\text{C}$ in the North Sea and age-specific herring distributions. Second, real changes in herring feeding ecology with age.

In relation to the first driver, Bierman et al., (2010) described the spawning origin of herring caught in the central and northern North Sea in summers of 2004–2007. At the latitudes of our sampling stations, autumn spawning herring (Banks, Buchan and Shetland herring) tended to be most abundant, but winter spawners from the southern North Sea (Downs herring) are also present. Autumn spawners spawn in several inshore areas to the west of the study region and young herring tend to stay in relatively shallow water (<100m) for at least their first year (typically weighing <30g). With age, they move further offshore, predominantly appearing in the study region at an age of 2 or 3 yr (typically 120-140 g). Winter spawners spend their first year in the southern and central North Sea. The spatial distribution of one measure of base $\delta^{13}\text{C}$ in the North Sea (Barnes, Jennings & Barry, 2009) varied from -17.6 to -18‰ in the study region, compared with -17.4 to -17.8‰ in the inshore areas used by young autumn spawning herring and -16 to -17‰ in the southern areas used by young winter spawners and adult winter spawners during their migrations. Consequently, autumn spawning herring that have just recruited to the study region may have marginally higher $\delta^{13}\text{C}$ than older herring, but the effect on estimates of the relative proportion of pelagic production and trophic level is likely to be small. For

winter spawning herring the effect may be much larger, and given interannual variation in the extent of mixing of autumn and winter spawners in the central North Sea (Bierman *et al.*, 2010), the effects of movement on an apparent increase in use of the pelagic pathway and decrease in trophic level cannot be discounted.

In relation to the effects of real changes in feeding ecology, the increase in the use of the pelagic pathway and decrease in trophic level with body mass in herring may reflect an increase in the prevalence of filter feeding with body mass. We are not aware that such a shift has been studied or documented with diet data (Petitgas, 2010), but methods for examining gut contents as used in existing diet studies are unlikely to record phytoplankton feeding effectively. For other clupeid species, where patterns of direct phytoplankton consumption have been a research focus, an increase in phytoplankton feeding and decrease in trophic level with body size results from increased filter feeding and decreased particulate feeding. In sardine, for example, Bode, Carrera, & Lens (2003) demonstrated that $\delta^{15}\text{N}$ of sardines ≥ 18 cm in total length fell with body size. This reduction in $\delta^{15}\text{N}$ is consistent with a decrease in trophic level (Bode *et al.*, 2007), which would result from increased feeding on phytoplankton by larger fish in cases when phytoplankton were abundant (Garrido *et al.*, 2007). Consumption of phytoplankton by filter feeding sardine may be considerable when large phytoplankton are abundant. For example, chain-forming diatoms may account for 99% of prey ingested by sardine during spring upwelling events off the Portuguese coast (Garrido, 2003). Despite the likely increase in the prevalence of phytoplankton in the diets of filter feeding fish, the absolute trophic levels of sardines (Bode *et al.*, 2017) and herring (Jennings & van der Molen, 2015) both imply that zooplankton still contribute substantially to assimilated diet of larger fish. In the future, studies to quantify the role of phytoplankton in ingested and assimilated diet of herring would be valuable. This is because confirmation of reductions in trophic level and increases in direct use of phytoplankton with body size would substantially alter our understanding of the structure and function of pelagic food webs in regions where herring are abundant. These regions include our study sites (Table 1) and the North Sea more widely (Sparholt, 1990).

Our analytical framework provides relative measures of the use of pelagic and benthic pathways. To generate these measures we assumed 99% use of the pelagic and benthic pathways by mackerel and plaice respectively (the source indicator species). While it is reasonable to assume from diet and stable isotope evidence that

mackerel primarily use the pelagic pathway and plaice primarily use the benthic pathway, their absolute use of either pathway is not known. For these reasons, we always refer to 'relative' use of a pathway. However, we do not expect absolute use of the pathways to differ markedly from our 99% assumptions given that mean depth in the study region was 170 m. Giraldo et al., (2017), for example, used C and N stable isotopes to demonstrate that coupling between pelagic and benthic systems decreases markedly with depth on another part of the northern European continental shelf. At 100m depth, the maximum depth at which they modelled results, the use of the benthic pathway by fishes feeding on the seabed was approximately 85% and the use of the pelagic pathway by pelagic piscivores was approximately 95%. Given plaice and mackerel are members of these feeding groups, and given that relationships between depth and use of pelagic or benthic pathways were still positive at 100m in the study of Giraldo et al., (2017), it is likely that the assumed 99% use of each pathway at a mean depth of 170m would be within a few percent of the true value (e.g. perhaps within 2% for the pelagic pathway and 10% for the benthic pathway). Thus the errors introduced by estimating pelagic or benthic use for the source indicator species are small in relation to the uncertainties in use of the pathways addressed and expressed in the Bayesian analyses. Since absolute use of the pelagic or benthic pathway by source indicator species is not known, estimates of use of the pelagic or benthic pathway by other species are tied to these. Consequently, conclusions about small changes in the use of pathways by these species through time may also be interpreted as changes in the use of pathways among species and may not indicate absolute changes in reliance on pelagic or benthic pathways at a system level.

In future, it would be desirable to develop the stable isotope methods to provide absolute estimates of pelagic or benthic affiliation in the study region. This would require the identification of species that are specialist feeders on phytoplankton and benthic detritus based food chains respectively and then to sample them with sufficient frequency to account for the short-term isotope dynamics which are evident in smaller individuals with fast turnover times (Wainright & Fry, 1994; Kürten *et al.*, 2013). An alternative is to simulate the seasonal dynamics of $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ in phytoplankton and benthic detritus with models to generate time-integrated estimates of source $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$, as now being attempted for $\delta^{13}\text{C}$ (Magozzi *et al.*, 2017)

and widely adopted already for $\delta^{15}\text{N}$ by biological oceanographers (Somes *et al.*, 2010).

The use of two end-member Bayesian mixing models with both C and S stable isotope data provided comparable estimates of the relative use of pelagic and benthic pathways by marine fishes in the North Sea, although uncertainty around modal estimates increased when C was used in isolation. The effects of adding S to the mixing model on the precision of the result was unsurprising given the low trophic fractionation of S (which would have minimised any variance in estimates of the relative use of pelagic and benthic pathways introduced by inaccurate estimates of trophic level) and the large and consistent differences between $\delta^{34}\text{S}$ of sulphates and sulphides (Barros *et al.*, 2010; Thode, 1991; Connolly *et al.*, 2004). Our conclusion that S led to more precise estimates of source contributions was consistent with the results of Connolly *et al.*, (2004), where a meta-analysis was used to assess the extent to which $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ distinguished sources in estuarine and marine food webs and affected the precision of estimates of source contributions to consumers. When our mixing models included both C and S the credible intervals around mean estimates of source contributions to consumers were reduced, even though S showed greater within source variability than C.

Relative use of pelagic and benthic pathways varied considerably among species, but more than two-thirds of the biomass in the total fish community was linked to food chains that were ultimately supported primarily by direct phytoplankton grazing rather than production recycled through benthic detrital pathways. Within the community, differences in the relative use of pelagic and benthic pathways by different species were largely consistent from year to year, despite potential fluctuations in planktonic activity, likely reflecting the relatively constrained habitats and diets of most species (Heessen, Daan & Ellis, 2015) as constrained by morphology and other species' characteristics determined on evolutionary time-scales (Reecht *et al.*, 2013).

Approximately 30% of total consumer biomass was linked to the benthic pathway, demonstrating that a substantial proportion of fish biomass, and by inference production, in the northern North Sea is supported by production that has passed through transformations on the seabed. All sampled species appear to use both pelagic and benthic pathways to some extent. Accessing both pathways is likely to provide a more resilient feeding strategy than reliance on one or other pathway because detrital-based production cycles are typically dampened and attenuated in

relation to cycles in primary production and, together, these out of phase cycles will stabilise temporal variance in total production (Ruardij & Van Raaphorst, 1995; Mussap & Zavatarelli, 2017) and thus food supply to a range of consumers (Darnell, 1961; Kopp *et al.*, 2015). Further, there is strong theoretical evidence to suggest that the presence and use of pathways supported by both primary production and detritus stabilise food webs (McCann, Rasmussen & Umbanhowar, 2005) and coupling between these pathways may increase food web resilience to human and environmental perturbations (Blanchard *et al.*, 2011).

3.5 Conclusion

Using $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ enabled the pelagic and benthic pathway to be differentiated and produced estimates of the contribution of the pelagic pathway to species. Approximately 70% of biomass was estimated to be supported by the pelagic pathway. Year and mass generally had a negative effect on individuals, although the size of the effect was larger for mass than year. At species level the effect of both year and mass was variable.

This study also revealed that method is a very important complement to diet studies, because it focuses not on the habitat preferences of the prey (benthic or pelagic), to define the importance of the pathway but on the extent to which production is channelled through benthic systems as opposed to passing directly from predator to prey within the pelagic zone. Thus even those species feeding on the seabed show significant use of pelagic production because their prey feed directly on phytoplankton.

As well as providing new insight into role of these species in the food web, our estimates of the importance of different pathways provide a basis for studies linking dynamics to dependence, provide evidence for coupling which has been predicted to have implications for food web stability. Future studies might aim to better understand environmental and ecological variables which affect species' affiliation to benthic and pelagic pathways.

Chapter 4. Comparative use of benthic and pelagic food web pathways by fishes in three northeast Atlantic shelf seas

4.1 Introduction

A primary aim in food web ecology is to identify processes and structures in food webs which impart persistence and stability (Rooney *et al.*, 2006). In marine food webs links between benthic and pelagic pathways (benthic-pelagic coupling) may contribute to these properties (Blanchard *et al.*, 2011; Kopp *et al.*, 2015; Woodland & Secor, 2013) One type of link is provided by consumers feeding from both pathways (Rooney *et al.*, 2006). Energy passes more slowly through benthic (detrital based) food web pathways than pelagic pathways supported directly by primary producers (Rooney & McCann, 2012). Mobile consumers integrate the pathways by switching between prey types associated with benthic or pelagic pathways. If the system is perturbed, the pathways are predicted to behave in an asynchronous fashion, with the pelagic pathway responding quickly whilst the benthic pathway is lagged, allowing a rapid yet stable recovery (Rooney *et al.*, 2006; Rooney & McCann, 2012). The extent to which consumers feed from benthic and pelagic pathways and the factors affecting their preferences are not well established. There are at least two reasons for this. First, conventional diet studies can demonstrate if consumers eat species coming from benthic or pelagic habitats, but this alone is not indicative of the pathways that support them. Many benthic bivalves, that provide food for bottom-dwelling fishes will, for example, consume phytoplankton in shallow shelf seas (Jumars, Dorgan, & Lindsay, 2015; Lehane & Davenport, 2002; Vedel, 1998). Second, efforts to assess the use of benthic or pelagic pathways by consumers rarely spanned a range of body sizes and trophic levels within and among species and spanned several regions with different environmental and oceanographic characteristics.

Carbon stable isotope analysis is a useful tool to assess the relative use of benthic and pelagic pathways by consumers (e.g. Davenport and Bax, 2002; Woodland and Secor, 2013; Kopp *et al.*, 2015) because consumers feeding on the benthic pathway are enriched in ^{13}C relative to pelagic feeders (Le Loc'h, Hily & Grall, 2008) (Kopp *et al.*, 2015). Isotopic differences occur due to microbial recycling and degradation occurring in the bottom nepheloid layer which enrich $\delta^{13}\text{C}$ in benthic systems (Le Loc'h, Hily & Grall, 2008) whilst the increased water turbulence pelagic systems are exposed supplies cells with fresh carbon at higher rates, promoting ^{13}C depletion

(France, 1995). The $\delta^{13}\text{C}$ values associated with benthic and pelagic pathways are to some extent conserved as they propagate through the food web (Mintenbeck *et al.*, 2008) because ^{13}C enrichment between a prey and its consumer is often small (0.5-1‰ per trophic transfer), although values of 1-2‰ may be typical for marine fish (Sweeting *et al.*, 2007a). Mixing models can be used to estimate the contribution of benthic and pelagic pathways to consumer tissue. Briefly, these are used to estimate the fractional contribution of the benthic or pelagic isotopic source to a tissue from the isotopic composition of the benthic and pelagic sources and the consumer tissues (e.g. Parnell *et al.* 2010; Chapter 1).

Relative use of benthic or pelagic pathways by consumers may be influenced by their behaviour, body size, location in the water column and morphology as well as external constraints imposed by the physical environment such as depth and mixing. For example, bottom dwelling species and surface living species may be expected to be more strongly affiliated with benthic or pelagic pathways than species which are loosely seabed associated or use the entire water column (Kopp *et al.*, 2015). Body size constrains feeding interactions (Cohen *et al.*, 1993b) and prey choice by small-bodied species or juvenile-stages are influenced by gape limits, behaviour choices such as predation risk, and detection and capture distances (Scharf, Juanes & Rountree, 2000b). Collectively, and perhaps within species, smaller individuals might have a higher dependence on the pelagic pathway, because prey are more accessible and productive (Woodland & Secor, 2013). Generally, larger individuals and species may not be subject to such strong foraging constraints and may switch between a wider range of more widely distributed prey types (Woodland & Secor, 2013). For many species, trophic level will increase with body size (Jennings & van der Molen, 2015) and this may require an increase in foraging area, resulting in spatially more connected food webs (Kopp *et al.*, 2015). Species at low trophic levels may rely either on the benthic or pelagic pathway, with species at a higher trophic levels tending to be generalist (Polis & Strong, 1996). This ability for species to feed from both pathways and on a broader range of prey sizes may be an important stabilising mechanism in food webs (Blanchard *et al.*, 2011; Rooney & McCann, 2012).

In marine systems, the volume of pelagic material reaching the seafloor is strongly related to depth (Martin *et al.*, 1987). If the sea is deep, less detritus reaches the seabed and benthic consumers are more likely to be supported by energy recycled

within the benthic community. If the sea is shallow, such as in a shelf sea, a large fraction of detritus reaches the seafloor, and generalist consumers may feed on prey dependent on the pelagic or benthic community or both (Blanchard *et al.*, 2011; Giraldo *et al.*, 2017). Further, in shallower waters both pelagic and benthic sources may be accessible to more consumers due to physical proximity (Kopp *et al.*, 2015; Miller, Brodeur & Rau, 2008).

The amount of mixing of the water column may also affect the strength of benthic-pelagic coupling. For example, water column circulation, horizontal and vertical mixing can affect the sinking rates of pelagic material and the amount of resuspension of material from the seafloor (Buesseler *et al.*, 2007; Griffiths *et al.*, 2017). Wind and storm events can also enhance vertical mixing, increasing nutrient availability through desorption from suspended sediment particles (Lawrence *et al.*, 2004). Well mixed waters can facilitate benthic-pelagic coupling as material from both benthic and pelagic sources will be available to consumers in any one location while physical barriers such as stratification can decrease mixing and potentially weaken benthic-pelagic coupling (Kopp *et al.*, 2015). The extent of mixing shows strong seasonality in many mid- and high-latitude shelf seas. For example, from May to October, large areas of the shelf seas around the United Kingdom become stratified with surface waters warming and bottom water remaining relatively cold (Huthnance, 2010).

This chapter aimed to use carbon stable isotope analysis to estimate the use of benthic and pelagic pathways by consumer fish species in three shelf seas around the United Kingdom. These seas differ in their geographic, oceanographic and physical characteristics and provide an opportunity to explore the effects of both ecological (species, body size and trophic level) and environmental (depth, salinity, bottom temperature) factors on the use of benthic and pelagic pathways. From the results inference is made about the extent to which consumers may contribute to stabilising the food webs in these shelf seas as a function of ecology and environment.

4.2. Methods

4.2.1. Sampling

The following data and is taken from Jennings & Cogan, (2015). Fish were sampled in the Celtic Sea, Irish Sea and English Channel in 2010. Fish were caught using a

Grande Ouverture Verticale bottom trawl or 4m beam trawls, both towed at approximately four knots for 30 minutes and positions of individuals caught were assigned to the longitude and latitude where the net was shot. The sampling aim was to catch up to six individuals from each of 7–12 length classes spanning body length ranges recorded in previous surveys in each sea area. Length classes ranged from 2 cm for the smallest species to 10 cm for the largest

Individual fish weights were recorded to the nearest 0.1g wet weight or to 1g for larger fishes heavier than one kilogram. Up to two cm³ of white muscle tissue from the dorsal musculature of each individual were dissected and immediately frozen to -20°C where it was stored frozen until it was freeze dried for further processing.

4.2.2 Stable isotope analysis

All freeze dried samples were ground to a homogenous fine powder using a pestle and mortar. After processing each individual sample all equipment was cleaned and the samples were transferred to a glass vial. The carbon and nitrogen isotopic composition of each sample was determined with a Europa Scientific 20-20 IRMS with a Europa Scientific Roboprep-CN preparation module operated by Iso-Analytical Ltd (Crewe, UK). After every four to six samples two reference samples, which were Iso-Analytical Standards IA-R014 (powdered bovine liver), IA-R005 (beet sugar) and IA-R045 and IA-R046 (ammonium sulphate), were analysed. Only carbon data isotope data were used in this study and the ¹³C composition was expressed in conventional delta notation ($\delta^{13}\text{C}$), relative to the abundance of ¹³C in Pee Dee Belemnite. Twenty percent of samples were processed in duplicate for quality control. Standard deviation for samples within batches for a duplicated pair tended to be slightly higher than replicates of reference material (<0.25‰) and the 95th percentile of the overall distribution of absolute differences for both isotopes in each duplicated pair was 0.21‰ for $\delta^{13}\text{C}$. Experimental precision for all batches of samples was < 0.1‰.

A number of methods are available to correct lipid content (e.g. Kiljunen *et al.*, 2006; Sweeting, Polunin and Jennings, 2006; Post *et al.*, 2007; Logan *et al.*, 2008). Lipid normalization was performed using the following equation from Sweeting *et al.*,

$$(2006), \delta_{protein} = \frac{(\delta_{sample} * C:N_{sample}) + (7 * (C:N_{sample} - 3.663))}{C:N_{sample}} \text{ for individuals with a C:N}$$

ratio higher than 3.5 (see Jennings & Cogan, (2015) for C:N values). This equation was refined using experimental data from European sea bass tissues and produces

estimates of $\delta^{13}\text{C}$ comparable with those based on chemical lipid extraction for fish tissue (Sweeting *et al.*, 2006).

Individual isotopic values were also corrected to a baseline $\delta^{13}\text{C}$ isoscape (Chapter 2). The baseline $\delta^{13}\text{C}$ value estimated at the sampling site (following methods in Chapter 2) was subtracted from the measured $\delta^{13}\text{C}$ and a mean baseline $\delta^{13}\text{C}$ value for each sea was added to allow absolute isotopic values to be compared with previous studies (Kopp *et al.*, 2015).

$\delta^{13}\text{C}$ isotopic values of fish consumers were also corrected to a ‘common’ trophic level to account for small trophic level differences which might influence the isotopic values of individuals, independent of any contribution of benthic and pelagic pathways. Median trophic level estimates for each individual, taken from Jennings & van der Molen (2015), were corrected for trophic fractionation as follows: $\delta^{13}\text{C}_{\text{corrected}} = \delta^{13}\text{C}_{\text{actual}} + (-1.74(\text{TL}_{\text{actual}} - 4.5))$ where $\text{TL}_{\text{actual}} - 4.5$ generates an arbitrary common baseline trophic level that is close to the mean for all sampled individuals and the multipliers represent the mean trophic fractionation of each isotope in teleost fish as reported in Sweeting *et al.* (2007). Further analyses were run both with trophic level corrected and uncorrected isotopic values (trophic level uncorrected results in Appendix B).

4.2.3 Use of $\delta^{13}\text{C}$ vs $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$

One ($\delta^{13}\text{C}$) or two ($\delta^{34}\text{S}$ and $\delta^{13}\text{C}$) isotopes can be used to differentiate between benthic and pelagic pathways (Chapter 3). Prior application of two end-member Bayesian mixing models with both CS and C stable isotope data for the North Sea provided comparable estimates of the relative use of benthic and pelagic pathways (Chapter 3), although uncertainty around modal estimates increased when C was used in isolation (Table 13).

Difference of 50% credible intervals	SC	C
Minimum	0.05	0.24
Maximum	0.11	0.3
Mean	0.07	0.27

Table 13: The minimum, maximum and mean difference of the 50% credible intervals from estimated relative contribution of the pelagic pathway to fish biomass by species (CPP) using $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ (SC) and $\delta^{13}\text{C}$ alone (C).

As available resources did not support $\delta^{34}\text{S}$ analysis for all individuals and the estimates of modal benthic and pelagic contributions with the one ($\delta^{13}\text{C}$) or two ($\delta^{34}\text{S}$)

and $\delta^{13}\text{C}$) isotope methods are similar only $\delta^{13}\text{C}$ was used in further analysis (Chapter 3).

4.2.4 Source indicator species

Relative contributions of benthic or pelagic pathways to consumer tissues were expressed in relation to source indicator species (SIS). Two source indicator species (SISs) were selected in each sea area, to characterise the isotopic composition associated with high dependence on the benthic or pelagic pathway. The affiliation of the remaining species in the community to these pathways was expressed in relation to the dependence of the SIS. Each SIS was initially identified using a combination of diet and stable isotope data. Diet data were obtained from the Integrated Database and Portal for Fish Stomach Records (DAPSTOM, Pinnegar 2014). All available diet records for the Irish, Celtic, North Sea and English Channel, were used to classify the prey of each fish species in the size-ranges sampled in this study. The prey of each fish species were classified as 'benthic', 'pelagic' or 'unknown' based on position in the water column. Benthic prey were assumed to be all species or groups living on or in the seabed which were more likely, overall, to consume material cycled through benthic pathways. Pelagic prey were assumed to be all species or groups living anywhere else in the water column, which were more likely to be supported by food chains based on living phytoplankton. The percentage of benthic and pelagic prey items were calculated by species based on numbers recorded, as DAPSTOM does not provide data on prey weights.

The stomach contents data suggested that plaice and lemon sole had consumed the highest percentage of benthic items (99.1 and 99.2% benthic prey by number respectively) and mackerel and scad consumed the highest percentage of pelagic items (Table 14). However, as the mean $\delta^{13}\text{C}$ values of plaice was lower than the mean for lemon sole (-17.9‰ vs -16.9‰), and that this difference would have held even after accounting for the small differences in trophic level between these species (Jennings & van der Molen, 2015), we took mackerel and plaice as the SIS for the Celtic Sea. In the Irish Sea and English Channel a lack of sampled individuals and differences in $\delta^{13}\text{C}$ data prevented mackerel and plaice being used as SIS. SIS for both seas were chosen based on mean $\delta^{13}\text{C}$, number of individuals sampled (count) and stomach contents data (Table 14). For the Irish Sea, herring and thornback ray were chosen for the pelagic and benthic SIS respectively. For the English Channel, scad and thornback ray were chosen for the pelagic and benthic SIS.

Sea	Species	m $\delta^{13}\text{C}$	Min $\delta^{13}\text{C}$	Max $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$	Count	% benthic
Celtic	Mackerel	-20.3	-16.3	-23.1	1.67	38	22.1
Celtic	Plaice	-17.2	-15	-20.4	1.35	24	99.1
Irish	Herring	-20.6	-19.5	-22.6	0.98	15	15.3
Irish	Thornback ray	-17	-12.1	-19.8	1.54	40	96.3
Channel	Scad	-18.9	-18.4	-19.1	0.24	7	23.6
Channel	Thornback ray	-17.5	-14.8	-20.1	1.03	68	96.3

Table 14: Source indicator species in the Celtic, Irish Sea and English Channel. Mean, minimum, maximum and standard deviation (SD) of $\delta^{13}\text{C}$ values, count of individuals sampled in each of the seas and % of benthic prey recorded in diet data.

4.2.5 Covariate variables

Annual bottom temperature, annual salinity and depth at each sampling location were estimated using the Cefas north-west European shelf seas 3D setup for the General Estuarine Transport Model (GETM; Burchard & Bolding, 2002; www.getm.eu), which covers an area from 46.4°N to 63°N and 17.25°W to 13°E with a resolution of 0.05° latitude and 0.02° longitude from 1995 to 2010. Monthly mean salinity and temperature values were extracted for the relevant years of fish sampling from the near-bottom and surface model layer and these were averaged across the year to give an annual measurement (Jennings & van der Molen, 2015). Median trophic level estimates for each individual were taken from Jennings & van der Molen (2015).

To understand whether species dependence on the pathways were related to habitat species were also grouped based on their morphology and where they tended to spend the majority of the time in the water column. Groupings followed Walker, Maxwell, Le Quesne, & Jennings (2017): 1- predominately buried in sediment; 2- predominately on the seabed (lumpiform); 3- predominately on the seabed (flat); 4- on or near the seabed (anguilliform/fusiform); 5 – predominately close to the seabed but not on it; 6- midwater species with some seabed association; 7 – pelagic.

4.2.6 Comparison of isotopic data across UK seas

A two end-member Bayesian mixing model was used to estimate the contribution of the benthic and pelagic pathways to fish biomass across the Irish, Celtic Sea and English Channel. The model was based on *simmr* (Parnell, 2016, <https://github.com/andrewcparnell>) using $\delta^{13}\text{C}$ values as inputs and was developed in R Studio (Version 0.99.486; R Development-Core-Team, 2007) using packages *plyr* (Wickham, 2011), *rjags* (Plummer, 2016), *siar* (Parnell & Jackson, 2013) and *devtools* (Wickham & Chang, 2016).

The model equations used were equations 1-4 in Parnell et al. (2013). The source values s_{jk} are assumed to be normally distributed based on the mean and standard deviation of the stable isotopic composition of the two SISs across the seas (Figure 12).

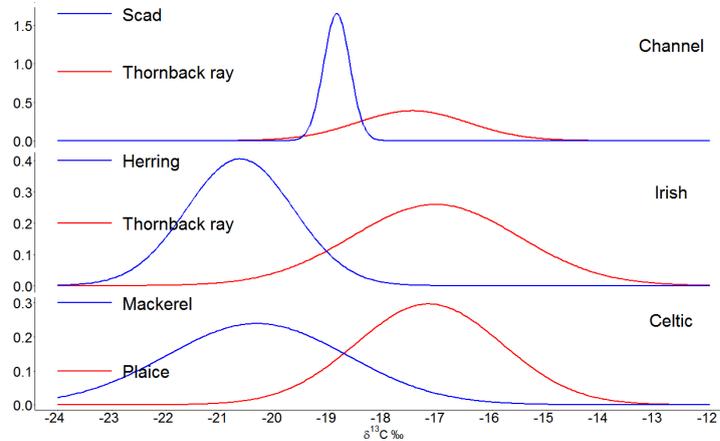


Figure 12: Distributions of isotopic values of benthic and pelagic SIS across UK seas

A prior is given for the dietary proportions of each individual i on source k (denoted p_{ik}) based on the centralised log-ratio normal distribution. The residual standard deviation (denoted σ_{ij} for isotope j) was given a uniform prior distribution from 0-100. Trophic fractionation factors or concentration dependencies were not included. The model did not include uncertainty and errors from machine measurements, trophic correction, lipid correction for $\delta^{13}\text{C}$, baseline correction and spatial isotopic variation of consumers.

Individuals were grouped by species and 100,000 iterations were run to generate a posterior probability density based on estimated contributions of the pelagic pathway to fish biomass. Output comprised estimates of the mode and 50% credible intervals of the posterior probability distribution of the relative contribution of the pelagic pathway to fish biomass by species.

The mixing model was further adapted to include covariates to examine the effects of consumer body mass, trophic level, depth, salinity and bottom temperature on species' affiliation to the pathways. The model was developed in R using packages R2jags (Su & Yajima, 2015) and plyr (Wickham, 2011). The model was run with 1,000,000 iterations grouping all species together to examine the effect of covariates on the whole community across seas. The model was also run with 100,000 iterations to examine the effect of covariates on individual species. Output comprised estimates of the mode, 50% and 90% credible intervals of the contribution of the

pelagic pathway in centralised log-ratio transformed space, R which describes model convergence, and an estimate for the amount of variation not explained by the parameters. Outputs where $R < 1.1$ at species level and < 1.3 at community level and were used for further analysis as model convergence had occurred.

4.3 Results

The relative contribution of the benthic and pelagic pathways to fish biomass by species varied across seas, with twenty-three species largely linked to the benthic pathway, five species linked to the pelagic pathway, and the remaining twenty-nine species with median contributions implying use of both pathways (Figure 13). Credible intervals were wide, reflecting high variation in use of the pathways among individuals within species and source indicator species. A similar but opposite contribution existed between the benthic and pelagic pathway and therefore the relative contribution of the pelagic pathway to fish biomass by species (CPP) was used in further analysis.

Correlation of modal CPP of species present in all seas was relatively strong, with ranked correlation of 0.42 between the Celtic and Irish Sea, 0.49 between Celtic Sea and English Channel and 0.57 between the Irish Sea and English Channel (p -values < 0.01). However, a weaker correlation existed between the mean modal CPP across all seas within the consumer groups based on depth preference and morphology ($r=0.29$, $p<0.03$).

Use of the benthic pathway increased strongly with trophic level in the Celtic Sea and English Channel, but the effect was weaker in the Irish Sea (Table 15). Across all seas trophic level was the ecological variable most strongly related to use of the benthic pathway, with an increase in trophic level causing a marked increase in benthic affiliation and a decrease in pelagic affiliation (Figure 14). A similar but weaker effect was also found with mass. For the environmental variables, the effect of salinity, depth and bottom temperature varied across the Celtic, Irish Sea and English Channel. The amount of variation not explained by the variables considered (σ) was greatest for the Irish Sea, followed by the Celtic Sea and English Channel.

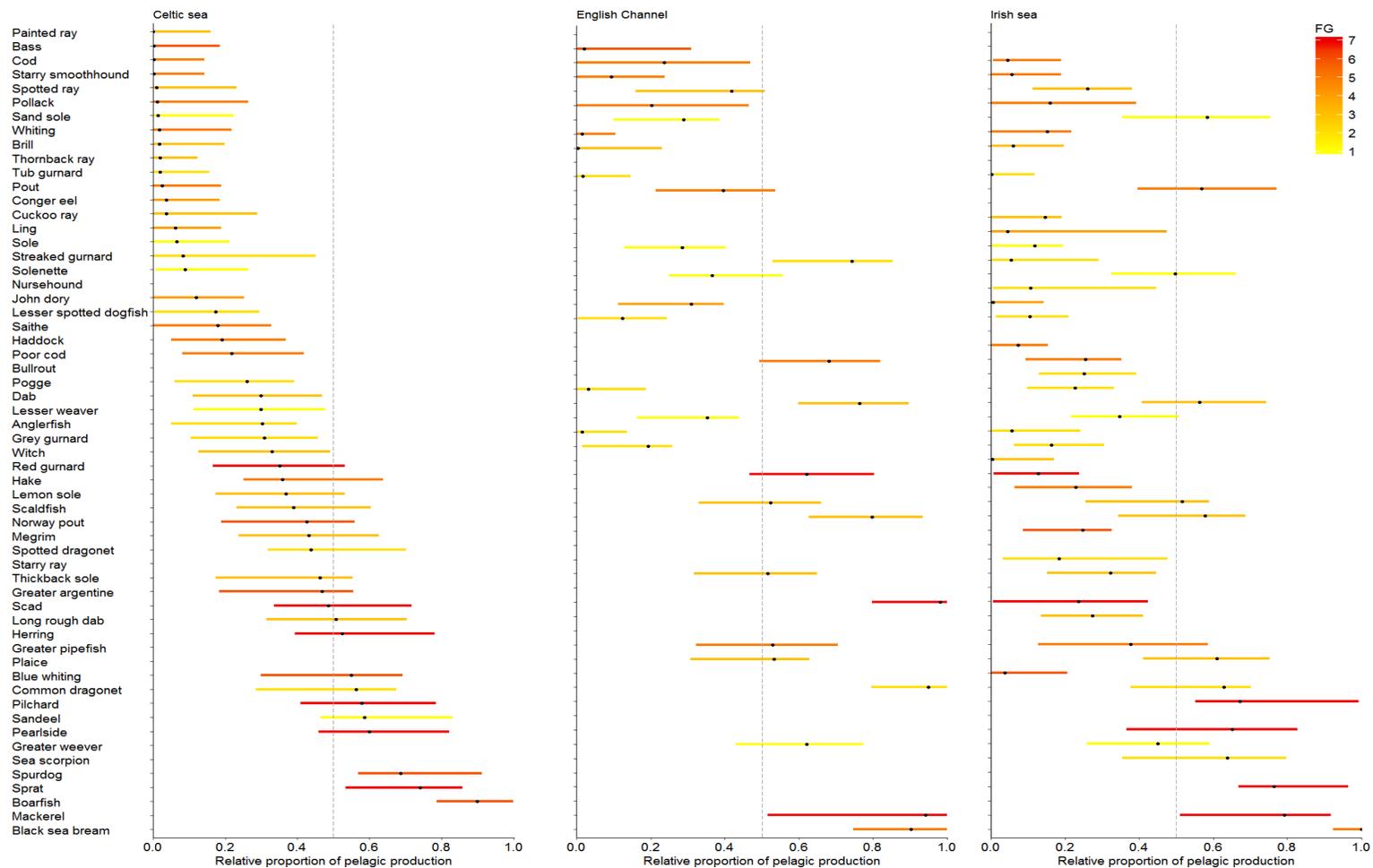


Figure 13: Estimated relative contribution of the pelagic pathway to fish biomass by species (CPP) across all seas ordered by CPP of the Celtic Sea (if absent ordered by values in first appearing panel). Points show the mode and bars the 50% credible intervals of the posterior distribution. Colours display the groups to which species are assigned based on location in the water column and morphology. (1 benthic – 7 pelagic, full description in 4.2.5)

Sea	Spearman	P-value
Celtic	-0.67	<0.001
Irish	-0.17	0.26
English Channel	-0.76	<0.001

Table 15: Results of ranked correlation between species' mean trophic level and CPP across the seas

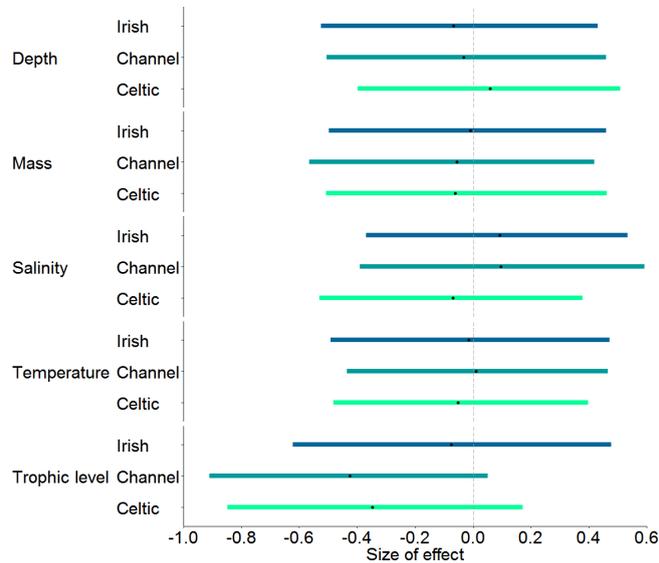


Figure 14: Estimated effect of depth, mass, salinity, temperature and trophic level on individuals' affiliation to the pelagic pathways across the Celtic, Irish Sea and English Channel. Points show the mode and bars the 50% credible intervals. σ (amount of variation not explained by the parameters) is 0.77, 0.78 and 0.58 respectively.

For the majority of species in all seas, use of the benthic pathway increased with trophic level and mass, although this effect was stronger for trophic level than mass, with many species having modes greater than -1 (Figure 15 & Figure 16). The species for which increases in trophic level led to the largest increases in use of the benthic pathway were predominantly bottom dwelling species: streaked gurnard (-1.87) and thickback sole (-1.64) in the English Channel, scaldfish (-1.25) in the Celtic Sea and lesser weaver (-1.49) in the Irish Sea. Only greater pipefish (in the Irish Sea) had a positive modal effect for trophic level. Conversely, several species such as sprat, pilchard, spotted dragonet, pogge, john dory, pout and sand sole had a positive modal mass effect across more than one sea. A larger negative effect of mass on CPP (where mode > -1) was found for poor cod in the Irish Sea and English Channel and long rough dab in the Celtic Sea.

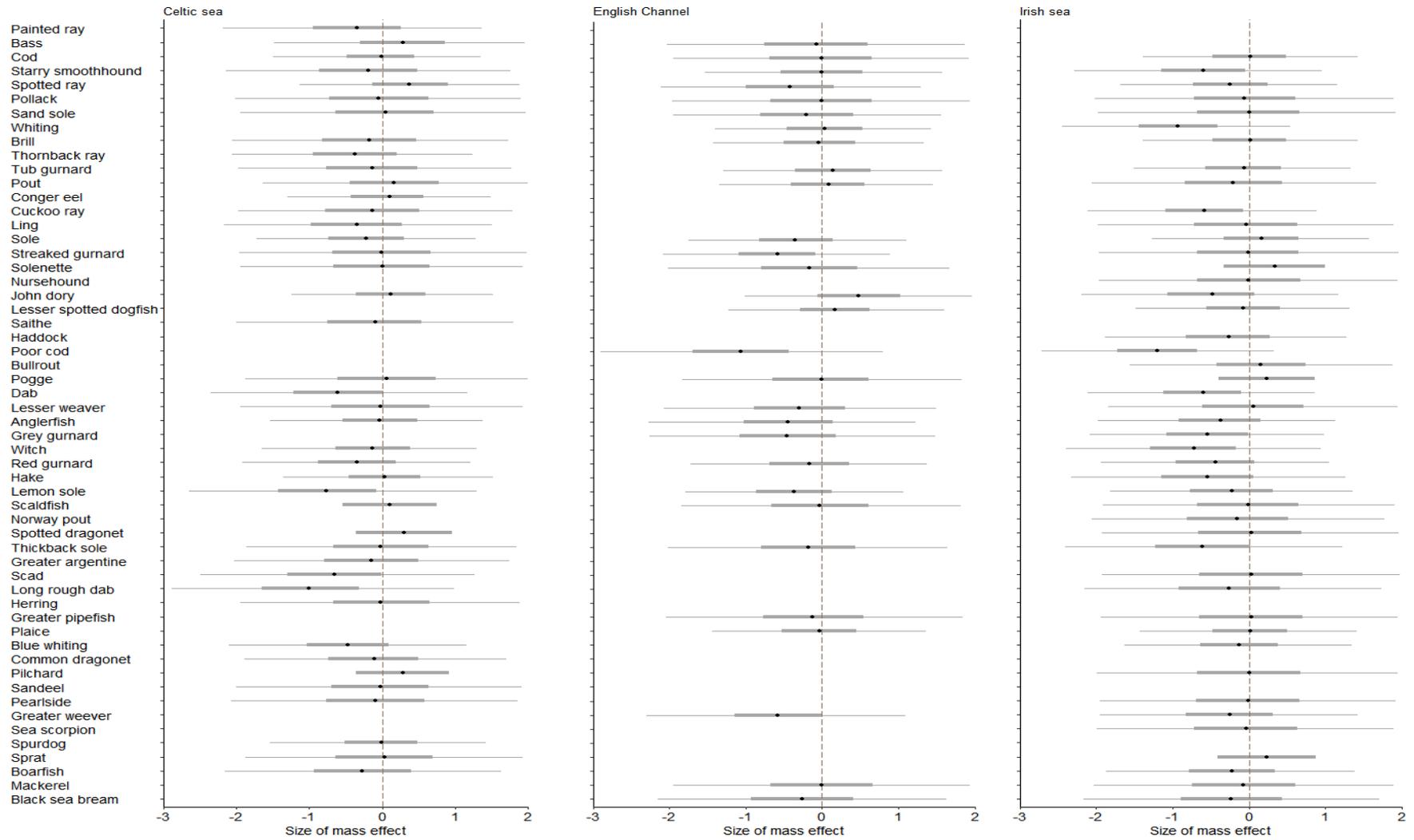


Figure 15: Estimated effect of body mass on CPP across all seas, points show the mode, bars and lines the 50% and 90% credible intervals respectively.

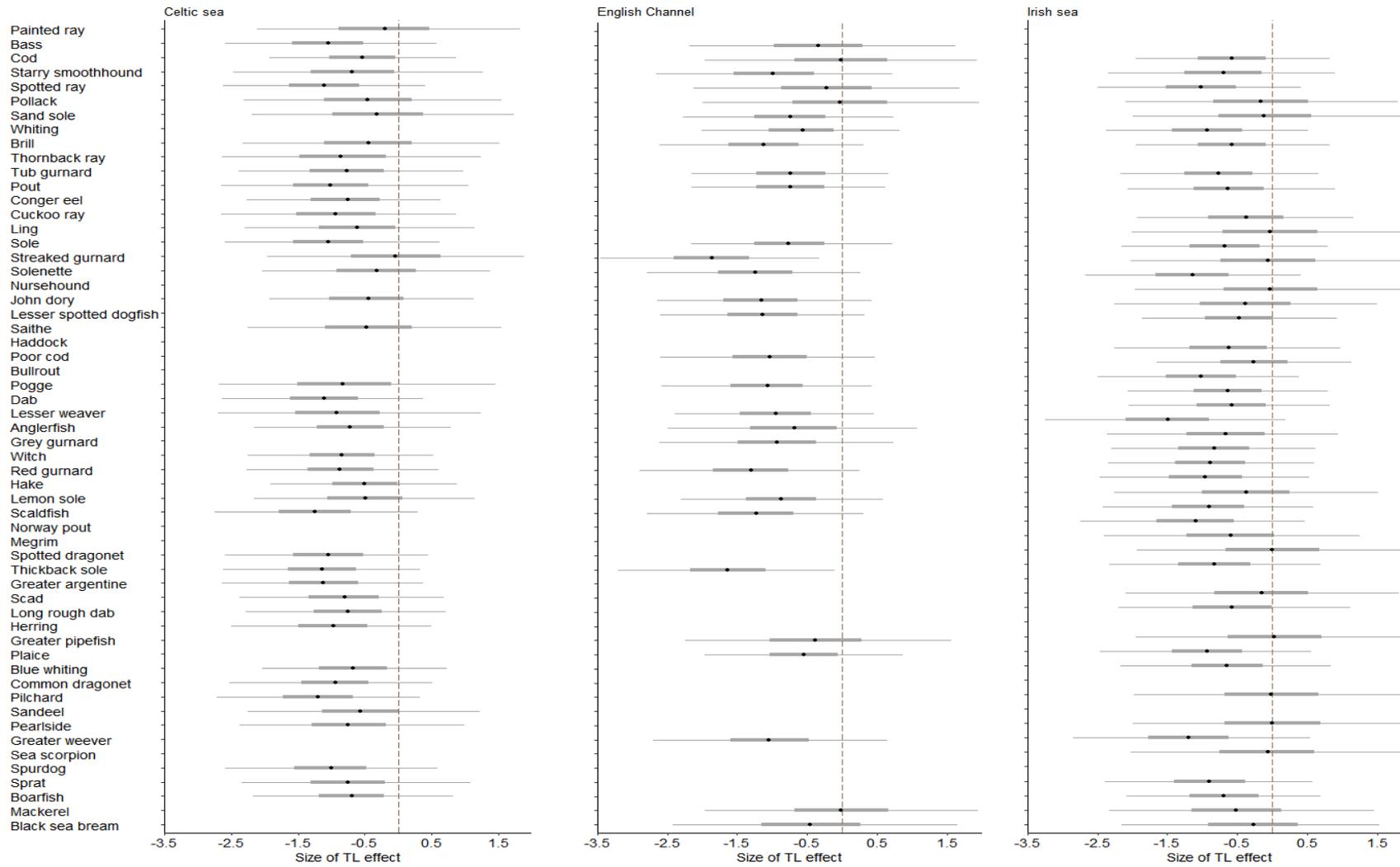


Figure 16: Estimated effect of trophic level on CPP across all seas, points show the mode, bars and lines the 50% and 90% credible intervals respectively.

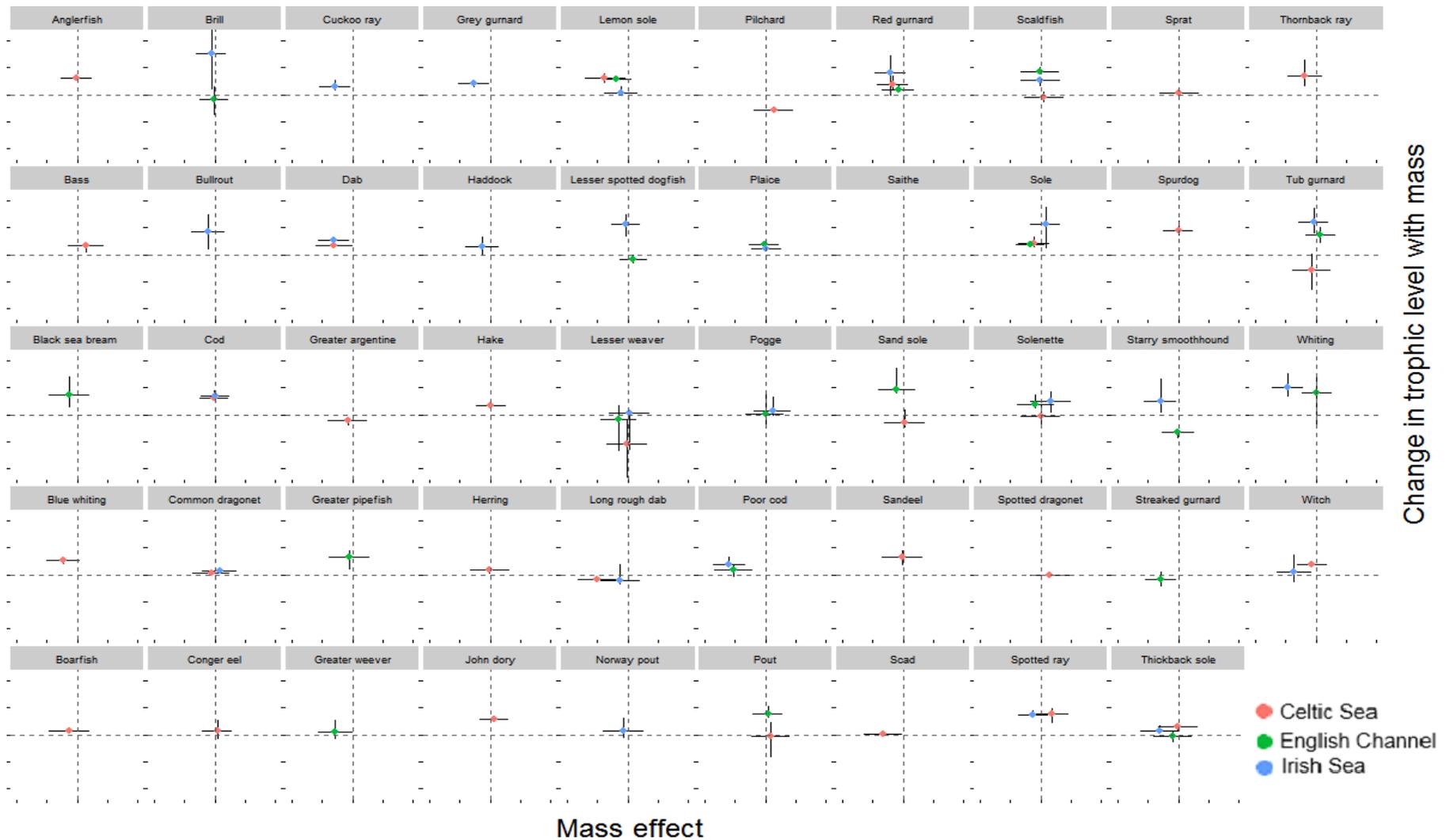


Figure 17: A comparison of the estimated effect of mass on CPP (x-axis) with the change in species' trophic level with mass (y-axis) across all seas. Points display the mode and bars the 50% credible intervals. For both axes the dashed lines represent the 0 intercepts and the tick marks represent - 2 to 2

Across all seas, change in species trophic level with mass was positive for most species, suggesting that as species increased in body mass, they also increased in trophic level, whilst also for most species the effect of body mass on CPP tended to be negative (Figure 17). Thus as species increase in mass both benthic affiliation and trophic level increase.

The impact of the environmental variables on use of the benthic or pelagic pathway tended to be small across the seas, ranging from -1.1 to 0.99 although the sign of the mean was variable across factors and seas (Table 16; Figure A.3- Figure A.5). For example, for the Irish Sea the mean modal effects of depth and salinity were negative, whilst in the Celtic Sea were positive.

	Depth			Salinity			Temperature		
	Ce	Ch	I	Ce	Ch	I	Ce	Ch	I
Minimum	-0.38	-0.36	-1.1	-0.22	-0.55	-0.76	-0.81	-0.66	-0.65
Mean	0.09	-0.01	-0.2	0.22	0.04	-0.05	-0.01	0.01	0
Maximum	0.54	0.32	0.09	0.99	0.52	0.61	0.46	0.51	0.64
Range	0.92	0.67	1.49	1.21	1.07	1.47	1.26	1.16	1.29

Table 16: The estimated minimum, mean, maximum and range modal effect of depth, salinity, bottom temperature on CPP across the Celtic Sea (Ce), Irish Sea (I) and English Channel (Ch)

Generally, the magnitude of the effects of mass, trophic level, salinity, depth and temperature on CCP varied across species. Weak or no correlations existed between the size of the effects by species across the Celtic, Irish Sea and English Channel (Table 17) although correlation between the adjacent Celtic and Irish Seas for trophic level and salinity were greater. There also tended to be little correlation between the size of the effect and the range of data although correlation was stronger for depth in the Irish Sea and salinity in English Channel (Table A.1).

Correlation	Mass	Trophic level	Salinity	Depth	Temperature
Celtic - Irish	0.18	0.55	0.4	0.09	0.16
Celtic - Channel	0.16	-0.07	-0.1	-0.21	0.17
Channel - Irish	-0.08	0.21	0.35	0.21	0.21

Table 17: Ranked correlation for the effect of variables between species present in the Celtic, Irish Sea and English Channel

4.4 Discussion

Fish communities in all these shallow shelf seas are dominated by species feeding from both benthic and pelagic pathways. Relative use of pathways varied substantially between individuals within species. Physical factors such as depth,

salinity and bottom temperature were weak predictors of the relative use of pathways. But, in all seas, species and individuals at higher trophic levels were more strongly affiliated with the benthic pathway. Use of the benthic pathway also increased with body size, but this effect was weaker than the effect associated with trophic level and small in relation to the variation in use of pathways among species and individuals. Fish morphology and location in the water column were weak predictors of use of the benthic or pelagic pathway. Overall, results suggest that most fish consumers are not reliant on one pathway or another at any locality and there are many species coupling the benthic (slow) and pelagic (fast) pathways in these shelf sea food webs. Based on existing theory, these shelf sea food webs are likely to be resilient in relation to food webs in deeper water where such coupling is much weaker (Rooney *et al.*, 2006; Blanchard *et al.*, 2011).

Our source indicator species (SIS) do not provide an absolute baseline for assessing the use of the two pathways and the use of benthic and pelagic pathways should be interpreted in relative rather than absolute terms. While it is reasonable to assume that the SIS in each sea area primarily use the benthic and pelagic pathway in each case, their absolute use of these pathways will not be 100% and will vary among seas. For these reasons we focus on rank comparisons and correlations for comparing the use of pathways in the different sea areas, and focus on analyses of the effects of ecological and environmental variables that assess relative changes in use of the pathways. Obtaining information on absolute use of benthic and pelagic pathways would be a good long-term aspiration, but would require the identification of species that are specialist feeders on phytoplankton and benthic detritus based food chains respectively and the sampling of these species with sufficient frequency to account for the short-term isotope dynamics which are evident in smaller individuals with fast turnover times (e.g. Kürten, Painting, Struck, Polunin, & Middelburg, 2013; Wainright & Fry, 1994). The spatial scales on which these baselines are set would also influence the results given food web connectedness at multiple scales.

Several processes may have increased uncertainty in the results. For example, the mixing model did not include uncertainty and errors associated with machine measurements, trophic correction, lipid correction for $\delta^{13}\text{C}$, baseline correction and spatial isotopic variation of consumers. The use of $\delta^{13}\text{C}$ alone, as opposed to using $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ to differentiate the pathways, also increased uncertainty around modal

estimates (Chapter 3). Different species were also used as SIS, which may have divergent feeding and migration patterns resulting in differences in SIS mean and standard deviations among seas and potentially affecting credible intervals and modal estimates. However, as shown in Chapter 3, the use of herring (>140g), whose movements are more constrained than mackerel, as a pelagic SIS produced very similar 50% credible intervals and modal estimates, with differences in the proportion of modal estimates always <0.17 and tending to be <0.08.

Species sampled, the number of samples and ranges of environmental variables also differed among seas. For example, the English Channel is shallower than the Celtic or Irish Sea. However, small sample sizes had little impact on the analysis; only three species had a smaller range across variables where less than ten samples were collected. Furthermore, little correlation was found between the range of environmental variables considered and the size of the effect, suggesting differing ranges of environmental conditions of the seas did not influence analysis. Given these uncertainties it may be prudent to recommend that although the results are ranked for visual ease, the wide credible intervals suggest species are separated by their use of production as either being benthic dominated, pelagic dominated and mixed use.

The stable isotope method complements diet studies because it indicates whether energy is transferred through benthic or pelagic systems rather than defining 'benthic' or 'pelagic' in terms of the habitat used by prey and the location where prey are consumed. Indeed, the assessment of the role of consumer morphology and location in the water column suggested that these factors were a weak predictor of the use of benthic or pelagic energy pathways. This is likely a consequence of the significant proportion of benthic animals that consume phytoplankton in shallow shelf seas (Jumars, Dorgan, & Lindsay, 2015; Lehane & Davenport, 2002; Vedel, 1998) and invertebrates and fish prey in the water column that feed on food chains supported by benthic detritus (Jumars, 2007; Marcus & Marcus, 1998; Mauchline, 1980). If described with diet data, the contribution of these feeding interactions to species' overall use of the benthic or pelagic pathways can only be elucidated by modelling all feeding interactions and hence the food web; and dietary data are usually not adequate to allow this to be achieved at the level of species or size classes.

The prevalence of species using both pathways suggests many species are feeding opportunistically, as demonstrated in other shelf-sea marine food webs (e.g. Chapter

3; Monteiro, Isidro and Lopes, 1991; Thomas and Cahoon, 1993; Woodland and Secor, 2013). This is also evidenced by the variation in species' affiliation to the pathways among seas and weak impact of environmental variables on relative use of the pathways. Such opportunistic feeding is possible in shelf seas because a large proportion of pelagic material reaches the seafloor where it may be consumed directly or reprocessed through detrital pathways (Blanchard *et al.*, 2011; Kopp *et al.*, 2015; Martin *et al.*, 1987). The switch towards the use of the benthic pathway with increasing trophic level and body mass is consistent with previous observations that smaller individuals are more dependent on the pelagic pathway than larger individuals (Woodland & Secor, 2013; Chapter 3). However, it is unlikely this relationship extends to the largest consumers which were not included in this study and are often observed to feed down the food web on pelagic prey that are relatively more productive (Jennings & Warr, 2003b). The weak effects of environmental factors on use of the pathways may be linked to our focus on relatively shallow and dynamic shelf-seas, with larger effects potentially found when comparing systems with greater environmental differences (Kopp *et al.*, 2015; Miller, Brodeur & Rau, 2008). For instance, a small isotopic distinction existed between benthic and benthopelagic demersal fish sampled in the northeastern North Atlantic continental slope at 500m but this separation increased with depth (Trueman *et al.*, 2014). This demonstrates there may be fewer opportunities to feed from both benthic and pelagic pathways in deeper and permanently stratified waters beyond the shelf edge (Polunin *et al.*, 2001; Reid *et al.*, 2012)

4.5 Conclusion

$\delta^{13}\text{C}$ was used to differentiate between the benthic and pelagic pathways in UK fish species. Bayesian mixing models were used to produce estimates of the relative contribution of the pelagic pathway to fish biomass by species (CPP) across three UK seas (Celtic and Irish Sea and English Channel).

The majority of species relied to some extent on both pathways and species' affiliations to the pathways varied across seas, suggesting that opportunistic feeding may be prominent. Also, correlation between CPP and functional groups was relatively weak, suggesting that a species' use of habitat may not be indicative of its dependence on a pathway, at least in a shelf sea setting.

Trophic level, body mass, depth, salinity and bottom temperature explained some variation in species' affiliations to the pathways, with trophic level and body mass generally having a negative effect on CPP and trophic level having the greatest effect. The sign of the effect of the environmental factors varied across species and seas and tended to be small, suggesting species may be able to respond to changes in local food availability. Shallow waters of shelf seas may provide access to both pelagic and benthic sources to most consumers and this strong benthic-pelagic coupling may make for strong community resilience.

Chapter 5. Higher dependence on pelagic food web pathways exacerbates fluctuations in fish populations

5.1 Introduction

Temporal variations in population abundance are widely reported and understanding the causes of these fluctuations has generated much debate over the past century (Schwartzlose *et al.*, 1999; Baumgartner, Soutar & Ferreira-Bartrina, 1992; McCann & Rooney, 2009). Many questions remain about the relative and interacting roles of environmental, food web and human drivers of these dynamics (Anderson *et al.*, 2008; Shelton & Mangel, 2011; Rooney & McCann, 2012; Cianelli *et al.*, 2006; Dunne *et al.*, 2005). These questions are still highly relevant today, as system fluctuations and the causes of them have significant implications for the conservation and management of natural resources (Clark, 2010).

Drivers of fluctuations can be a result of stochastic and deterministic events (Bjørkvoll *et al.*, 2012). Stochasticity includes random variation in the environment, which in turn influences variation in vital rates such as growth or survival (Shelton & Mangel, 2011), or demographic stochasticity in the reproduction and survival of individuals (Lande, Engen & Sæther, 2003). Deterministic drivers include competition and predator-prey interactions and changes in age structure and density-dependent responses in populations which influence, and are influenced by, food web structure (Caswell, 2001; May & McLean, 2007; Shelton & Mangel, 2011). These processes are further affected, directly and indirectly, by humans. For fished populations with age-truncated structures, for example, population dynamics may become unstable owing to changing demographic parameters such as intrinsic rates of increase and growth (Anderson *et al.*, 2008; Rouyer *et al.*, 2012).

Food web theory has been fundamental in evaluating mechanisms which affect stability in population dynamics (Monteiro & Faria, 2016). In marine food webs, several factors will interact to influence stability (Shelton & Mangel, 2011). One factor expected to increase stability is the presence of benthic (detrital) and pelagic (planktonic) pathways and coupling between them (Moore *et al.*, 2004). The benthic pathway provides food webs with stability, as energy passes through slower than the pelagic pathway, which provides efficiency (Rooney & McCann, 2012). Coupling of these pathways can occur when consumers feed from both pathways (Rooney *et al.*, 2006). Coupling may be particularly strong in shallow shelf seas where most consumers have access to both benthic and pelagic sources of production,

irrespective of their depth preferences (Kopp *et al.*, 2015). In these and other systems, highly mobile consumers can also draw on benthic and pelagic food sources (McCann & Rooney, 2009; Woodland & Secor, 2013). Theoretical analyses suggest that when a coupled system is disturbed, the pathways behave in an asynchronous fashion; the pelagic pathway responds quickly following disturbance while the response of the benthic pathway is lagged. Collectively, these out of phase responses stabilise the resource base for consumers that can use both pathways (Rooney & McCann, 2012; Rooney *et al.*, 2006).

Life history strategies and use of pelagic or benthic food web pathways may be linked, because material in the pelagic pathway tends to be more labile and spatially homogenous than in the benthic pathway. This creates a competitive environment where the most successful strategy is growing fast and reproducing quickly (Rooney & McCann, 2012), a strategy which will also reduce predation risk more rapidly in an environment where food chains are strongly size-structured (Dickie, Kerr & Boudreau, 1987). Bjørkvoll *et al.* (2012), for instance, suggested that Barents Sea fish species with greater dependence on the pelagic pathway had faster life-histories than those species dependent on the benthic pathway.

Life histories also influence population responses to climate variability and additional mortality such as fishing (Shelton & Mangel, 2011). For example, the abundance of fast growing species is more reliant on individual recruitment events, resulting in quick responses to environmental changes and larger population fluctuations than longer-lived species (Anderson *et al.*, 2008; Bjørkvoll *et al.*, 2012). Fishing can further increase fluctuations in abundance (Beddington & May, 1977; May *et al.*, 1978; Anderson *et al.*, 2008) because selective removal of larger individuals truncates age structure and thus increases the impact of changes in recruitment on population abundance and modifies demographic parameters (Anderson *et al.*, 2008).

The main aim of this chapter was to understand the potential causes of fluctuations in abundance of 15 shelf sea fish in the North Sea over a quarter century (1990/1991 to 2015/2017). Three factors were examined: benthic-pelagic coupling, life history characteristics and variability in fishing pressure over time.

5.2 Methods

5.2.1 Datasets

Two datasets were used to describe temporal fluctuations in fish species abundance. The first dataset was from the North Sea International Bottom Trawl survey (NS-IBTS). Data were downloaded from https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx. The first quarter survey data for the years 1991-2017 were chosen due to the completeness of data. Fifteen shelf fish species (plaice, starry ray, lemon sole, long rough dab, whiting, dab, haddock, scad, norway pout, saithe, herring, mackerel, grey gurnard, cod, anglerfish) were selected because the use of pelagic food-web pathways by these species had already been assessed and because they accounted for most of the total abundance of the fish community (Chapter 3). Data for Roundfish Area 1 (a defined stratum used in the survey design, boundaries roughly -4° to 4° , 62° to 58°) were used because survey hauls were from similar locations to those used to collect the stable isotope data used to assess use of the pelagic pathway. The catch per unit effort (CPUE) per length per haul data were used to provide an index of abundance in further analysis for each species.

The second dataset used were stock assessments for the main commercially fished stock in the North Sea from 1990-2015, as downloaded from <http://standardgraphs.ices.dk> (ICES, 2017). Eight species were included for which use of the pelagic pathway had been determined (Chapter 3) and for which annual spawning stock biomass estimates were available. These stocks were:

- Plaice Subarea IV (North Sea)
- Whiting Subarea IV (North Sea) and Division VIIId (Eastern Channel)
- Herring in Subarea IV and Divisions IIIa and VIIId (North Sea autumn spawners)
- Norway pout in Subarea IV (North Sea) and IIIa (Skagerrak - Kattegat) – Autumn assessment
- Cod (*Gadus morhua*) in Subarea IV and Divisions VIIId and IIIa West (North Sea. Eastern English Channel. Skagerrak)
- Saithe in Subarea IV (North Sea) Division IIIa West (Skagerrak) and Subarea VI (West of Scotland and Rockall)
- Haddock in Subarea IV and Divisions IIIa West and VIa (North Sea. Skagerrak and West of Scotland)
- Mackerel in the Northeast Atlantic (combined Southern, Western and North Sea spawning components).

5.2.2 Acquiring variables: Benthic-pelagic coupling, life history parameters, fishing pressure

The metric used to measure the strength of benthic-pelagic coupling for each species was the estimated relative contribution of the pelagic pathway to fish biomass (CPP). CPP was calculated for each species using stable isotope data ($\delta^{13}\text{C}$) collected in the North Sea from 2002-2006 as outlined in Section 3.2. To test sensitivities of CPP estimates, yearly $\delta^{13}\text{C}$ values were used as well as combined $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values from 2006 which have much smaller uncertainty surrounding the modal estimates. $\delta^{13}\text{C}$ values of fish consumers were corrected to a 'common' trophic level (TL) to account for small trophic level differences which might influence the isotopic values of individuals, independent of any contribution of benthic and pelagic pathways. Further analyses were run both with TL corrected and uncorrected isotopic values (TL uncorrected results in Appendix B).

Asymptotic weight W_{∞} , in the von Bertalanffy Growth Equation was used as a metric to describe species' life history. This parameter is correlated with many other fish life history parameters including intrinsic rates of increase, size and age at maturity, natural mortality and longevity. A literature search was conducted to find estimates of W_{∞} from the period for which survey and stock assessment data were collated (Table 18).

Species	Jennings et al. 2008	García-Carreras et al. 2016	Speirs et al. 2016	Jennings et al. 1999	Mean	Log ₁₀
Anglerfish	18045			16646.25	17345.63	4.24
Cod	19380	21012.43	19218.58	19218.58	19707.40	4.29
Dab	211		621.93	203.14	345.36	2.54
Grey gurnard	886		773.12	824.74	827.95	2.92
Haddock	3075	686.97	2776.96	3186.27	2431.30	3.39
Herring		286.87	246.01		266.44	2.43
Lemon sole	551	465.88		624.62	547.17	2.74
Long rough dab	133			120.02	126.51	2.10
Mackerel		436.76			436.76	2.64
Norway pout	68	71.27	51.63	99.18	72.52	1.86
Plaice	1465	434.14	897.00	1518.58	1078.68	3.03
Saithe	8271	13134.99	4838.87		8748.29	3.94
Scad	950				950.00	2.98
Starry ray	2348			2392.45	2370.23	3.37
Whiting	594	507.17	705.63	657.73	616.13	2.79

Table 18: W_{∞} values (g) for species from the literature and the resultant mean and log₁₀ values

Given some variation in estimates among studies and years, mean values were taken when more than one estimate was available. In some cases W_{∞} values were

derived from estimates of L_{∞} using the relationship $W=aL^b$, with parameters a and b from Silva et al. (2013).

Variability in recruitment was used as an additional life history parameter.

Recruitment is the number of fish surviving to enter the fishery and can be highly variable for short-lived species (ICES 2016b). Recruitment rates (with a unit of thousands of individuals) were obtained from the ICES stock assessment dataset.

Variation in fishing mortality was used as the metric for variability in fishing pressure. Fishing mortality is an index of the proportion of fish in a year class killed by fishing in one year, averaged over the dominant year classes in the catches (ICES 2016b). Fishing mortality rates were obtained from the ICES stock assessment dataset.

All metrics used are modelled estimates and have uncertainties and potential errors associated with their calculation. For example, when calculating stock assessments and associated metrics, assumptions were made such as maturity-at-age and natural mortality-at-age remaining constant for plaice (ICES, 2016a). Therefore cautious interpretation of results is needed.

5.2.3 Data analysis of trawl survey data

Species length classes were converted from mm to cm and individuals smaller than 12cm were removed from the analyses because they are poorly selected by the survey gear (Walker *et al.*, 2017). The dataset provided CPUE in numbers by length class. Length classes were converted to weight classes with the relationship $W=aL^b$, with parameters a and b from Silva et al. (2013). Biomass by species by year was estimated by multiplying individual body mass by numbers at length per haul, and summing these quantities by species by year.

To ensure species biomass variance was not affected by the size of population biomass, species' biomass was \log_{10} transformed so variance was independent of mean biomass. In addition, spatial and temporal autocorrelation was tested to examine if species' variance was affected by space and time. For example, shoaling species such as herring may cluster together at a particular time or location, which might or might not be sampled by the trawl survey and the patchiness of the data may not be an accurate representation of overall population variance.

Spatial autocorrelation was tested using variograms and found not to be present for any species. Autocovariance was tested using the Kwiatkowski–Phillips–Schmidt–

Shin (*KPSS*) test and showed temporal autocorrelation in three species (anglerfish, grey gurnard and cod). A linear mixed effect model with a correlation structure was used to quantify the logged biomass of species whilst removing potential effects from the temporal autocorrelation: $\text{lme}(\text{logbiomass} \sim 1, \text{random}=\sim 1|\text{Species}, \text{correlation}=\text{corAR1}(\text{form}=\sim 1|\text{Species}))$. As model fit was enhanced with the correlation structure compared to without (Table A.2) the residuals from this model were extracted.

For species without temporal autocorrelation a linear mixed effect model was used to quantify the logged biomass of species with the following structure: $\text{lme}(\text{logbiomass} \sim 1, \text{random}=\sim 1|\text{Species})$. Residuals by species were extracted from the model and the standard deviations (SD) of residuals were calculated to use as a metric for variability in species abundance. The relationship between the SD of residuals with CPP and W_∞ was plotted and the linear relationship between the variables were examined.

5.2.4 Data analysis of stock assessment data

A loess curve with a span of 0.7, which was tested as being best model fit whilst not overfitting the model, was fitted to modelled stock size across years by species and SD of the residuals were calculated, to use as a metric for variability in species abundance. To estimate variability in fishing pressure and recruitment a loess with a span of 0.7 was fitted to the estimated fishing mortality and recruitment across years by species and SD of the residuals were calculated. The relationship between the SD of residuals from stock size and CPP, W_∞ , SD of residuals from fishing pressure and recruitment was examined using linear models.

All data analysis was conducted in R Studio (Version 0.99.486; R Development-Core-Team, 2007) using packages *plyr* (Wickham, 2011), *ggplot2* (Wickham, 2009), *mgcv* (Wood, 2011), *gstat* (Pebesma, 2004), *sp* (Pebesma & Bivand, 2005), *astsa* (Stoffer, 2016), *xts* (Ryan & Ulrich, 2014) and *nlme* (Pinheiro *et al.*, 2017).

5.3 Results

The relationships between fluctuations in species' abundances and benthic-pelagic coupling, W_∞ , variability in fishing pressure and recruitment across the two datasets were variable (Figure 18). A strong positive relationship was found between fluctuations in species' abundance and the relative contribution of the pelagic pathway to fish biomass (CPP) across both datasets, although this was less

pronounced with the stock assessment dataset (SA) which included fewer species (Table 19). CPP estimates derived from mean, yearly $\delta^{13}\text{C}$ values or combined $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ estimates did not significantly impact the significance of the p-values when examining the effect of CPP on fluctuations in species' abundances (Table 20).

A weak negative relationship existed between W_{∞} and fluctuations in species' abundances (Table 19) and use of mean W_{∞} from a collection of scientific studies as opposed to W_{∞} from a single study did not affect the qualitative result (Table 21). A strong negative correlation existed between recruitment and W_{∞} (-0.68, p-value 0.06). Variability in recruitment was negatively related to fluctuations in species' abundance when modelled with other variables, although when modelled alone the effect was positive (Table 19). When modelled with W_{∞} , p-values were smaller for recruitment variability compared to W_{∞} (Table 19).

Variability in fishing pressure was negatively related to fluctuations in species' abundance when modelled with other variables, although when modelled alone the effect was positive (Table 19). AIC was used to determine model fit, with higher AIC suggesting worsening model fit. Variability in fishing pressure had the weakest relationship with fluctuations in species' abundance, with high AIC and p-values (Table 19).

The addition of W_{∞} , variability in fishing pressure and recruitment to CPP did not improve the model, with the added variables causing an increase in AIC and decrease in the level of significance of p-values across both datasets (Table 19). Furthermore, results from ANOVA comparing CPP against other models across both datasets suggested the addition of the other variables did not significantly alter the model outcome (Table A.4).

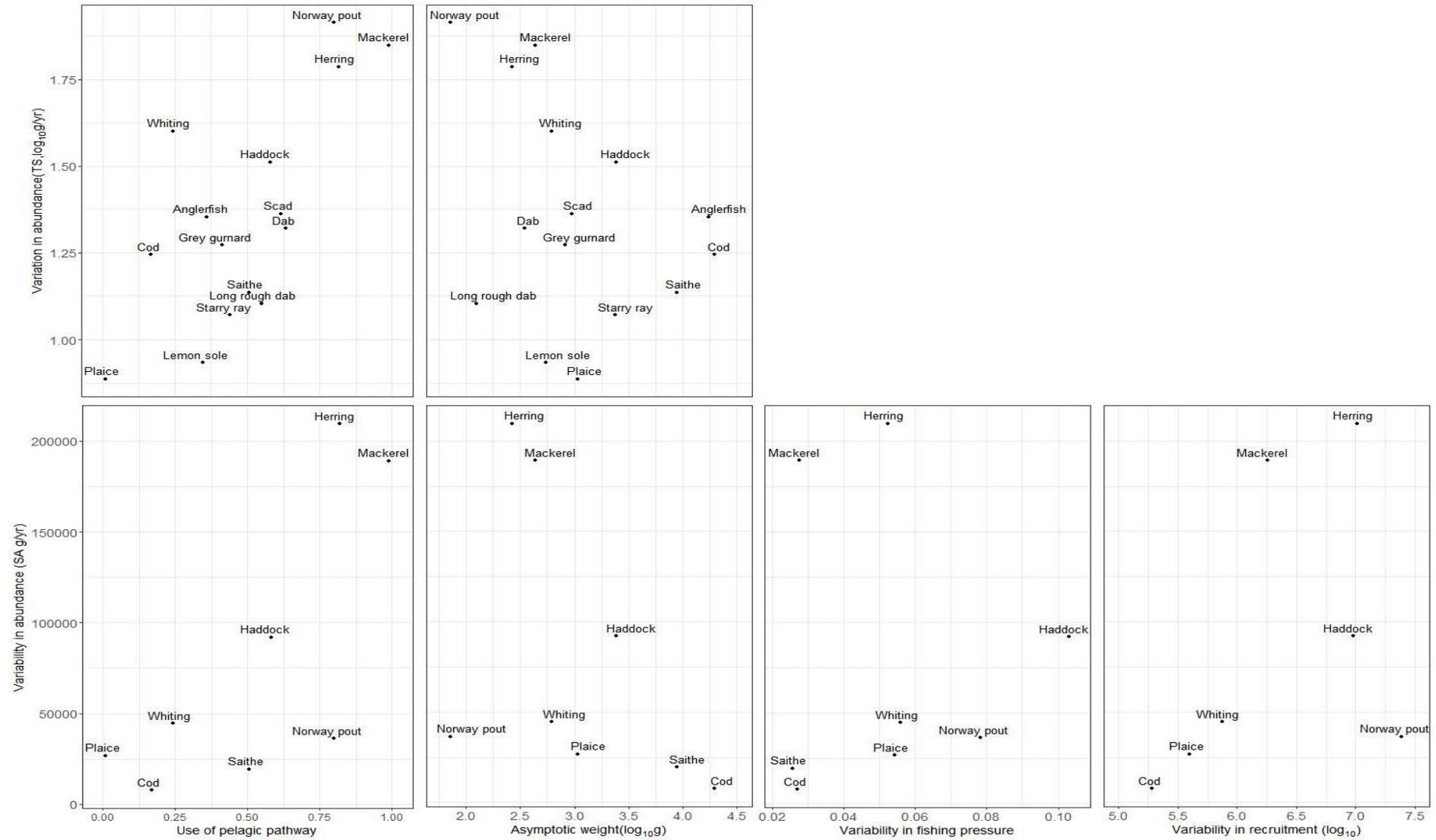


Figure 18: Plots of fluctuations in species' abundances against the relative contribution of the pelagic pathway to fish biomass, asymptotic weight, variability in fishing pressure and recruitment based on stock assessment (SA) and trawl survey (TS) data

Dataset	Model	Coefficients	P-value of coefficients and overall model (m)	AIC
SA	CPP+ FP +W _∞ + R	207400, 771000, -39900, -0.00735	0.09,0.55,0.39,0.22, m 0.26	202.84
SA	CPP + FP +W _∞	150992,-333279,-14212	0.17,0.77,0.76, m 0.31	205.62
SA	CPP + W _∞ + R	186200,-41130,-0.00542	0.07,0.33,0.19, m 0.13	201.95
SA	CPP+ FP + R	231800,822700,-0.00545	0.048,0.51,0.27, m 0.18	203.1
SA	CPP + W _∞	155463,-8696	0.12,0.82, m 0.14	203.81
SA	CPP + FP	167625,-189290	0.06,0.84, m 0.14	203.83
SA	CPP + R	209800,-0.00333	0.03, 0.31, m 0.08	202.07
SA	CPP	166270	0.04	201.91
SA	W _∞	-45267	0.25	206.19
SA	Recruitment	0.00117	0.76	207.95
SA	Fishing pressure	5497	1	208.08
TS	CPP + W _∞	0.88,-0.00	0.01,0.99, m 0.01	4.61
TS	CPP	0.88	<0.01	2.61
TS	W _∞	-0.16	0.19	11.3

Table 19: Results of linear models exploring fluctuations of species' abundances against the relative contribution of the pelagic pathway to fish biomass (CPP),W_∞, variability in fishing pressure (FP) and recruitment (R) based on trawl survey (TS) and stock assessment (SA) data. Full statistics available in Table A.3.

	Mean C (2002-2006)	C (2002)	C (2003)	C (2004)	C (2005)	C (2006)	SC (2006)
SA	0.04	0.02	0.02	0.06	0.09	0.03	0.05
TS	<0.01	0.01	0.02	<0.01	<0.01	<0.01	<0.01

Table 20: P-values from modelled fluctuations of species' abundances against the relative contribution of the pelagic pathway to fish biomass (CPP). To calculate CPP mean and individual yearly (2002-2006) δ¹³C (C) values were used in addition to δ¹³C and δ³⁴S combined (SC) in 2006

Study	Mean W _∞		W _∞	
	Coefficient	p-value	Coefficient	p-value
Jennings et al, 2008	-0.1	0.39	-0.1	0.36
Garcia-Carreras et al, 2016	-0.29	0.12	-0.23	0.2
Speirs et al,2016	-0.27	0.07	-0.27	0.07
Jennings et al, 1999	-0.09	0.51	-0.08	0.54

Table 21: Coefficients and p-values of models exploring fluctuations of species' abundances against mean log₁₀ W_∞ and log₁₀ W_∞ values from different studies based on trawl survey data

5.4 Discussion

Species with increased use of the pelagic pathway, a small asymptotic weight (W_∞), increased variability in fishing pressure and recruitment are linked to greater fluctuations in abundance. The most important factor driving increased fluctuations in abundance was use of the pelagic pathway, followed by recruitment variability, W_∞

and lastly by variability in fishing pressure although the linkage between these factors remains unclear.

Species primarily using the pelagic pathway such as mackerel and herring exhibited larger fluctuations in abundance than species using both pathways or the benthic pathway. Within the food web the consequence of species using the benthic pathway may be to deflect some energy away from the strong and fast unstable interactions of the pelagic pathway, potentially providing a powerful stabilising force (Rooney *et al.*, 2006; Rooney & McCann, 2012). Consumers which feed from both pathways may also have more stable population dynamics because they have options when one pathway becomes less productive (Blanchard *et al.*, 2012; Woodland & Secor, 2013). Thus, the results show that the strength of benthic-pelagic coupling affects population fluctuations. We expect that this, in turn, will influence the resilience of food webs to perturbations, with strong coupling stabilising population dynamics and providing the fastest return to steady-state (Blanchard *et al.*, 2012; Woodland & Secor, 2013; Post, Connors & Goldberg, 2000).

The correlation coefficients between increased use of the pelagic pathway and W_{∞} (TL corrected -0.5, TL uncorrected -0.22) and recruitment variability (TL corrected 0.53, TL uncorrected 0.31) from this study suggested those abundant North Sea species which use the pelagic pathway tended to have faster life-histories with increased recruitment variability than those using the benthic pathway. This concurs with a previous study conducted in the Barents Sea which found that pelagic species such as blue whiting and Barents Sea capelin had the shortest generation time (Bjørkvoll *et al.*, 2012). While species with short generation times and faster life histories are expected to show larger fluctuations in abundance owing to the greater effects of recruitment variation (Bjørkvoll *et al.*, 2012; Shelton & Mangel, 2011; Rooney & McCann, 2012), our results suggest this life history effect has a smaller influence on population variability than the use of the pelagic pathway. There are many important questions about the mechanisms by which the use of the pelagic pathway drives greater fluctuations in abundance, for example the life stages of the populations most affected by changes in pelagic production and links between changes in abundance and changes in competition and predation and thus growth and mortality.

It may be possible that the correspondence between the use of the pelagic pathway and population variability is both a direct and indirect effect. Production in the pelagic pathway is more variable across years, both in amplitude and timing of production due to variability in phytoplankton blooms (Wiltshire *et al.*, 2008). This may impact the amount of energy entering the system and even consumers feeding at higher trophic levels will be dependent on recent pelagic production due to the fast nature of the pathway (Woodland & Secor, 2013). Conversely, in the benthic pathway production is partly driven from the recycling of pelagic fallout which is processed on many different time-scales. For example, production may be consumed by suspension feeders, many with longer lifespans and slower turnover than zooplankton dependent on pelagic production and the sediment will also act as a store for production and will be recycled very slowly (Griffiths *et al.*, 2017). Thus the supply of energy in the benthic system may be smoothed and attenuated across many years in relation to the pelagic system (Smith, Mincks & DeMaster, 2006) and therefore the effects of population variability may be direct in the pelagic pathway and increasingly indirect in the benthic pathway.

Variability in fishing mortality seemed to have relatively little effect on fluctuations in species' abundances. Shelton & Mangel (2011) also found that variability in fishing mortality contributed little to population variability, rather recruitment variability was a substantial influence, which was also found to some degree in this study. Variability in fishing mortality on a given species will be driven by the response of the fisheries management system to changes in the abundance of that species, particularly if the management measures are adaptive (i.e. reviewed annually in light of last year's mortalities) and therefore can include stochastic events in subsequent management measures. Another driving factor can also be changes in the abundance of other species, because species are often caught together in mixed fisheries.

Consequently, as variation in fishing mortality may be bounded by regulations, we might expect that it may both track variation in abundance and be a response to it. In the context of the present study, however, our results suggest that changes in fishing mortality are primarily a response to fluctuations in abundance that increase in species making greater use of the pelagic pathway.

There are several limitations in the data. For example, there were differences between the datasets in fluctuations of species' abundances such as norway pout

and whiting, which had relatively higher variability in the trawl survey (TS) dataset compared to that in the stock assessment (SA) dataset. These differences may be related to how the abundance data were estimated: the TS dataset biomass was based on catch per unit effort across trawled areas, whereas the SA dataset referred to the whole stock and was estimated based on the spawning-stock biomass. These differences may result in the TS dataset potentially encompassing increased variability of species' abundance across years compared to the SA dataset, as CPUE is only one input to the stock assessment process. Another limitation was that W_{∞} values were means from four scientific studies ranging from 1997 to 2016. As these values are not set and change over time, mean W_{∞} values across a collection of studies may best represent true values. Also no single study provided W_{∞} values across all species, although the mean W_{∞} from the studies did not differ greatly from those derived from one study. A further limitation was that data on fishing mortality and recruitment was only available from the stock assessment dataset and for eight exploited species and so the full relationship between variability in fishing pressure and recruitment and fluctuations in species' abundance may not be explored. Furthermore, all metrics used and the stock assessments are modelled estimates and have uncertainties and potential errors associated with their calculation. However, the use of two independently measured datasets, two life history metrics and different $\delta^{13}\text{C}$ and combined $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ values which did not significantly alter the results may help strength the interpretation of our results.

As it is unlikely for a single factor to be responsible for driving variability in population sizes (Shelton & Mangel, 2011) the interaction between those tested and other non-tested factors may also influence population stability. These might include the capability of individuals to alter trophic positions throughout their lifetimes (Blanchard *et al.*, 2011), environmental stochasticity and other anthropogenic pressures such as the homogenisation of resources, habitat fragmentation and the removal of higher order consumers (McCann & Rooney, 2009). Future studies may investigate more in-depth and further factors which may influence the stability of the ecosystem.

5.5 Conclusion

This study found a significant positive relationship between fluctuations in species' abundance and the relative contribution of the pelagic pathway to fish biomass in

North Sea species. W_{∞} and variability in fishing pressure had a less significant effect and use of the pelagic pathway is probably related to W_{∞} . Use of both pathways potentially stabilises the food supply to consumers, which could improve the resilience of food webs to perturbations. As it is unlikely for a single factor to be responsible for causing fluctuations in populations future studies may investigate additional factors such the ability of individuals to change trophic positions and other anthropogenic impacts.

6. Conclusions

6.1 Introduction

This thesis aimed to increase understanding of the extent and consequences of benthic-pelagic coupling in shelf seas by (1) establishing the extent to which fish species are affiliated with the benthic and pelagic pathways across four UK seas (North Sea, Celtic Sea, Irish Sea and English Channel), (2) examining factors which might affect the strength of benthic-pelagic coupling and (3) ascertaining how benthic-pelagic coupling might affect the stability of populations. Stable isotope analysis was the main tool used to provide estimates of the extent to which species are affiliated to the benthic and pelagic pathways as it provides insight into realised long-term integrated feeding relationships.

6.2 Main findings and implications for research

6.2.1 *Stable isotope methodology*

To account for baseline isotopic spatial variation and allow for comparisons of fish species' isotopic values across UK seas this study created baseline isoscapes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. To create the isoscapes an empirical method was established to model queen scallop isotopic values and predictor variables, with bottom temperature and distance to UK shore used for $\delta^{13}\text{C}$ and bottom temperature and salinity for $\delta^{15}\text{N}$. Small variance across the isoscapes and a consistent relationship with published lion's mane jellyfish isoscapes of the North Sea suggested the scallop baseline isoscapes were suitable to correct sampled fish individuals' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

As variance might have increased in areas with few samples it would be beneficial to gain a better understanding of the causes of baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic variation, enabling the development of more accurate isoscapes. For this study physical variables were used for prediction and the relationships are unlikely to be casual and are not synonymous with ecological explanations. In terms of future study designs, developing a hybrid method which combines a geostatistical method, such as sampling at regular spatial intervals and interpolating, with an empirical method, such as uneven sampling distribution and using environmental predictors, may be useful in providing accuracy at both small and large scales (Bowen and Wilkinson, 2002).

To assess how benthic and pelagic pathways contributed to fish production I developed an analytical method using $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$. Source indicator species (SIS) were chosen because they were expected and shown, using diet data, to have high dependence on the benthic or pelagic pathway. The affiliation of the remaining species in the community to these pathways was expressed in relation to the dependence of the source indicator species using bayesian mixing models. The use of two isotopes ($\delta^{13}\text{C}$ and $\delta^{34}\text{S}$), as opposed to one isotope ($\delta^{13}\text{C}$), reduced uncertainty in estimates of the use of the pathways, although the rank order of use of pelagic pathways was almost identical for both methods. This consistency of rank suggested that $\delta^{13}\text{C}$ alone could be used in further analysis when higher numbers of samples had to be processed more quickly or when the higher costs of $\delta^{34}\text{S}$ analysis were a constraint. The analyst, however, would have to accept that any savings linked to omitting $\delta^{34}\text{S}$ analysis will increase uncertainty in estimates of use of the pathways.

This stable isotope method complements diet studies because it indicates whether energy is transferred through benthic or pelagic systems rather than defining 'benthic' or 'pelagic' in terms of the habitat used by prey and the location where prey are consumed, which as shown in this study, may be a weak predictor of the use of benthic or pelagic pathways. If described with diet data, the contribution of these feeding interactions to species' overall use of the benthic or pelagic pathways can only be elucidated by modelling all feeding interactions and hence the food web; and dietary data are usually not adequate to allow this to be achieved at the level of species or size classes.

However, there are several sources of variance for this method, potentially increasing error and uncertainty, which can originate from: machine measurements, trophic correction, lipid correction for $\delta^{13}\text{C}$, baseline isoscape correction and spatial isotopic variation of consumers. The SIS chosen also do not provide an absolute baseline for assessing the use of the two pathways and should be interpreted in relative rather than absolute terms. While it is reasonable to assume that the SIS in each sea area primarily use the benthic and pelagic pathway in each case, their absolute use of these pathways will not be 100% and will vary among seas. The use of different species as SIS in different sea areas can also introduce uncertainty as they have divergent feeding and migration patterns resulting in differences in SIS mean and

standard deviations among seas and potentially affecting credible intervals and modal estimates.

As this stable isotope method only provides relative pelagic or benthic affiliations to the pathways (i.e. relative to the source indicator species) it would be beneficial to develop a method to provide absolute estimates of pelagic or benthic affiliation of species. This might require the identification of species that are specialist feeders on phytoplankton and benthic detritus respectively and then to sample them with sufficient frequency to account for the short-term isotope dynamics which are very strong in smaller individuals with fast turnover times (Wainright & Fry, 1994; Kürten *et al.*, 2013). Alternatively seasonal dynamics of $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ in phytoplankton and benthic detritus could be simulated with models and used to generate time-integrated estimates of source $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ (Magozzi *et al.*, 2017).

6.2.2 Ecosystem perspective

Using this analytical stable isotopes method, I found that total fish consumer biomass in the northern North Sea in 2006 was linked to approximately 70% and 30% of biomass to pelagic and benthic pathways respectively. This analysis demonstrated that a substantial proportion of fish biomass and production is supported by production that has passed through transformations on the seabed. Furthermore, using estimates of the relative contribution of the pelagic and benthic pathways to species and biomass estimates from trawl survey and stock assessment data, I found that over the past thirty years the majority of fish biomass has been sustained by energy passing through pelagic planktonic pathways (Figure 19, A & B). This is also displayed in the proportion of biomass supported by the pelagic pathway (Figure 21A). Of course, these analyses only reflect the effects of changing species composition of the community and not any changes in the use of pathways by the individual species. But, I also note that, the rank importance of benthic and pelagic pathways changed rather little within species at the North Sea sites where we had access to five years' of sampling data.

Estimates of the use of benthic and pelagic pathways were different when calculated with stock assessment and survey data. An analysis based on stock assessment data suggested a higher and less variable proportion of use of the pelagic and benthic pathways across the years than that suggested by the results of an analysis based on trawl surveys (Figure 19A & B; Figure 21A). Relative biomass of individual species also differed between data collection methods, with herring, saithe and

haddock dominating biomass from trawl surveys whilst mackerel and herring comprised the majority of fish biomass according to stock assessments (Figure 19, C & D). These differences reflect the different regions covered by the trawl survey and assessment data, which provide information on local biomass at the time of the survey and total biomass of a stock across its entire range respectively.

Previous studies assessing changes in North Sea food web structure and function also suggest pelagic derived biomass accounts for the majority of biomass in the fish components of the food web. For example, during the period 1973 – 2000 the whole fish assemblage became more planktivorous, with a decline, in particular, of demersal piscivores and increases in planktivores (Figure 20, A; Heath, 2005a).

To calculate the food web biomass fluxes, Heath (2005a) used fishery landings data and based the contribution of the benthic and pelagic pathways on diet and abundance data from Greenstreet *et al.* (1997). However, the present study found only a rather weak correlation in the relative contribution of the pelagic pathway to fish production (CPP) between that determined by stable isotope and gut contents analysis. Correlation between CPP and functional groups was also relatively weak. Because the functional groups were categorised according to their habitat preferences, this suggests that the stable isotope method is a very important complement to diet studies, because the habitat preferences of the prey (benthic or pelagic) may not relate to the importance of the pathway. For example, some benthic fauna feed extensively from grazing pelagic phytoplankton or zooplankton (Jumars, Dorgan, & Lindsay, 2015; Lehane & Davenport, 2002; Vedel, 1998) and nektobenthic organisms can be important prey of pelagic fishes such as herring (Casini, Cardinale, & Arrhenius, 2004). Therefore a method which focuses on the extent to which production is channelled through the benthic or pelagic systems should be utilized.

The differences in diet and stable isotope methods for elucidating use of benthic and pelagic pathways is also shown in differences between the relative production of fish guilds based on Heath (2005a), and this study's analysis of stock assessment and trawl survey data (Figure 20). The species recorded in the trawl surveys and stock assessments can be placed into the same fish guilds defined in Heath (2005a) which were (1) benthivores: plaice, dab (NA - unavailable for trawl surveys or stock assessments), lemon sole (NA); (2) planktivores: herring, norway pout, sprat (NA), sandeel (NA); (3) demersal piscivores: cod, haddock, whiting, saithe; and (4) pelagic piscivores: mackerel, scad (NA).

The stock assessment biomass was dominated by pelagic piscivores and planktivores, with a particular increase in pelagic piscivores since 2007 (Figure 21B). Conversely, the trawl surveys were dominated by mainly demersal piscivores, followed by planktivores, similar to Heath (2005a) although with reversed dominance (Figure 21B). This suggests that pelagic species may still be the dominant guilds over time although the different methods of data collection and different geographical foci may affect guild composition.

These changes in the North Sea guilds over time may be a result of both climatic changes and fishing (Heath, 2005a; Planque *et al.*, 2010). For example, Heath (2005a) suggested the benthic food web was controlled by top-down processes, with the depletion of benthic fish through fishing resulting in a shift towards zooplankton consumption and also a release of benthic invertebrates from predation pressure producing a rise in macrobenthos production (Heath, 2005a; Heath *et al.*, 2012). Conversely the pelagic food web was regulated by bottom-up processes, with significant positive correlations between pelagic fish and zooplankton production suggesting a link to climatic factors (Heath, 2005a, 2005b). Individual pelagic species seemed to be functionally interchangeable within the guild, with boom and bust phases of herring, sprat, norway pout and sandeels responding to changes in fishing and climate (Heath *et al.*, 2012). This may suggest that pelagic feeding is more “generic”, with larger plasticity among pelagic species, whilst demersal feeding is more specialised (Planque *et al.*, 2010). Therefore, within the same geographic area, different fractions of the food web may exhibit fundamentally diverse control mechanisms and potentially different responses to climatic changes, with a shift to a more pelagic based structure potentially making the ecosystem more responsive to fluctuations in climate (Heath *et al.*, 2012).

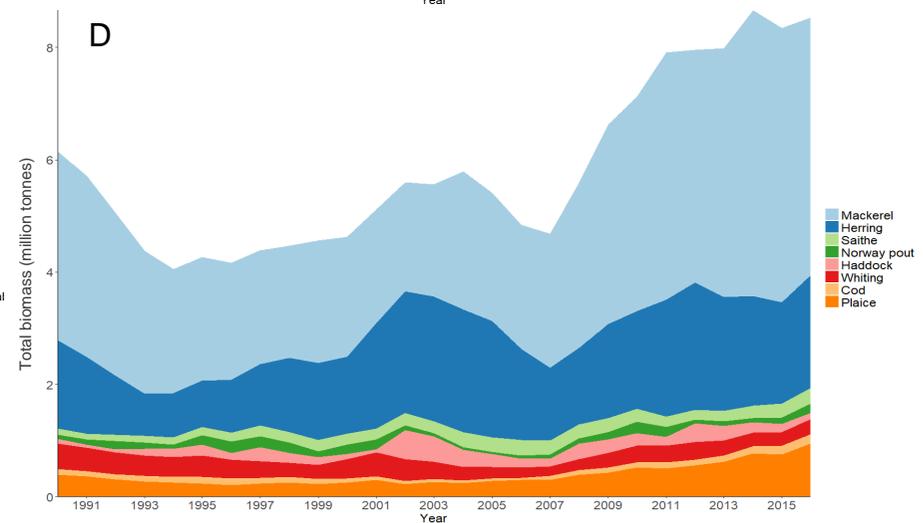
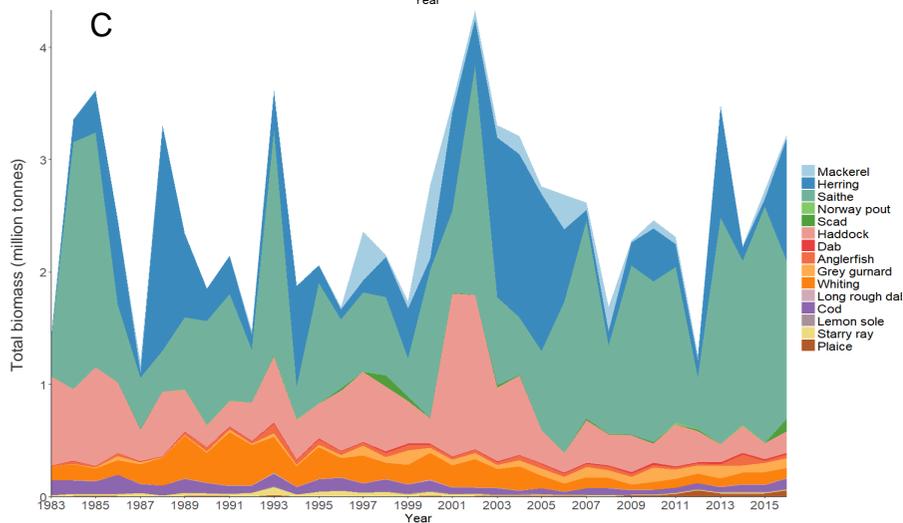
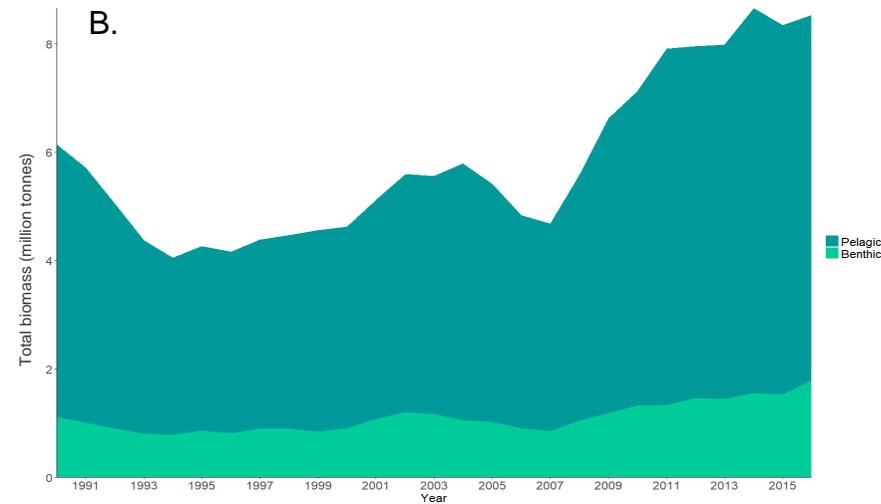
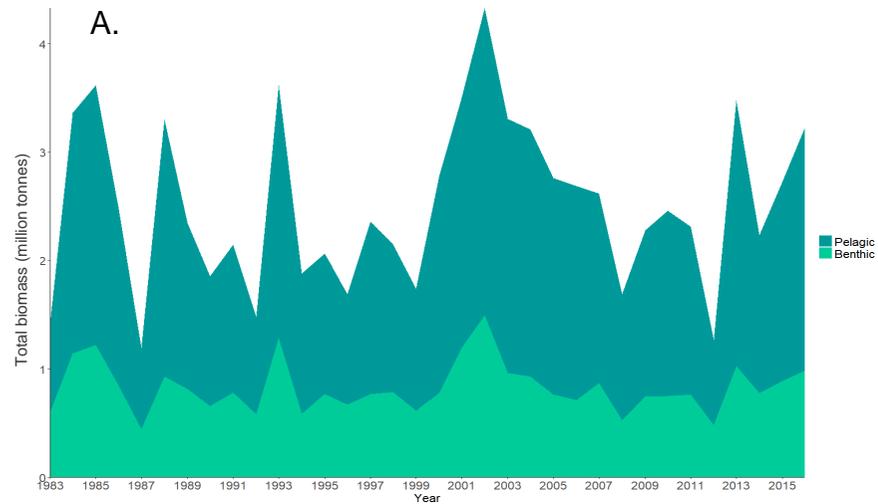


Figure 19: Total biomass (million tonnes) by year derived from the pelagic and benthic pathway in the North Sea estimated from A. trawl surveys (NS-IBTS) and B. stock assessments (ICES 2017) and biomass derived from species estimated from C. trawl surveys and D. stock assessments

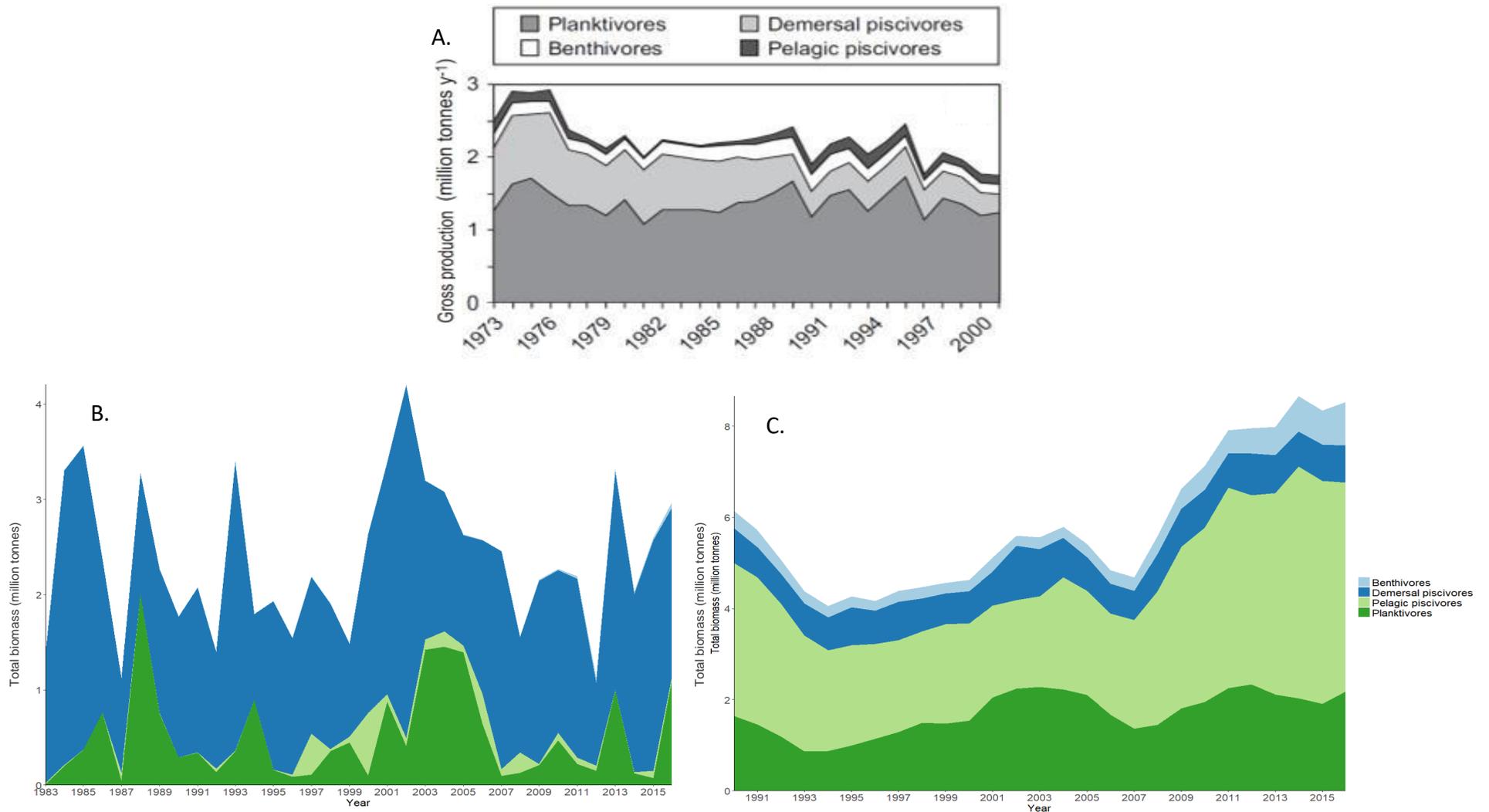


Figure 20: A. Gross production of each fish guild estimated from the STATLANT landings data (reproduced from Heath, 2005). Total biomass of each fish guild estimated from B. trawl surveys (NS-IBTS) and C. stock assessments (ICES, 2017)

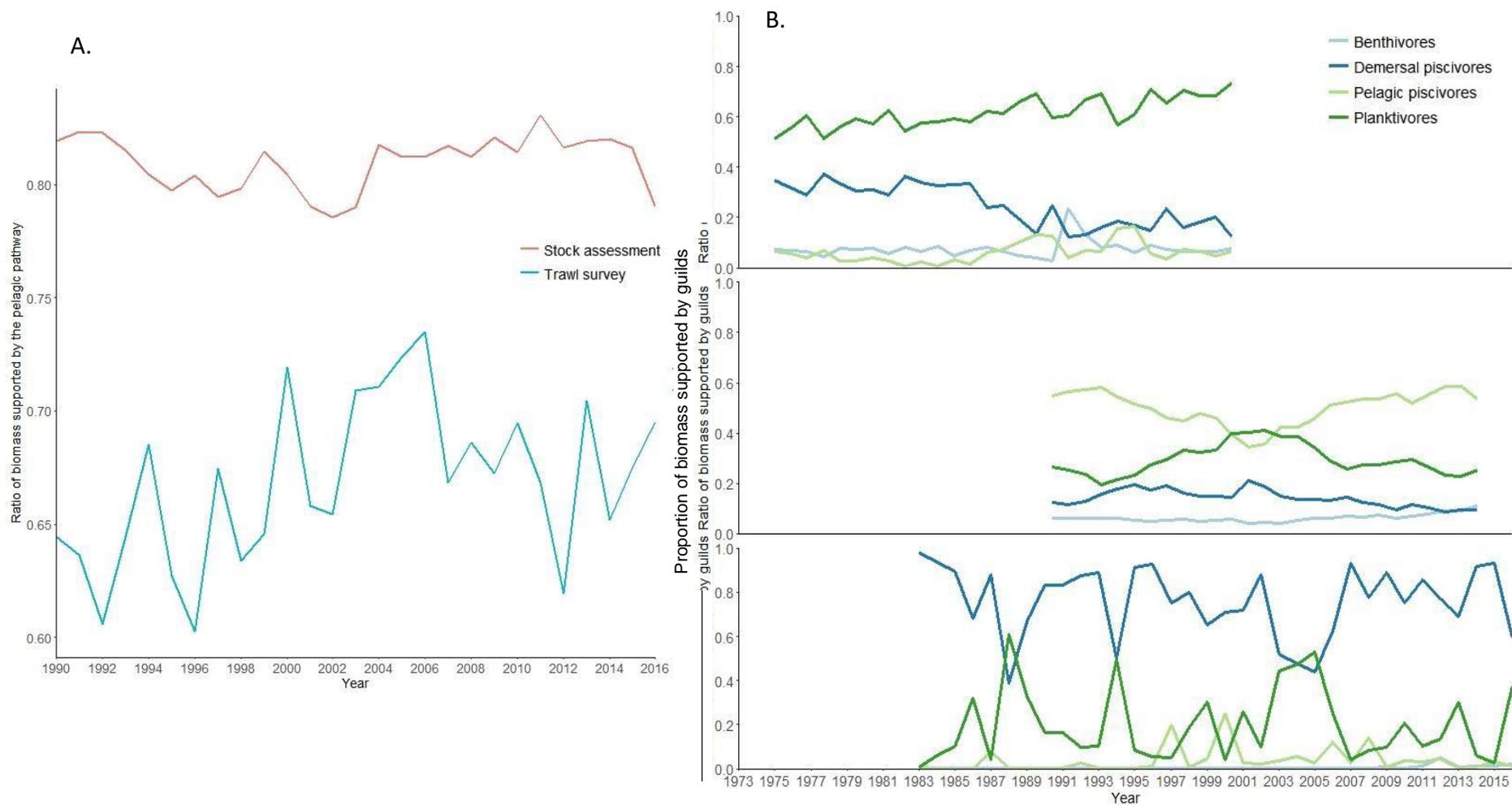


Figure 21: A. Proportion of biomass supported by pelagic pathway based on stock assessments and trawl surveys. B. Proportion of biomass supported by fish guilds based on data from Heath, 2005 (upper), stock assessments (middle) and trawl surveys (lower)

6.2.3 Anthropogenic pressures

Anthropogenic pressures will impact benthic-pelagic coupling both directly and indirectly through their effects on the biological (e.g. communities, species, functional traits) and physical (e.g. oxygen, salinity, temperature) elements of ecosystems (Griffiths *et al.*, 2017). For example, Griffiths *et al.*, (2017) suggest three significant processes affect benthic-pelagic coupling in the Baltic Sea including sedimentation, nutrient release from sediments and biological processes which all respond to widespread interacting anthropogenic pressures such as climate change, fishing and nutrient loading.

In UK seas, the present study found effects of depth, salinity and bottom temperature on benthic-pelagic coupling across the Celtic and Irish Seas and English Channel were small and inconsistent, suggesting species may be able to respond to changes in local food availability. Comparing these results with systems with greater environmental differences such as deeper permanently stratified waters may result in environmental factors having a greater impact (Kopp *et al.*, 2015; Miller, Brodeur & Rau, 2008). In the present study, body mass and trophic level had a greater effect than environmental variables with generally a marked decrease in pelagic affiliation and an increase in benthic affiliation across all seas, concurring with conclusions from previous studies (Woodland & Secor, 2013; Kopp *et al.*, 2015) that small individuals (which generally have low trophic levels) are more dependent on the pelagic pathway than larger individuals (with higher trophic levels). However, as the data used in this study were mainly for larger fishes it would be beneficial to compare the affiliations of juveniles and adults to the pathways as it might be expected that the juveniles have a higher dependence on the pelagic pathway (Woodland & Secor, 2013). Focusing more on differences in individuals across the full size range within species would also enable better understanding of whether UK shelf sea fish species have a curvilinear relationship with trophic level and the pathways, with the largest individuals occupying the highest trophic levels tending to depend on both pathways (Rooney *et al.*, 2006; Woodland & Secor, 2013).

The effects of exploitation and climate on fish populations are likely to be not just additive but also interacting (Planque *et al.*, 2010). Removing the largest individuals can also promote increasing turnover rates, reduce rates of predation and increase the dominance of smaller organisms (Gislason, 2002; Bianchi *et al.*, 2000). Exploited communities dominated by small organisms which are largely dependent on the

pelagic pathway may have reduced top-down processes, with bottom-up processes playing a more significant role leading to greater impacts of climatic variability on the community structure (Planque *et al.*, 2010).

Strong benthic-pelagic coupling may improve community resilience to perturbations. For example, the present study found a significant positive relationship between variability in species' abundances and CPP. This was consistent with previous suggestions that species with a high dependence on the pelagic pathway have larger temporal variability than species dependent on both pathways or on the benthic pathway, the last two potentially providing a stabilising force and improving the resilience of food webs to perturbations (Bjørkvoll *et al.*, 2012; Rooney & McCann, 2012). The present results show that most species across the UK seas relied to some extent on both pathways, potentially due to opportunistic feeding and the shallow waters of shelf seas which may provide access to both pelagic and benthic sources to most consumers. Therefore, the UK shelf sea food web is expected to be relatively resilient to perturbations.

When examining variability in species' abundances, weaker non-significant relationships were found with life history characteristics and variability in fishing pressure. This also concurs with previous studies that these dynamics alone will not drive changes in abundances and it is likely that a combination of factors such as overfishing, climatic variability and life history characteristics will cause a population to move from a steady to fluctuating state (Bjørkvoll *et al.*, 2012; Pinsky & Byler, 2015; Shelton & Mangel, 2011). However, as only one dataset calculated variability in fishing pressure it would be beneficial, if possible, to replicate analysis with long term datasets in other regions or seas to further understand the potential causes of variation of species abundance. Furthermore, additional factors which may influence population stability could be investigated such as the capability of individuals to alter trophic positions across their lifetimes and other anthropogenic impacts (Blanchard *et al.*, 2011; McCann & Rooney, 2009).

Future changes to ecosystems affected by anthropogenic influences are hard to predict. If fishing continues to remove high-trophic level species, ecosystem resilience may decline and the greater influence of bottom-up processes could result in larger impacts on community structure due to climate variability. Warming of the southern North Sea and Celtic Sea could see a continuation of colonization of Lusitanian species and departure of Boreal species to deeper and northern UK

waters (Heath *et al.*, 2012). The regime shift to a warmer biological regime in the North Sea in the late 1980s which led to increases in phytoplankton and most pelagic species may also suggest in the future the continued warming of the seas could lead to increased abundances of pelagic species (Engelhard *et al.*, 2011). However some pelagic species such as herring may decline potentially due to its main prey *C. finmarchicus* also declining in warmer regimes in the past (Beaugrand & Ibanez, 2004).

Species unable to adapt their distributions due to strict habitat association such as the lesser sandeel may be most threatened by severe impacts and are at risk of local extinction (Holland *et al.*, 2005). As species may not exhibit fixed feeding preferences due to changing prey availability it is also difficult to predict the probable indirect effects of climate change and ocean acidification (Le Quesne & Pinnegar, 2011).

6.2.4 Management measures

The analytical stable isotope method I developed in this study provides the first quantitative insights into the use of the pelagic and benthic pathways by shelf-sea species. In time, such measurements may prove to be useful indicators of processes and functioning in shelf-sea ecosystems which can be utilised to support the development of ecosystem indicators for fisheries management. Indicators are necessary to assist the implementation of ecosystem-based management (EBM), which aims to consider the overall status of fisheries and their role within the ecosystem (Heath, 2005b), through supplying evidence of the state of the ecosystem (Jennings, 2005). However, before this method can become a useful indicator, long-term variation of species use of the pelagic and benthic pathways needs to be ascertained as well as their relationship with other functional properties of the food webs and ecosystems.

Improved knowledge of ecosystem structure and the effect of anthropogenic influences may help shift regulation of fisheries from single species catch control to EBM. This will be beneficial to future management as weak regulation of fishing may promote a more pelagic-based structure, potentially causing the ecosystem to be more vulnerable to external and internal forcing (Heath, 2005b; Hsieh *et al.*, 2006). Furthermore, as fractions of the ecosystem may respond differently to climatic changes, such as the bottom-up and top-down processes influencing the pelagic and benthic pathways respectively (Heath, 2005a, 2005b), stability is increased by preserving diversity at individual and population levels (Planque *et al.*, 2010).

To maintain both pelagic and benthic pathways, management strategies need to be responsive to the combined effects of climate and exploitation on fish populations. If management can respond rapidly to decreases in productive potential of stocks (e.g. from falling recruitment or low rates of somatic growth) then this may ameliorate the risk of collapse and reduce fluctuations linked to climate. Changing the management system to support small but frequent adjustments to target estimates and management measures could ensure effective conservation of the populations as delays in management responses could increase the probability of a collapse (Pinsky & Byler, 2015). However, this comes at a cost in terms of demands on the assessment and feedback (monitoring) systems and risks may also be reduced by more conservative management strategies.

Ensuring the age-structure is preserved rather than concentrating on only abundance and biomass could also increase population resilience to climate variation and anthropogenic pressures. This may be partly due to juvenile fish relying more on the pelagic pathway whilst larger, higher-trophic level individuals are more dependent on both pathways (Planque *et al.*, 2010; Woodland & Secor, 2013). Therefore, only restoring population biomass or abundance may not be sufficient to re-establish the same patterns of population resilience. Instead other population characteristics such as spatial and demographic structures also need to recover (Planque *et al.*, 2010). This may be achieved through the protection of larger and older individuals as well as young individuals potentially through measures such as the use of marine protected areas or regulating fishing capacity (Planque *et al.*, 2010).

The strength of benthic-pelagic coupling can also affect the resilience of the ecosystem. For example, removal of the mobile top predators which couple the pathways increases the vulnerability of food webs to perturbations (Blanchard *et al.*, 2011). Furthermore, this study found that species which are dependent on the pelagic pathway seem to have larger temporal fluctuations than species dependent on both or the benthic pathway. Therefore, future management measures should ensure that top predators which couple the food web remain within the ecosystem and more attention is given to pelagic species. As suggested by Heath (2005a) some pelagic species in the North Sea may be interchangeable within the guild and therefore, if possible, it may be effective to have flexibility within management strategies to switch the focus between species, capitalising on the boom phases within the guild and allowing species in the bust phase to recover.

6.3 Conclusion

This thesis aimed to gain a better understanding of the use of benthic and pelagic pathways, and benthic-pelagic coupling, by UK shelf sea fish species. Stable isotope analysis was the main tool used to establish the extent to which species are affiliated to the pathways. Using a method which focused on how production is channelled through the pathways was imperative, as habitat preferences of the prey may not relate to the importance of the pathway.

The North Sea food web structure was found to be dominated by pelagic derived biomass, potentially making the ecosystem more responsive to fluctuations in climate. The strength of benthic-pelagic coupling across UK seas was most affected by trophic level and body mass, with smaller, low trophic level individuals more dependent on the pelagic pathway. High dependence on the pelagic pathway also led to larger temporal variability of species abundance. Across UK seas strong benthic-pelagic coupling was found for most species, suggesting strong community resilience to perturbations.

Maintaining both pelagic and benthic pathways is likely to improve the ecosystem's resilience to climate variation and anthropogenic pressures. This requires management measures focused on an ecosystem approach to ensure overexploitation of either pathway does not occur. This may also be possible with single species management, provided that mortality rates of species could be separated so that other species, particularly benthic species, are not overfished when closely associated and more productive species are targeted. Preserving the age-structure and top mobile predators would also be beneficial to maintaining strong benthic-pelagic coupling.

Appendices

Appendix A

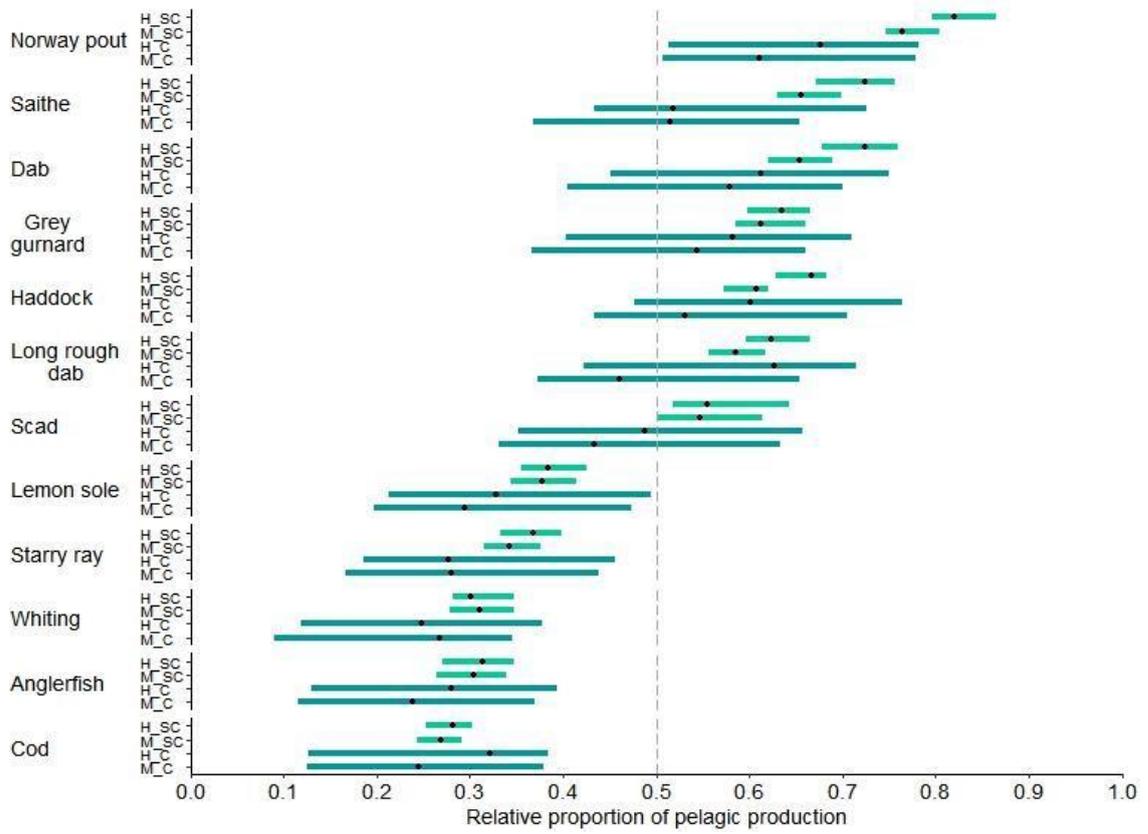


Figure A.1: Comparisons between estimates of the relative contribution of the pelagic pathway to fish biomass by species in 2006 when using herring (H) greater than 140g or mackerel (M) as pelagic source indicator species. Results are presented for $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ isotopes (SC) or just $\delta^{13}\text{C}$ (C). Points show the mode and narrow bars the 50% credible intervals of the posterior distribution.

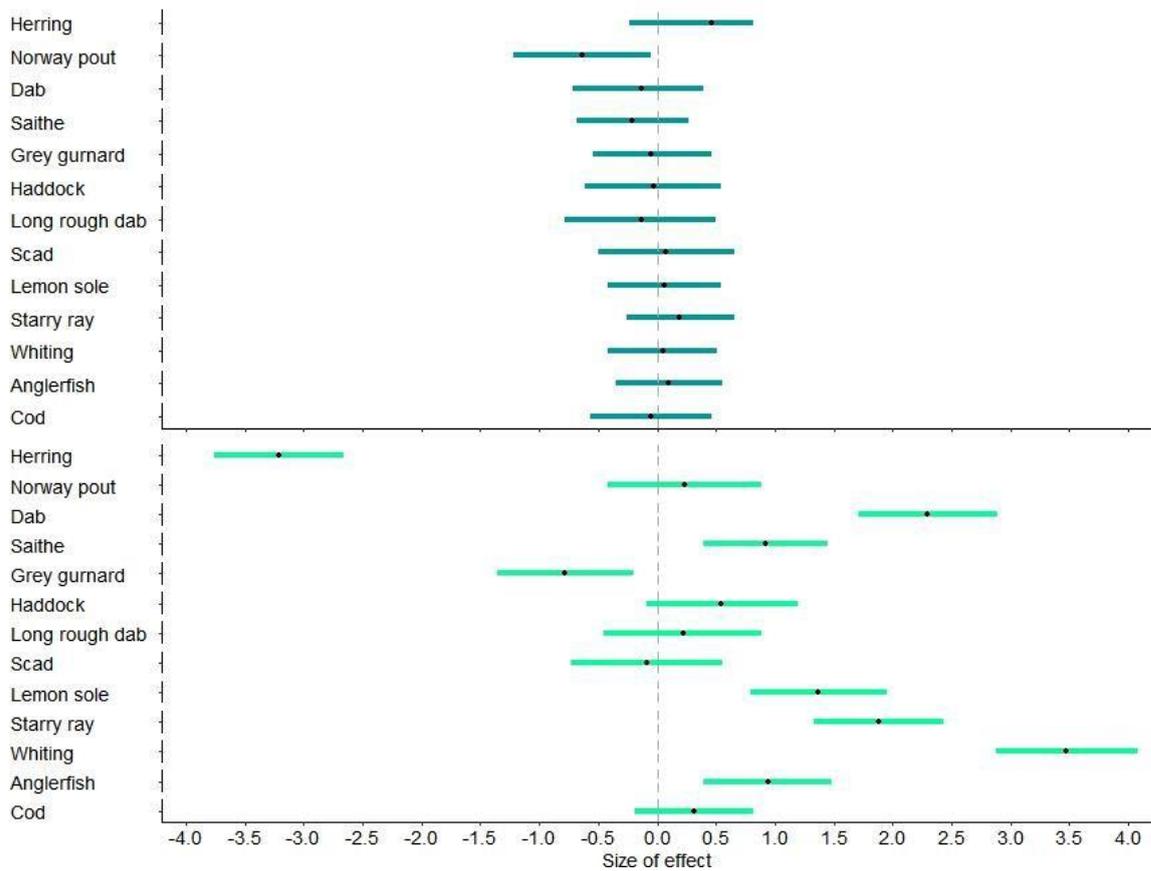


Figure A.2: Effects of body mass (bottom) and year (top) on the use of benthic pathways by North Sea fish species during 2006. Points show the mode and bars the 50% credible intervals. Positive values indicate increasing reliance on the pelagic pathway with increasing body mass or year. Modal values of σ ranged from 0.8 to 1.37 across species.

Sea	Depth	Salinity	Temp	Mass	TL
Celtic	0.05	0.04	0.18	0.05	-0.11
Channel	0.37	0.43	0.15	-0.11	-0.04
Irish	-0.46	0.25	0.03	-0.16	-0.20

Table A.1: Spearman’s ranked correlation for the size of the effect and range of data used across the English Channel, Irish and Celtic Sea

	AIC	BIC	logLik
Without corAR1	119382	119407.5	-59688.02
With corAR1	99971.77	100005.7	-49981.89

Table A.2: Model fit of equation lme (logbiomass ~ 1, random=~1|Species) with and without correlation structure corAR1.

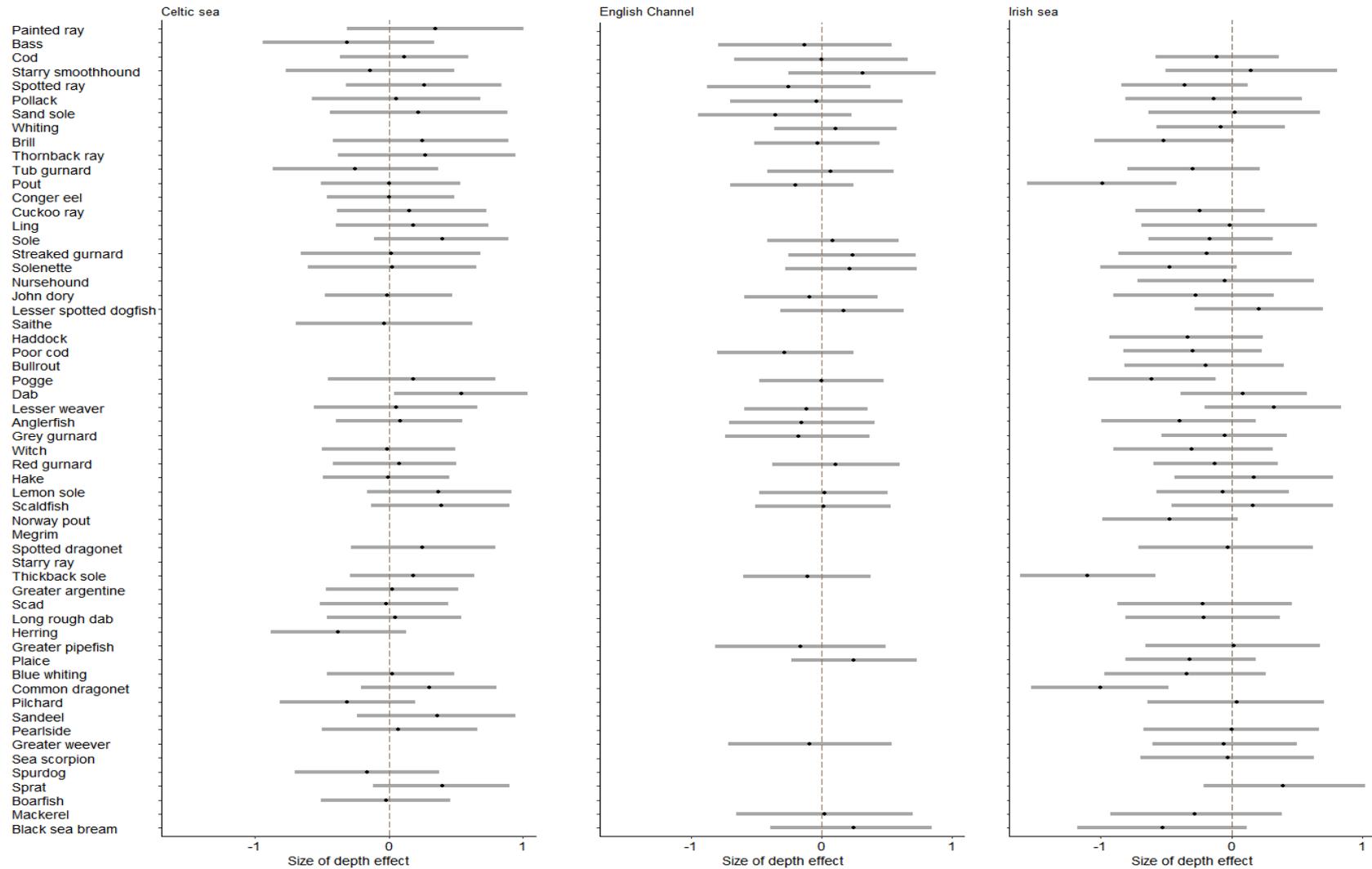


Figure A.3: Estimated effect of depth on CPP across all seas, points show the mode and bars the 50% credible intervals

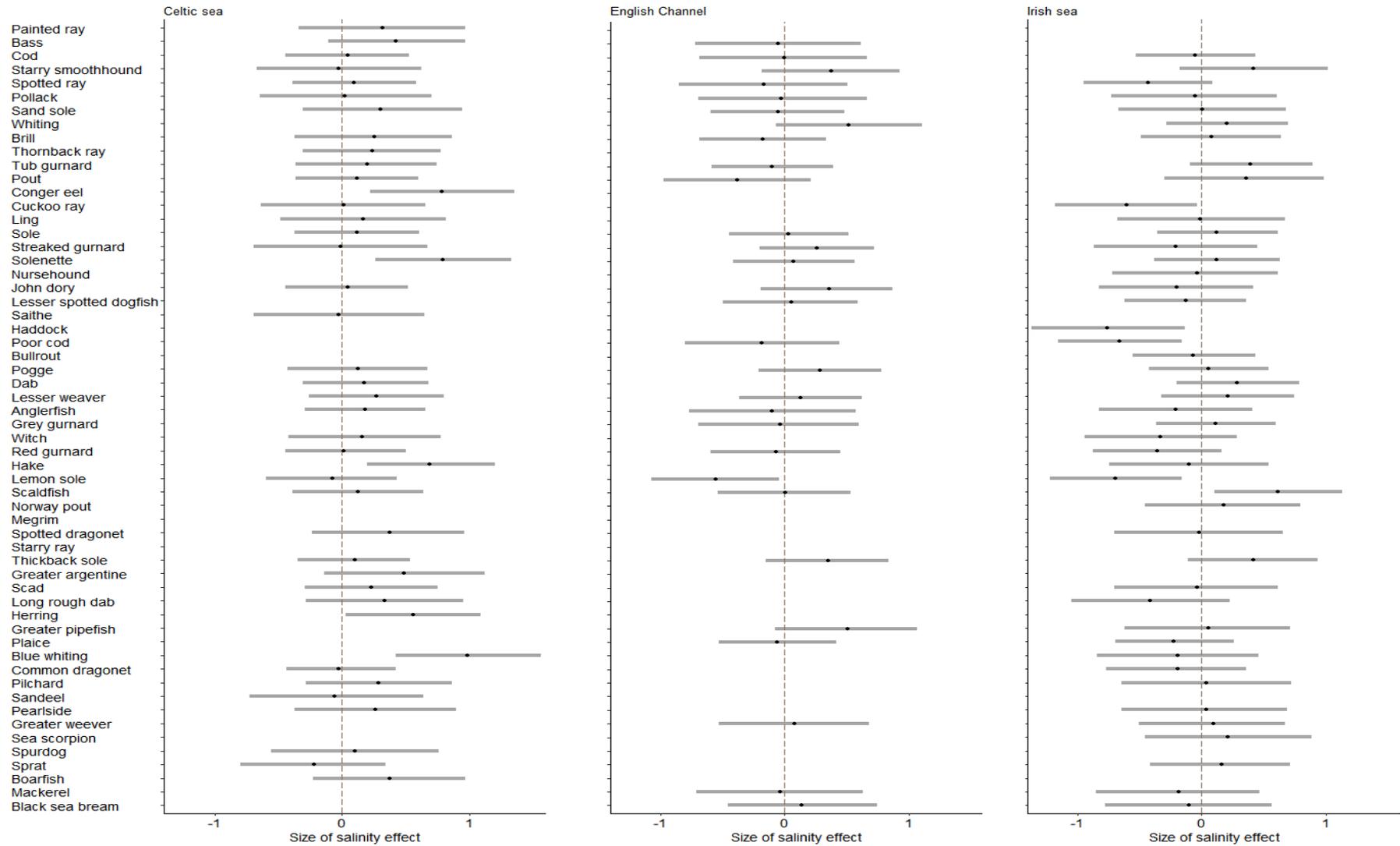


Figure A.4: Estimated effect of salinity on CPP across all seas, points show the mode and bars the 50% credible intervals

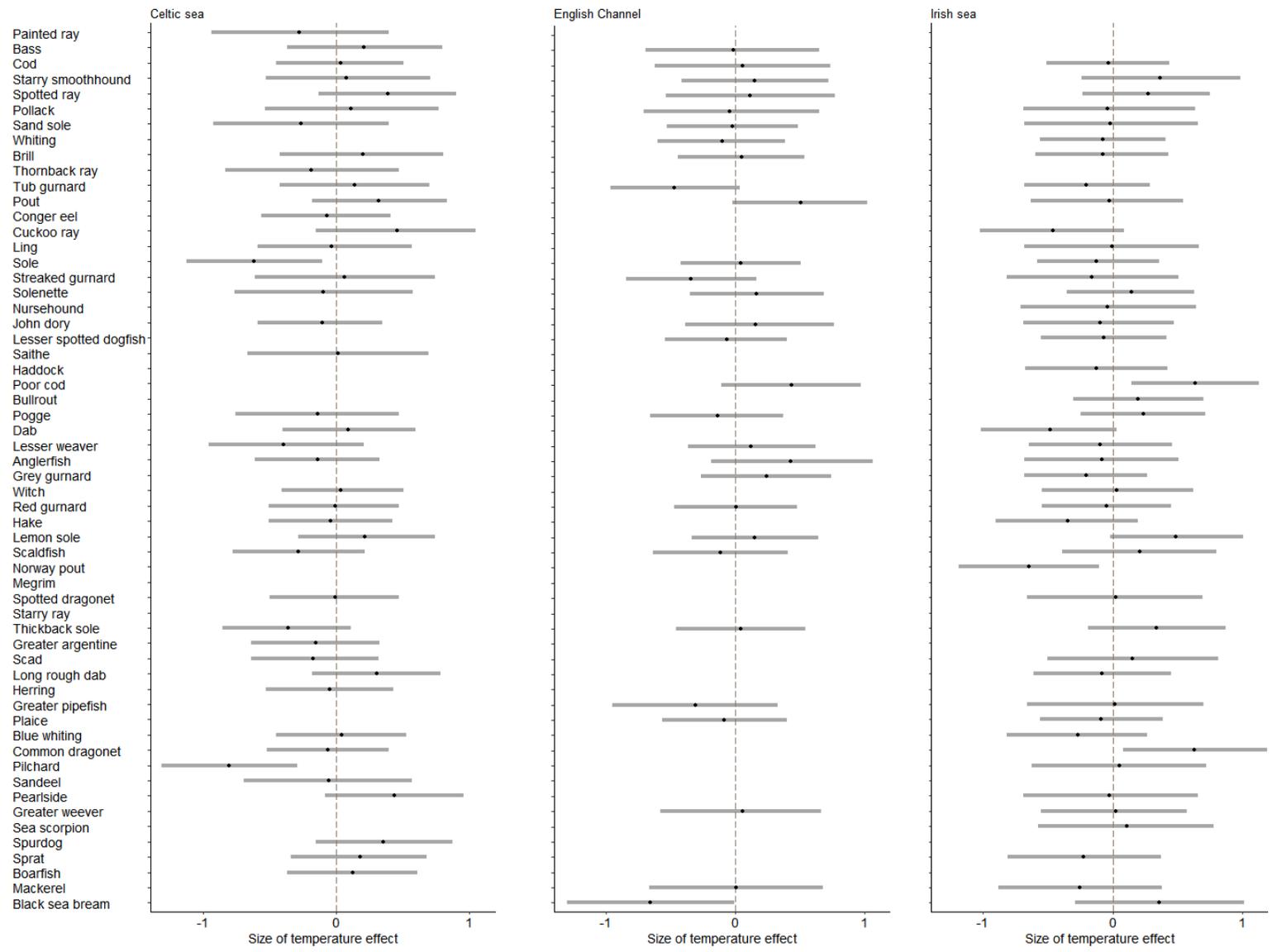


Figure A.5: Estimated effect of temperature on CPP across all seas, points show the mode and bars the 50% credible intervals

Dataset	Model	Coefficients	P-value of coefficients and overall model (m)	Adjusted R2	Multiple R2	AIC	F statistic
SA	CPP+ Fishing pressure + W_{∞} + Recruitment	207400, 771000, -39900, -0.00735	0.09,0.55, 0.39, 0.22, m 0.26	0.43	0.75	202.84	2.31 on 4 & 3 DF
SA	CPP + Fishing pressure + W_{∞}	150992,-333279,-14212	0.17,0.77, 0.76, m 0.31	0.22	0.55	205.62	1.55 on 3 & 4 DF
SA	CPP + W_{∞} + Recruitment	186200,-41130,-0.00542	0.07,0.33, 0.19, m 0.13	0.51	0.72	201.95	3.395 on 3 & 4 DF
SA	CPP+ Fishing pressure + Recruitment	231800,822700,-0.00545	0.048,0.51, 0.27, m0.18	0.43	0.67	203.1	2.761 on 3 & 4 DF
SA	CPP + W_{∞}	155463,-8696	0.12,0.82, m 0.14	0.43	0.51	203.81	6.31 on 2 & 12 DF
SA	CPP + Fishing pressure	167625,-189290	0.06,0.84, m 0.14	0.36	0.54	203.83	2.96 on 2 & 5 DF
SA	CPP + Recruitment	209800,-0.00333	0.03, 0.31, m 0.08	0.49	0.63	202.07	4.302 on 2 & 5 DF
SA	CPP	166270	0.04	0.46	0.54	201.91	6.99 on 1 & 6 DF
SA	W_{∞}	-45267	0.25	0.08	0.21	206.19	1.6 on 1 & 6 DF
SA	Recruitment	0.00117	0.76	-0.15	0.02	207.95	0.1 on 1 & 6 DF
SA	Fishing pressure	5497	1	-0.17	<0.01	208.08	<0.01 on 1 & 6 DF
TS	CPP + W_{∞}	0.88,-0.00	0.01,0.99, m 0.01	0.43	0.51	4.61	6.31 on 2 & 5 DF
TS	CPP	0.88	<0.01	0.47	0.51	2.61	13.66 on 1 & 13 DF
TS	W_{∞}	-0.16	0.19	0.06	0.13	11.3	1.95 on 1 & 13 DF

Table A.3: Results from linear models exploring variability of species' abundance against the relative contribution of the pelagic pathway to fish biomass (CPP), W_{∞} , recruitment and variability in fishing pressure based on trawl survey (TS) and stock assessment (SA) data.

Dataset	Model	P-value
TS	CPP + W_{∞}	0.99
SA	CPP + Fishing pressure	0.83
SA	CPP + W_{∞}	0.81
SA	CPP + Recruitment	0.26
SA	CPP + W_{∞} + Recruitment	0.28
SA	CPP + Fishing pressure + Recruitment	0.43
SA	CPP + Fishing pressure + W_{∞}	0.93
SA	CPP + Fishing pressure + W_{∞} + Recruitment	0.45

Table A.4: Results from ANOVA comparing models using CPP alone and including other variables based on trawl survey (TS) and stock assessment (SA) data.

Appendix B

The following tables and figures provide estimates of the contribution of pelagic and benthic pathways and associated analytical statistics when no correction is made to the $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values to account for differences in trophic level (please see main text). They are presented in this supplement to demonstrate the robustness of the results to the assumptions about the effects of trophic level and fractionation.

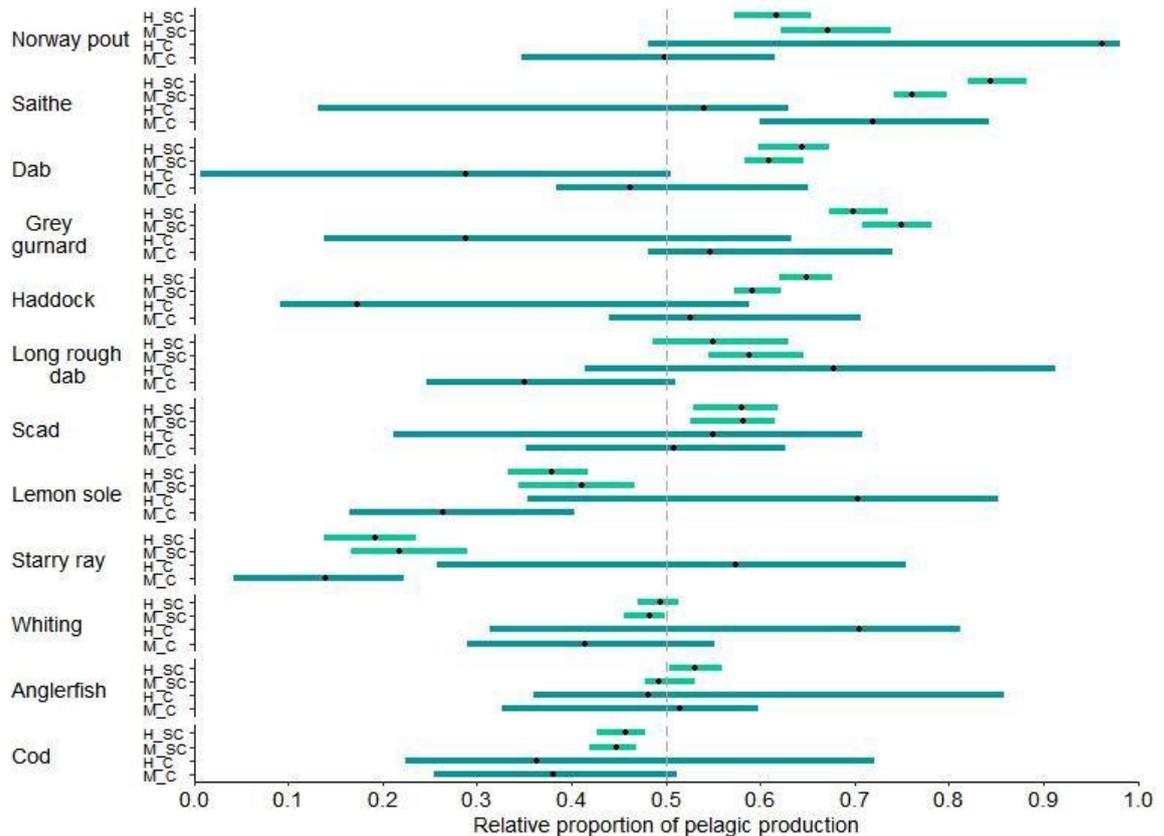


Figure B.1: Comparisons between estimates of the relative contribution of the pelagic pathway to fish biomass by species in 2006 when using herring (H) greater than 140g or mackerel (M) as pelagic source indicator species. Results are presented for $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ isotopes (SC) or just $\delta^{13}\text{C}$ (C). Points show the mode and narrow bars the 50% credible intervals of the posterior distribution.

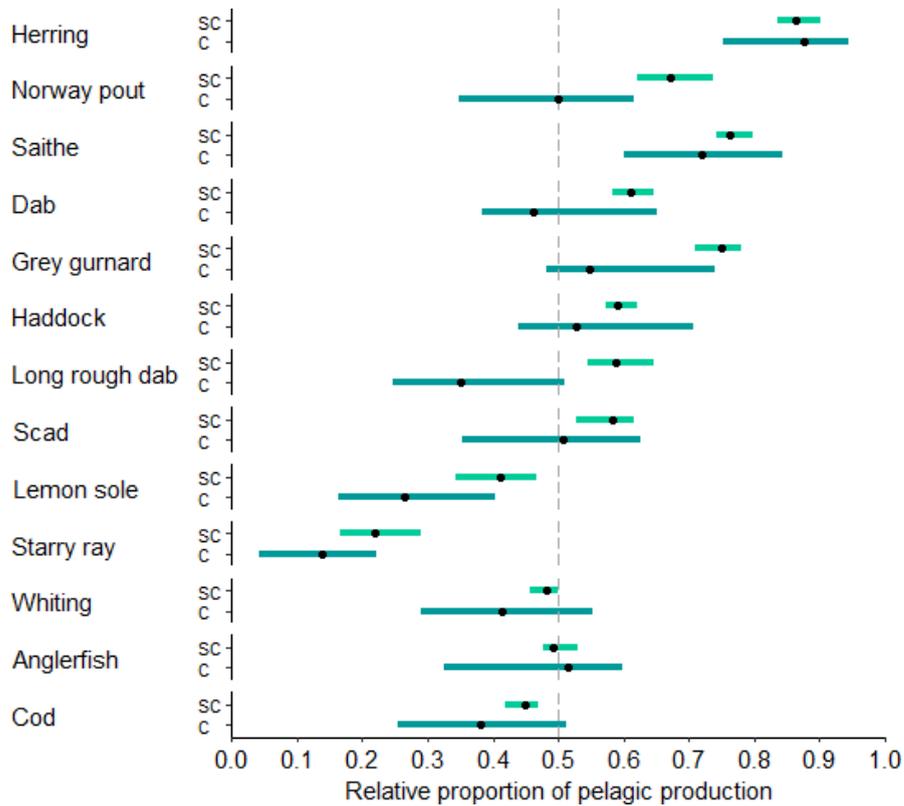


Figure B.2: The estimated relative contribution of the pelagic pathway to fish biomass by species in 2006 using both $\delta^{34}\text{S}$ and $\delta^{13}\text{C}$ isotopes (SC) or just $\delta^{13}\text{C}$ (C). Points show the mode and narrow bars the 50% credible intervals of the posterior distribution.

Common name	Biomass (t)	Biomass "pelagic" (t) $\delta^{34}\text{S}$ & $\delta^{13}\text{C}$	Biomass "pelagic" (t) $\delta^{13}\text{C}$
Mackerel	324104	320863	320863
Herring	643212	554862	562770
Norway pout	144739	97109	72198
Saithe	1460296	1112304	1051129
Dab	62670	38213	28934
Grey gurnard	99286	74447	54264
Haddock	261692	154651	137827
Long rough dab	30328	17824	10653
Scad	2508	1461	1274
Lemon sole	6830	2807	1806
Starry ray	4892	1069	680
Whiting	90294	43546	37365
Anglerfish	26976	13274	13899
Cod	26554	11901	10098
Plaice	7317	73	73
	(3191700)	(2444405)	(2303834)

Table B.1: Estimated contribution of pelagic pathways (modal SC and C estimates) to total biomass (tonnes) in the sampling area (estimated contribution to pelagic pathway by mackerel and plaice was assumed to be 0.99 and 0.01 respectively).

	$\delta^{13}\text{C}$ & $\delta^{34}\text{S}$			$\delta^{13}\text{C}$		
	25%	Mode	75%	25%	Mode	75%
Body mass[p]	-1.11	-0.35	0.55	-0.46	0.05	0.57
Body mass[b]	-0.54	0.34	1.11	-0.55	-0.04	0.47
σ	0.73	0.74	0.75	0.82	0.84	0.86

Table B.2: Effects of body mass on use of pelagic (p) and benthic (b) pathways in the North Sea during 2006. Positive values indicate increasing reliance on the relevant pathway.

Year	2002	2003	2004	2005	2006
2002	-	0.85	0.76	0.91	0.81
2003		-	0.82	0.92	0.83
2004			-	0.8	0.8
2005				-	0.8
2006					-

Table B.3: Correlations, between years, of modal contributions of pelagic pathways to species' biomass. Based on $\delta^{13}\text{C}$ data that have not been corrected to account for potential trophic fractionation.

	25%	Mode	75%
Body mass [p]	-3.01	-2.41	-1.80
Body mass [b]	1.80	2.41	3.02
Year [p]	-0.69	-0.20	0.29
Year [b]	-0.30	0.19	0.68
σ	0.91	0.92	0.93

Table B.4: The effect of mass and year on the contribution of pelagic (p) and benthic (b) pathways to North Sea fish biomass from 2002-2006 (mode and 50% credible intervals). Positive values indicate increasing reliance on the relevant pathway with increasing body mass or year.

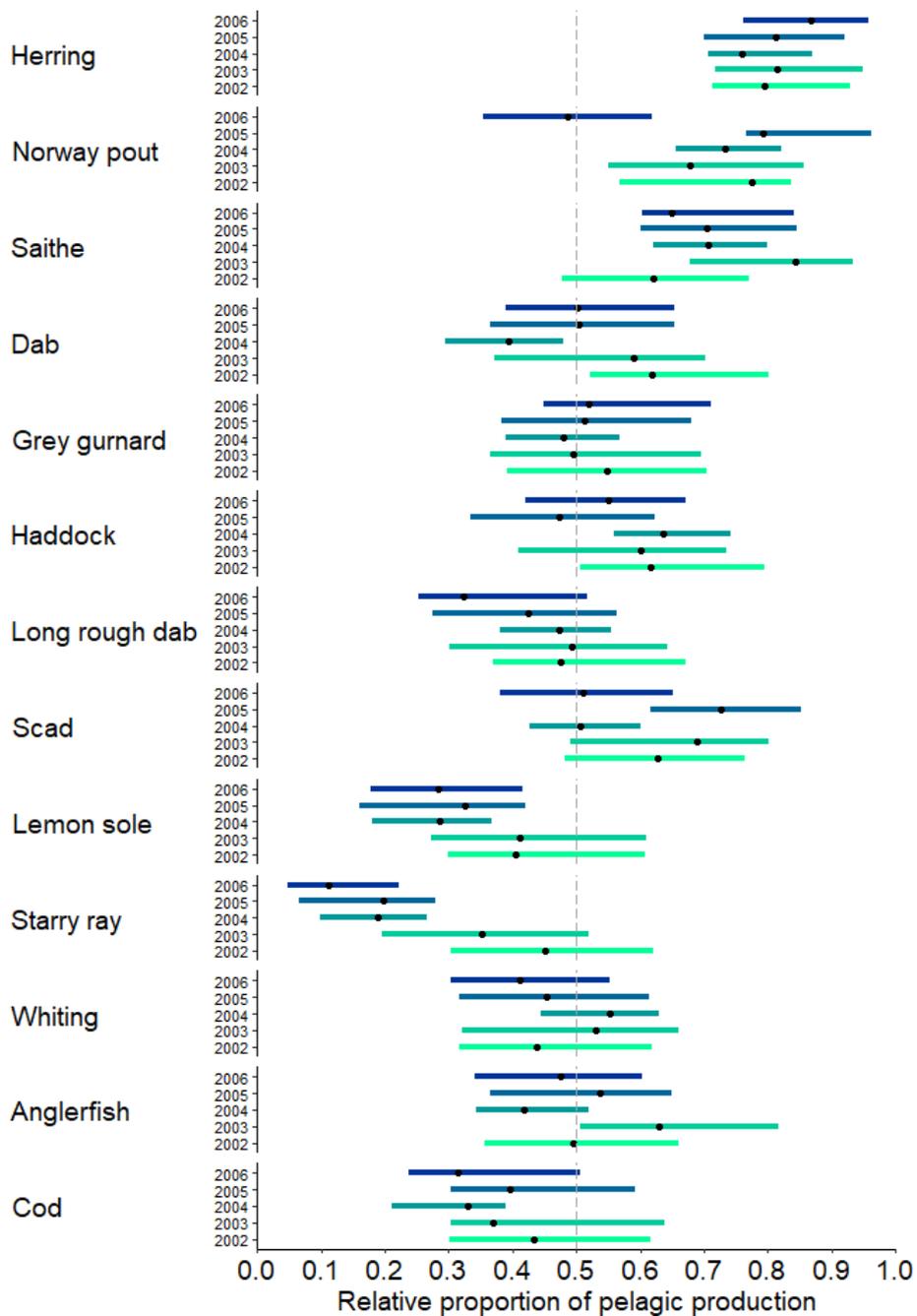


Figure B.3: The estimated contribution of the pelagic pathway to fish biomass by species from 2002 to 2006 based on $\delta^{13}\text{C}$ analysis. Points show the mode and narrow bars the 50% credible intervals of the posterior distribution.

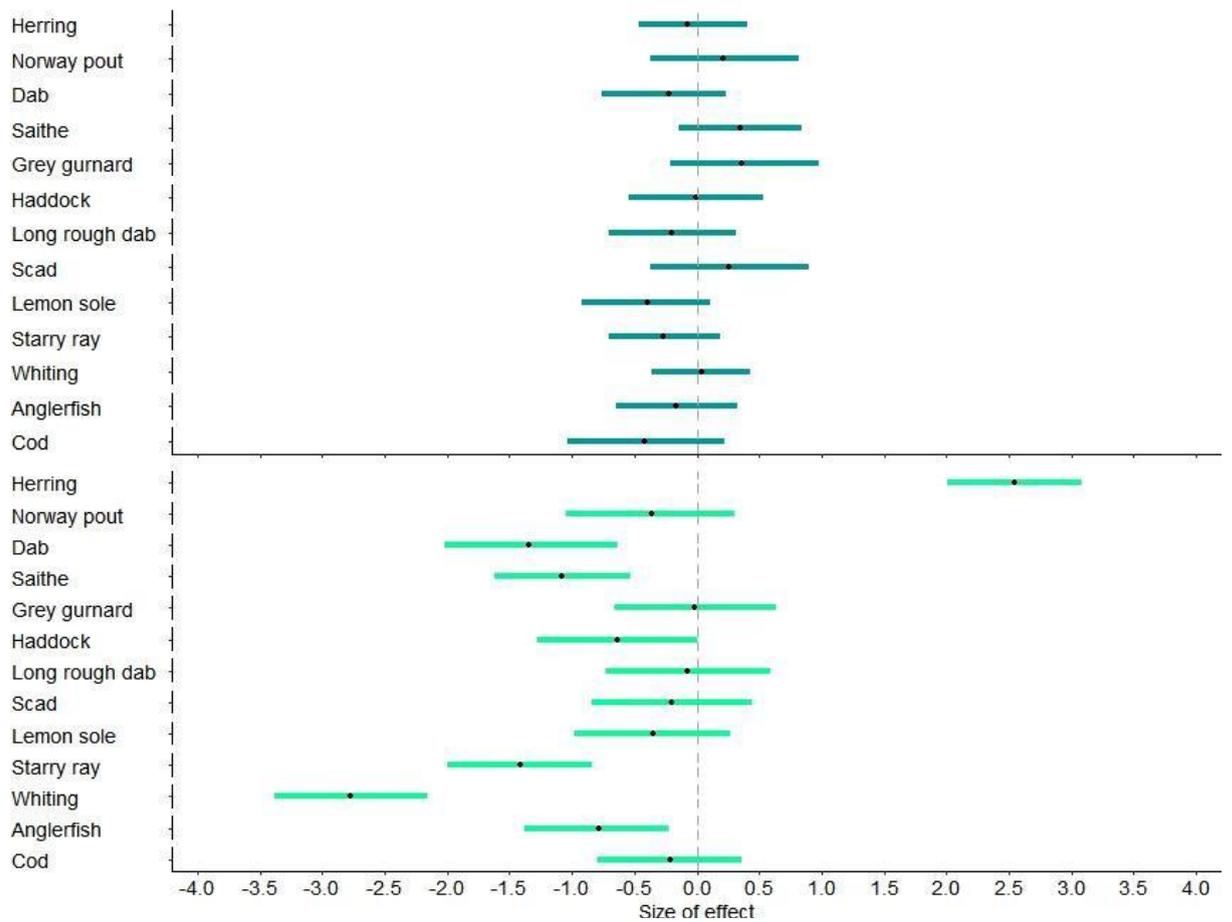


Figure B.4: Effects of body mass (bottom) and year (top) on contributions of the pelagic pathway to species' biomass from 2002-2006. Points show the mode and bars the 50% credible intervals. Modal values of σ ranged from 0.55 to 0.91 across species. Positive values indicate increasing reliance on the pelagic pathway with increasing body mass or year.

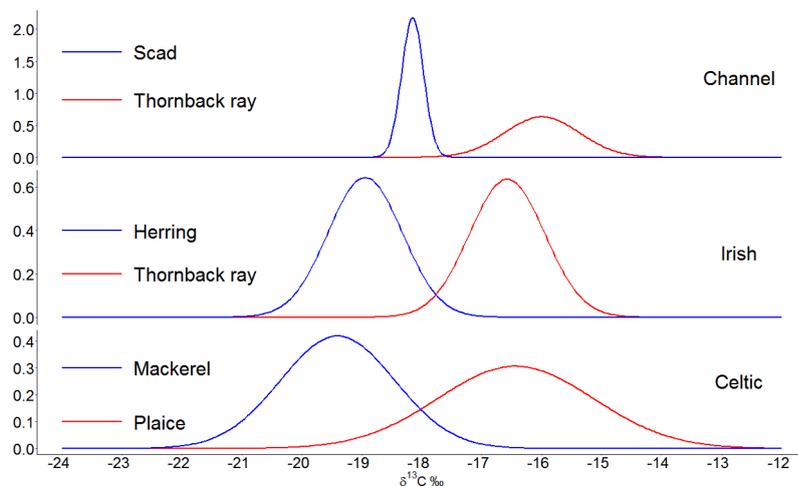


Figure B.5: Distributions of isotopic values of benthic and pelagic source indicator species (SIS) across UK seas

Seas	Spearman	P value
Celtic – Irish	0.38	0.06
Celtic – Channel	0.57	0.003
Irish - Channel	0.52	0.009

Table B.5: Correlation between the English Channel, Irish and Celtic Sea based on CPP of species present in all three seas. Correlation between the mean modal CPP across all seas and functional groups was 0.45, $p < 0.001$.

Sea	Spearman	P value
Celtic	-0.23	0.11
Irish	-0.06	0.67
English Channel	0.1	0.57

Table B.6: Results of Spearman rank correlation between species trophic level and CPP across UK seas.

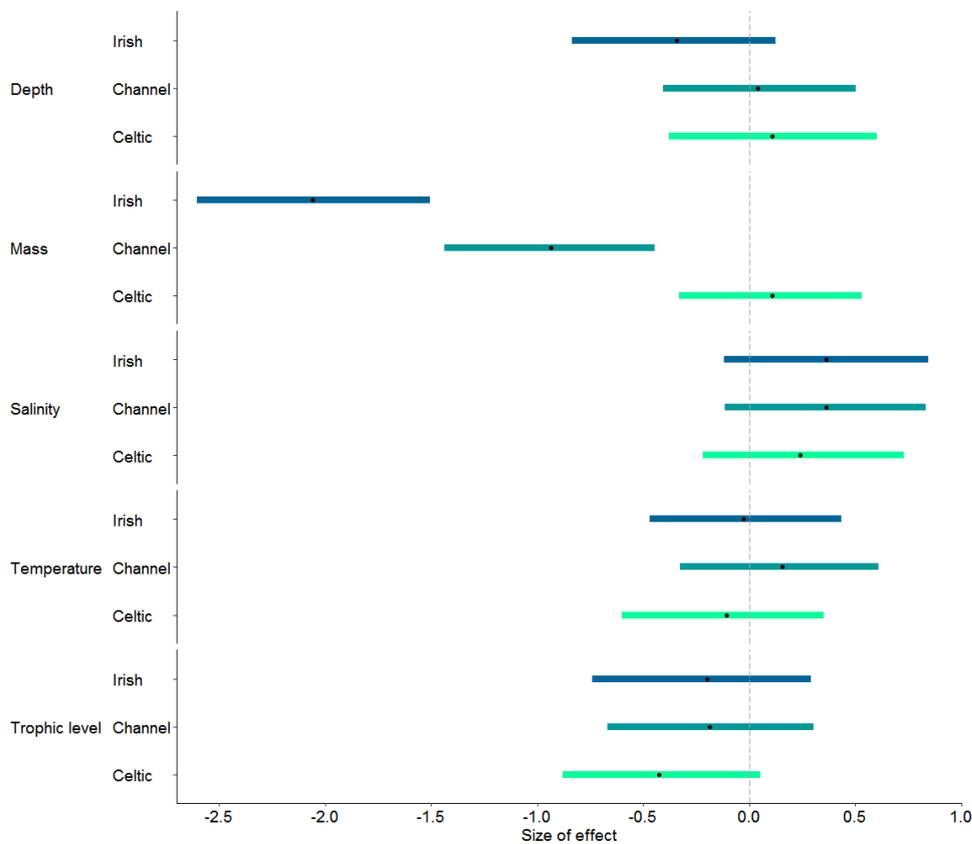


Figure B.6: Estimated effect of depth, mass, salinity, temperature and trophic level on individuals' affiliation to the pelagic pathways across the Celtic, Irish Sea and English Channel. Points show the mode and bars the 50% credible intervals. σ (amount of variation not explained by the parameters) is 0.76, 0.73 and 0.56 respectively.

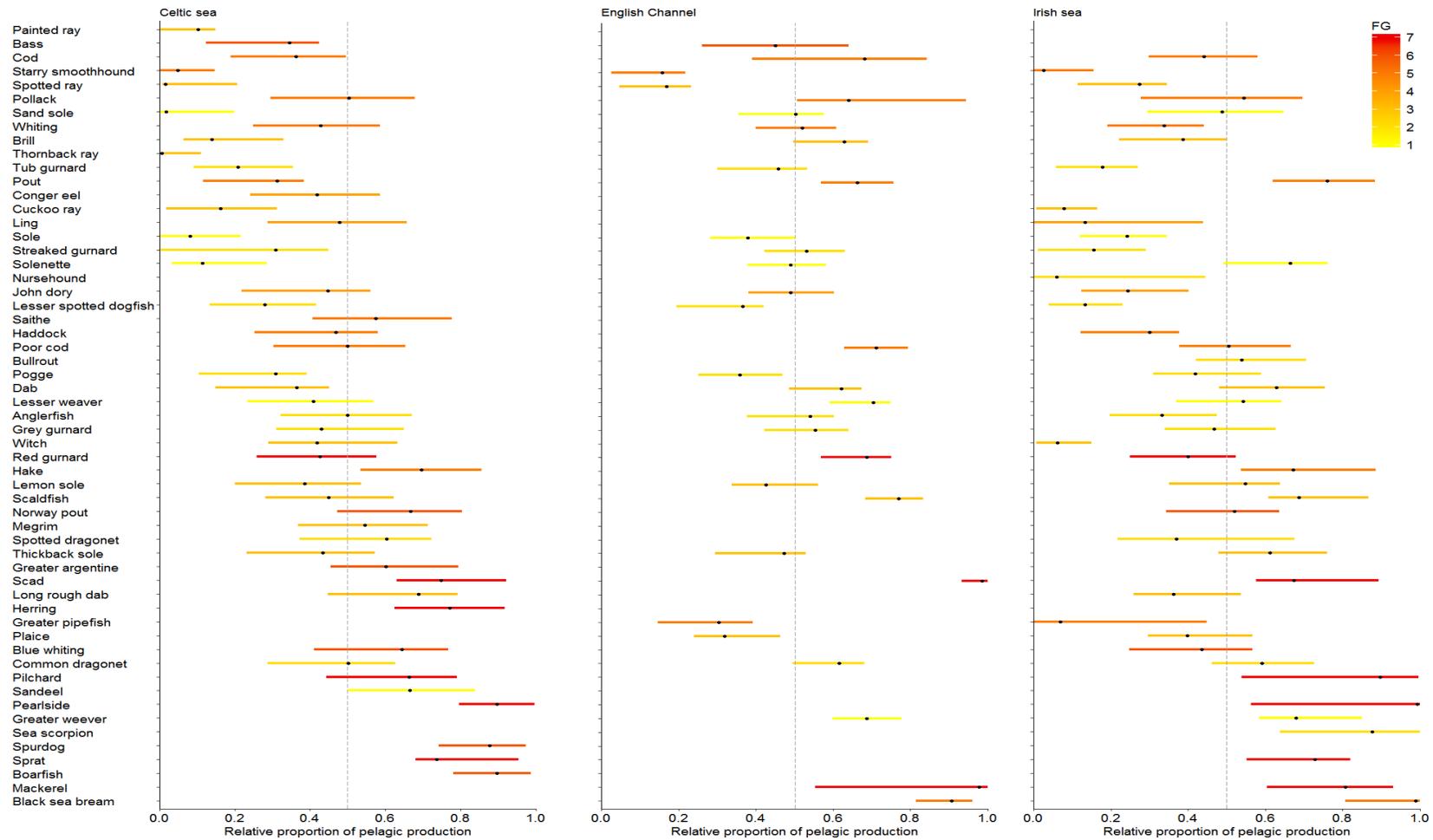


Figure B.7: Estimated relative contribution of the pelagic pathway to fish biomass by species (CPP) across all seas ordered by CPP across the Celtic Sea (if absent ordered by values in first appearing panel). Points show the mode and bars the 50% credible intervals of the posterior distribution. Colours display the functional groups (FG) (1 benthic – 7 pelagic)

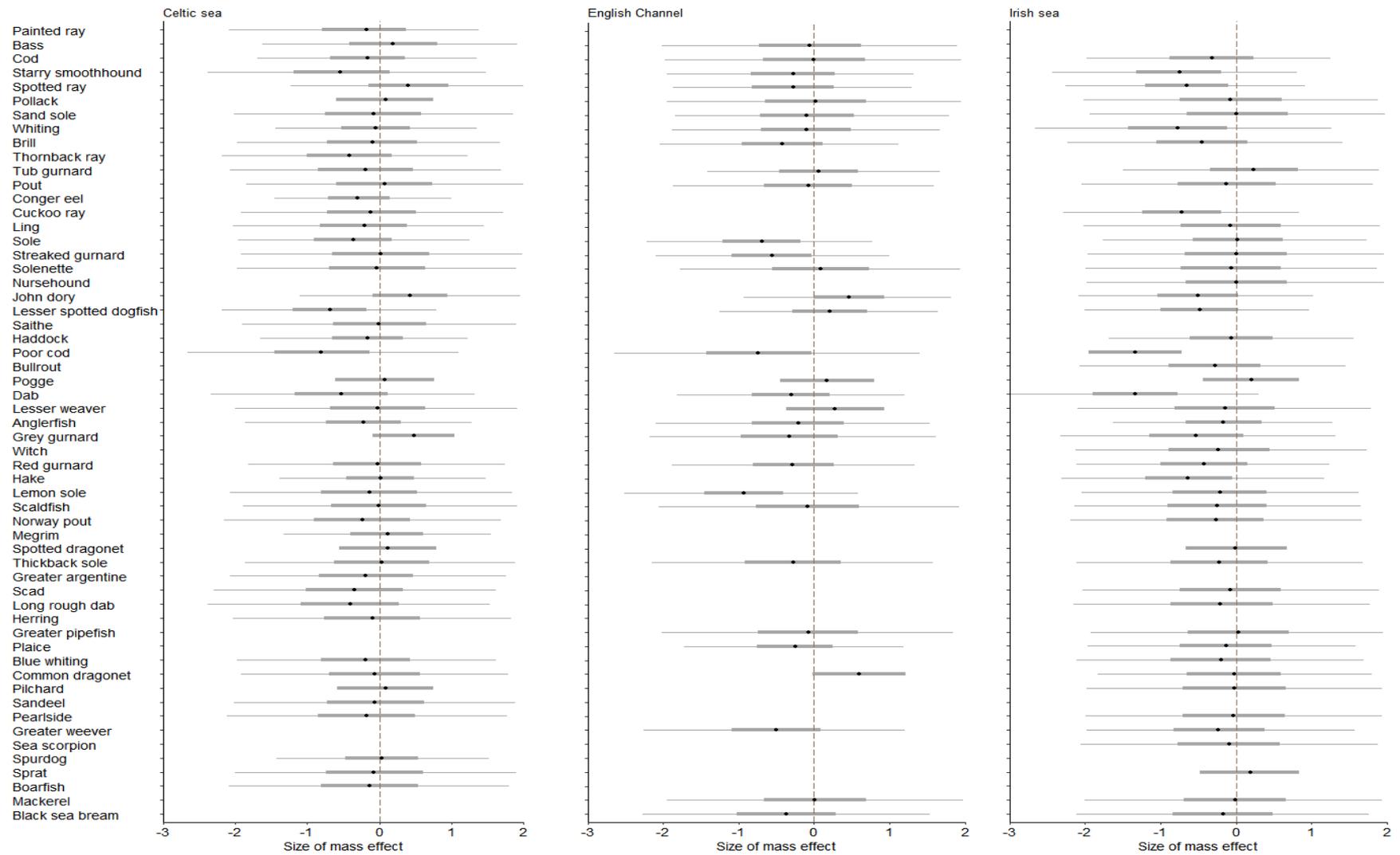


Figure B.8: Estimated effect of body mass on CPP across all seas, points show the mode, bars and lines the 50% and 90 % credible intervals respectively

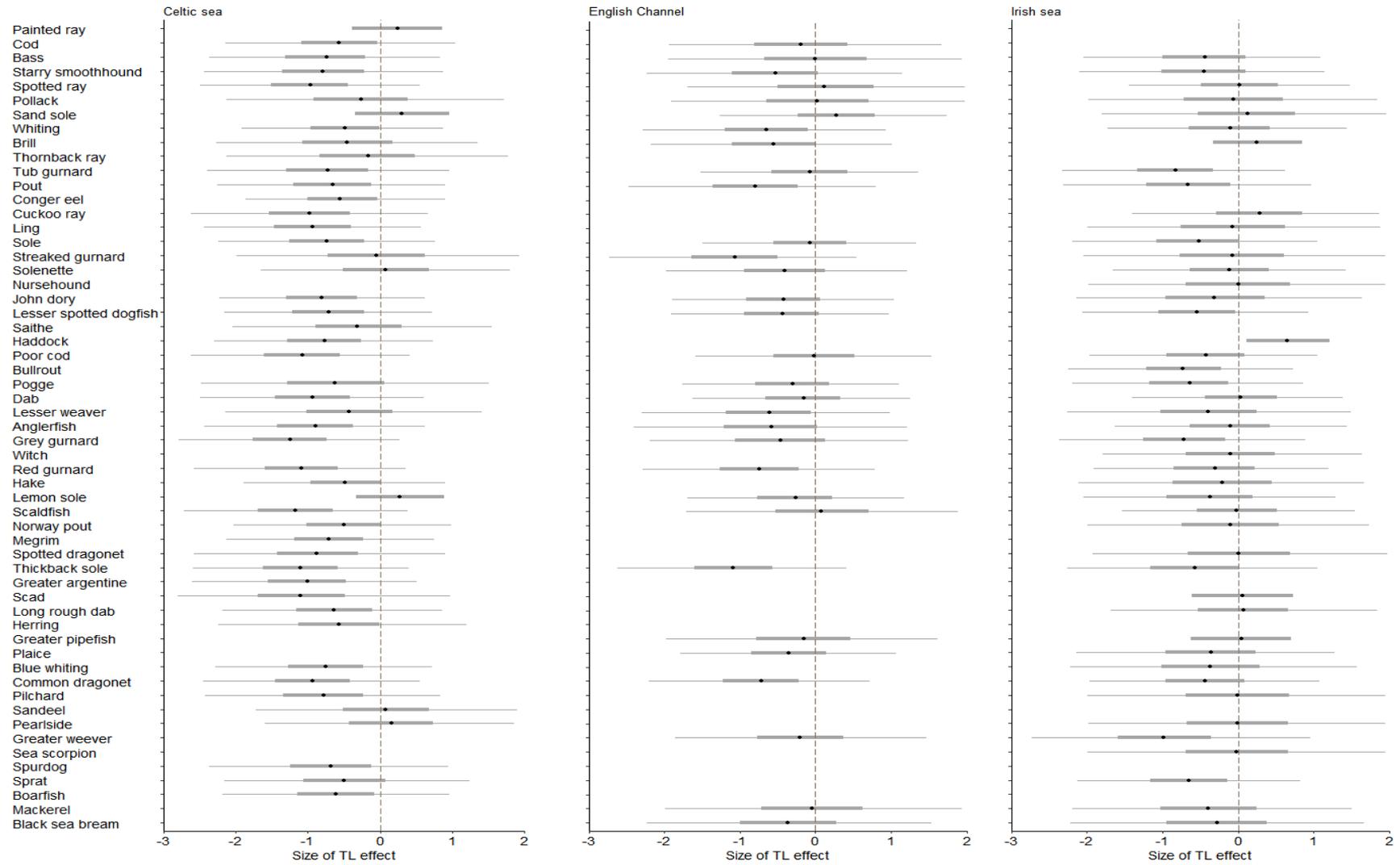


Figure B.9: Estimated effect of trophic level on CPP across all seas, points show the mode, bars and lines the 50% and 90 % credible intervals respectively

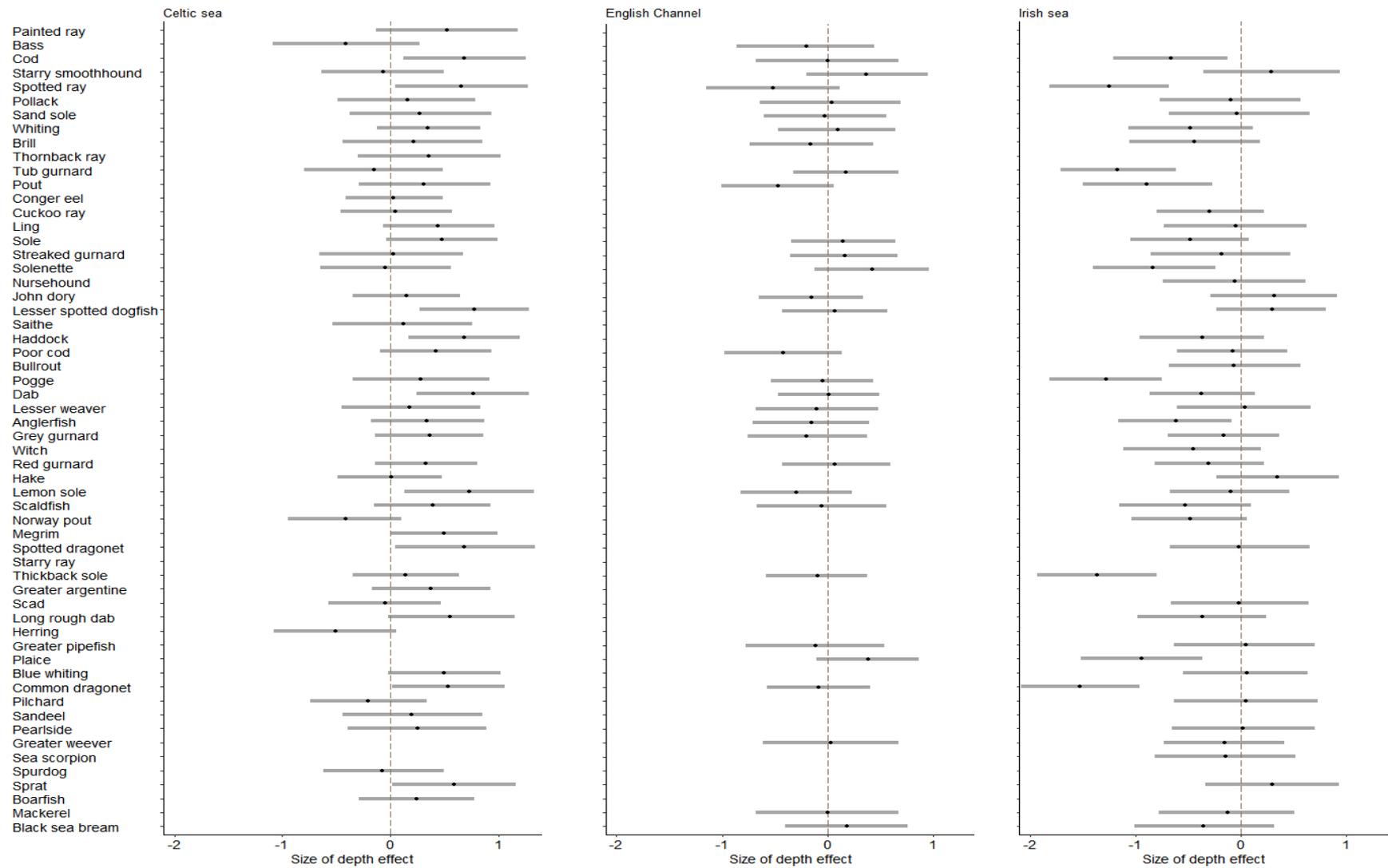


Figure B.10: Estimated effect of depth on CPP across all seas, points show the mode and bars the 50% credible intervals

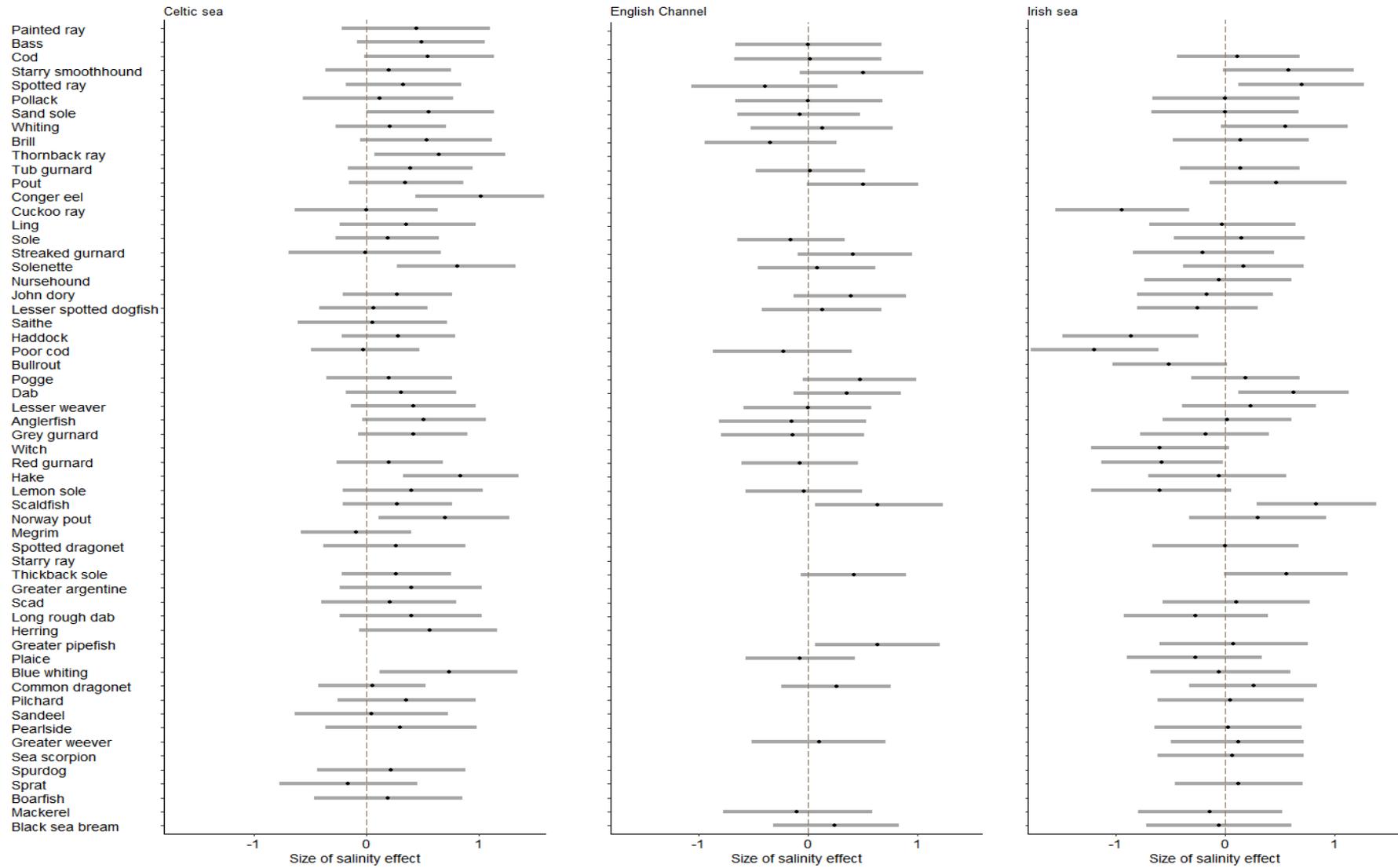


Figure B.11: Estimated effect of salinity on CPP across all seas, points show the mode and bars the 50% credible intervals

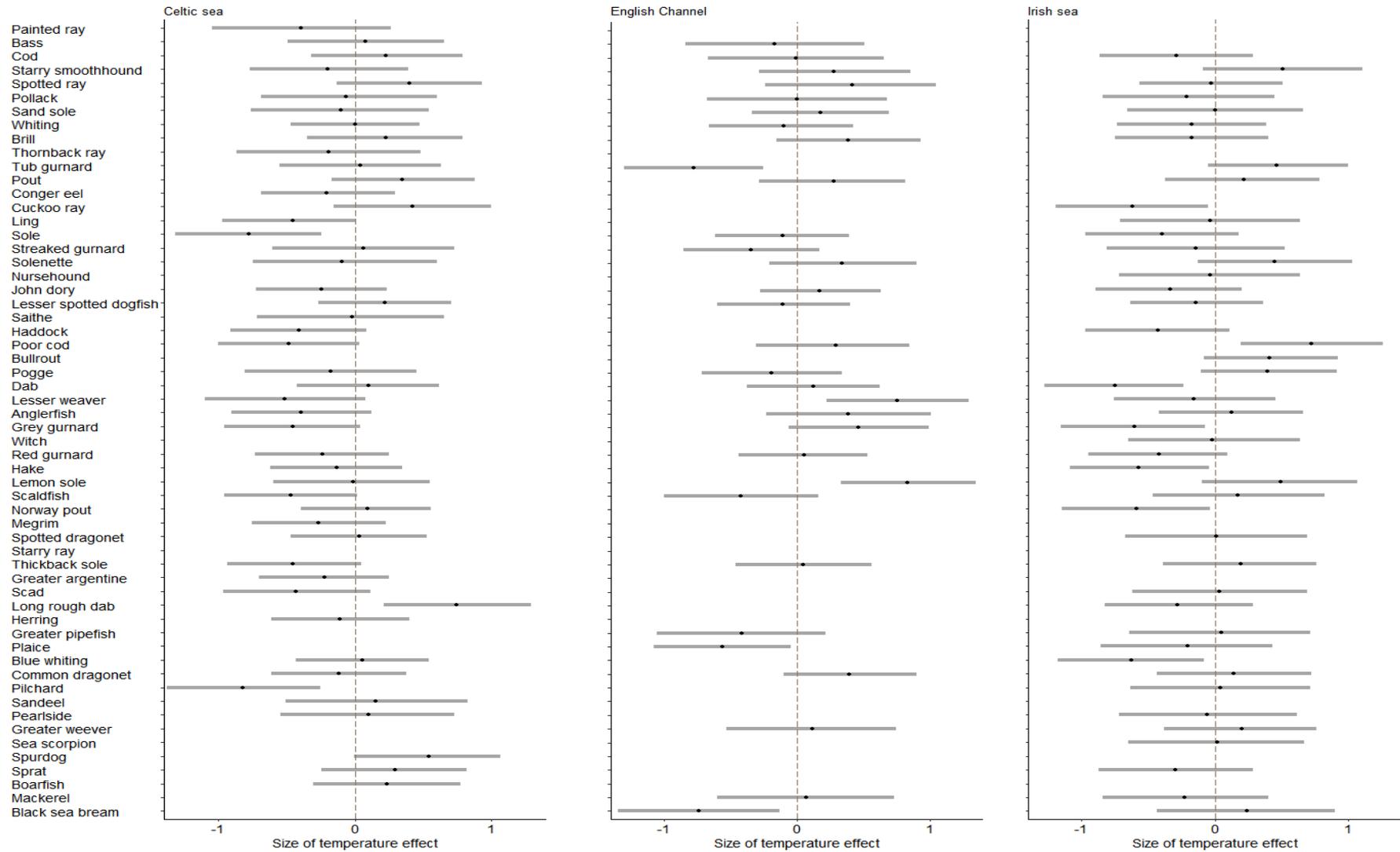


Figure B.12: Estimated effect of temperature on CPP across all seas, points show the mode and bars the 50% credible intervals

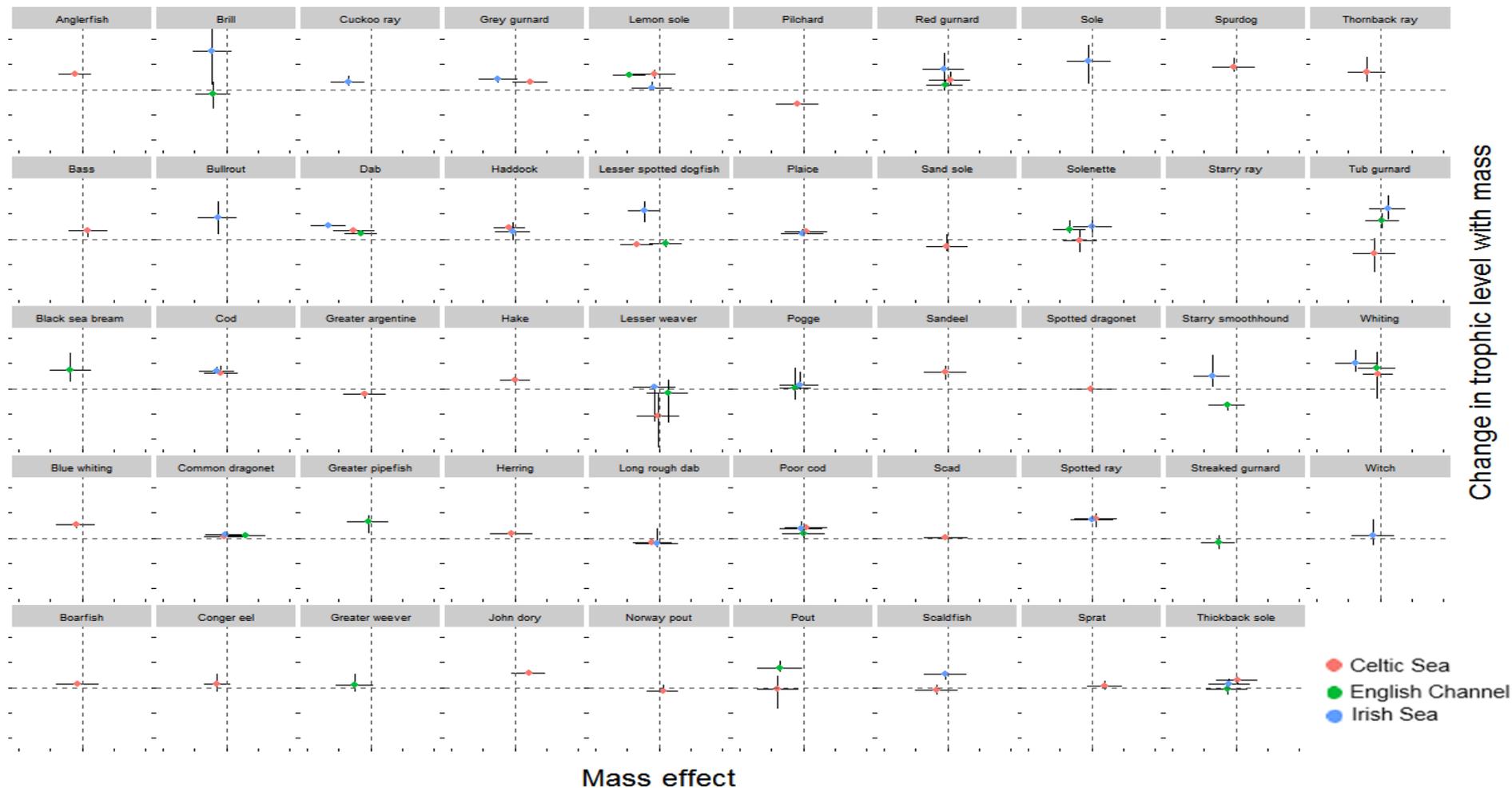


Figure B.13: A comparison of the estimated effect of mass on CPP (x-axis) with the change in species trophic level with mass (y-axis) across all seas. Points display the mode and bars the 50% credible intervals. For both axes the dashed lines represent the 0 intercepts and the tick marks represent - 2 to 2

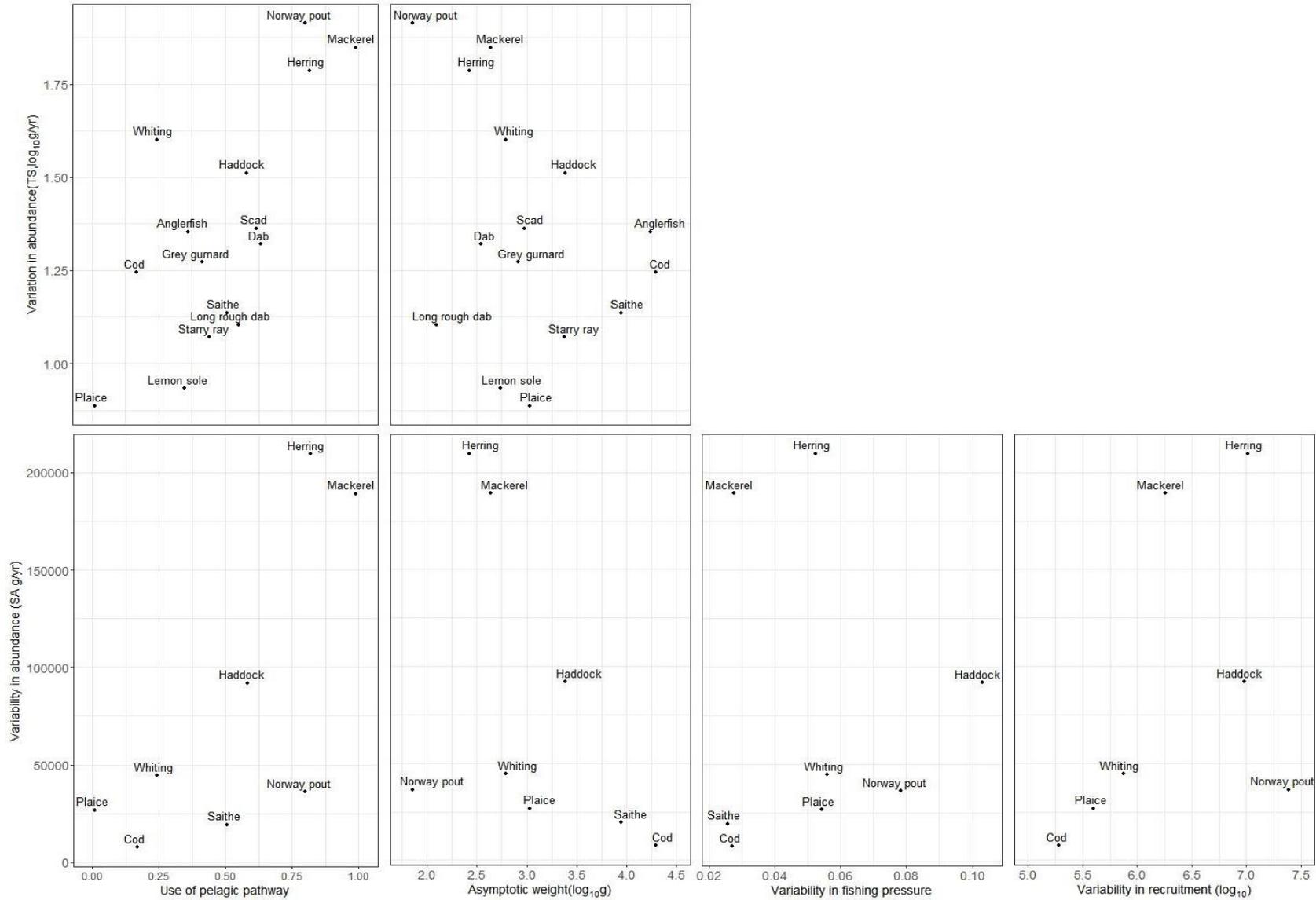


Figure B.14: Relationships of variability in species' abundance against the relative contribution of the pelagic pathway to fish biomass (CPP), W_{∞} , variability in fishing pressure and recruitment based on stock assessment (SA) and trawl survey (TS).

	Depth			Salinity			Temperature		
	Ce	Ch	I	Ce	Ch	I	Ce	Ch	I
Minimum	-0.51	-0.51	-1.53	-0.16	-0.39	-1.2	-0.82	-0.78	-0.75
Mean	0.26	-0.03	-0.33	0.33	0.12	-0.01	-0.09	0.05	-0.06
Maximum	0.77	0.43	0.35	1.02	0.64	0.83	0.74	0.83	0.73
Range	1.28	0.94	1.87	1.18	1.03	2.02	1.57	1.61	1.48

Table B.7: The estimated minimum, mean, maximum and range modal effect of depth, salinity, bottom temperature on CPP across the Celtic Sea (Ce), Irish Sea (I) and English Channel (Ch).

Correlation	Mass	Trophic level	Salinity	Depth	Temperature
Celtic - Irish	0.14	0.23	0.11	-0.02	-0.04
Celtic - Channel	0.24	0.07	-0.26	-0.36	-0.06
Channel - Irish	0.3	0.26	0.43	0.05	0.09

Table B.8: Ranked correlation for the effect of variables between species present in the Celtic, Irish Sea and English Channel

Sea	Depth	Salt	Temp	Mass	TL
Celtic	0.20	0.32	0.04	-0.05	-0.35
Channel	0.01	0.41	0.04	0.03	-0.04
Irish	-0.37	0.35	-0.23	0.03	-0.38

Table B.9: Spearman's ranked correlation for the size of the effect and range of data used across the English Channel, Irish and Celtic Sea

	Mean C (2002-2006)	C (2002)	C (2003)	C (2004)	C (2005)	C (2006)	SC (2006)
SA	0.07	0.08	0.12	0.1	0.11	0.03	0.08
TS	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01

Table B.10: P-values from modelled fluctuations of species' abundances against the relative contribution of the pelagic pathway to fish biomass (CPP). To calculate CPP mean and individual yearly (2002-2006) $\delta^{13}\text{C}$ (C) values were used in addition to $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ combined (SC) in 2006

Dataset	Model	P-value
TS	CPP against CPP + W^∞	0.26
SA	CPP against CPP + Fishing pressure	0.8
SA	CPP against CPP + W^∞	0.43
SA	CPP + Fishing pressure + W^∞	0.77

Table B.11: Results from ANOVA comparing models based on trawl survey (TS) and stock assessment (SA) data.

Dataset	Model	Coefficients	P-value of coefficients and overall model (m)	Adjusted R ²	Multiple R ²	AIC	F statistic
SA	CPP+ Fishing pressure +W _∞ + Recruitment	190000, 813200, -53800, -0.006	0.17,0.6,0.33,0.35,m 0.41	0.19	0.65	205.64	1.406 on 4 & 3 DF
SA	CPP + Fishing pressure +W _∞	150520,-119272,-28049	0.21, 0.92,0.53,m 0.36	0.15	0.51	206.32	1.41 on 3 & 4 DF
SA	CPP + W _∞ + Recruitment	171800,164100,-54060,-0.004	0.13, 0.27,0.36, m 0.24	0.32	0.61	204.48	2.115 on 3 & 4 DF
SA	CPP+ Fishing pressure + Recruitment	-71100,210300,829200,-0.003	0.12,0.6,0.6, m 0.38	0.12	0.5	206.6	1.32 on 3 & 4 DF
SA	CPP + W _∞	153593,-26067	0.14, 0.46,m 0.17	0.32	0.51	204.34	2.63 on 2 & 5 DF
SA	CPP + Fishing pressure	179,505,241,076	0.09 ,0.81,m 0.22	0.24	0.46	205.2	2.16 on 2 & 5 DF
SA	CPP + Recruitment	183900,-0.0008	0.1,0.81,m 0.22	0.24	0.46	205.2	2.104 on 2 & 5
SA	CPP	176870	0.069	0.36	0.45	203.3	4.91 on 1 & 6 DF
SA	W _∞	-45267	0.25	0.08	0.21	206.19	1.6 on 1 & 6 DF
SA	Recruitment	0.001174	0.76	-0.15	0.02	207.95	0.1 on 1 & 6 DF
SA	Fishing pressure	5497	1	-0.17	0	209.08	<0.001 on 1 & 6 DF
TS	CPP + W _∞	1.03,-0.09	<0.001,0.28,m 0.001	0.61	0.67	-1.19	12.11 on 2 & 12 DF
TS	CPP	1.09	<0.001	0.61	0.63	-1.68	22.48 on 1 & 13 DF
TS	W _∞	-0.16	0.19	0.06	0.13	11.3	1.95 on 1 & 13 DF

Table B.12: Results of linear models exploring fluctuations of species' abundances against the relative contribution of the pelagic pathway to fish biomass (CPP), W_∞, variability in fishing pressure (FP) and recruitment (R) based on trawl survey (TS) and stock assessment (SA) data

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