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# Trophic ecology of large gadiforms in the food web of a continental shelf ecosystem

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**Abstract :**

Human activities affect continental shelves, especially due to the harvest of living marine resources. Understanding their functioning and dynamics has become a growing concern in recent decades, especially through use of trophic modelling approaches. Studying the feeding ecology of key component species also improves this understanding by providing accurate information on trophic processes, particularly the dependence on trophic pathways. This study focuses on the trophic ecology of four large gadiforms (cod, haddock, whiting and hake) found on the continental shelf of the Celtic Sea. The study combines information on recently ingested prey (gut content analysis) and a more integrated indicator of food sources (stable isotope analysis). Two size classes of each species were considered (small and large - split around 20 cm for haddock, whiting and hake and 60 cm for cod), as were shallow and deep zones. The four gadiforms show distinct feeding niches and strategies, which limit interspecific competition. Cod and haddock relied mainly on the benthic trophic pathway but differed in favouring piscivory and invertivory, respectively. Hake fed mainly on the pelagic trophic pathway, while whiting seemed to feed on both pathways. Ontogenetic shifts from invertivory to piscivory were observed for whiting in both zones and for hake and cod in the deep zone. An unexpected shift from the pelagic to the benthic trophic pathway was observed from small to large haddock in the deep zone. Taking into account the descriptions of diets made in adjacent ecosystems throughout the year, the four species show trophic plasticity towards one of the trophic pathways or the other. Differences between the shallow and deep zones were related to benthic and pelagic prey characteristics, which themselves are driven by the sedimentary and hydrological context, especially thermal stratification.

**Highlights**

► Cod and haddock relied mainly on the benthic trophic pathway. ► Hake relied mainly on the pelagic trophic pathway. ► Whiting feed on both pathways. ► Shifts with size for whiting in both zones and for hake and cod in the deepest one.

**Keywords** : Celtic Sea feeding gut content stable isotopes ontogeny habitat comparison

# 1 Introduction

Continental shelf ecosystems provide many goods (*e.g.* fish harvests or raw materials) and services (*e.g.* breeding and nursey habitats, or carbon sequestration) that are threatened by global change, terrestrial inputs and anthropogenic activities. Among the variety of marine ecosystems, they are impacted the most by human activities (Halpern et al., 2008), especially due to the harvest of living marine resources, which is supported by the strong biological productivity of these areas. Thus, understanding their functioning and trophic dynamics has become a growing concern in recent decades. Trophic functioning in these areas is linked to terrigenous inputs that stimulate primary production and, as a result, benefit organisms of higher trophic levels and thus fisheries. In these ecosystems, the food web is structured mainly around interconnected pelagic and benthic pathways (Blanchard et al., 2011, Kopp et al., 2015). In the pelagic pathway, nutrients fuel the primary production consumed by zooplankton grazers that are themselves preyed on by invertebrate predators and pelagic fish. From 15-50% of the primary production and other pelagic material (faeces and remains of pelagic organisms) sinks to the bottom (Stahl et al., 2004; Glud, 2008). Some of this detrital material forms the base of the benthic pathway (Woodland and Secor, 2013), which also includes bottom primary production, but only in the euphotic zone. Detritivores and scavenger invertebrates eat the detritus and are themselves preyed on by benthic and demersal fish. The benthic pathway turns over more slowly than the pelagic pathway, and the use of these two pathways has a stabilizing effect on consumer populations (Rooney et al., 2006).

Trophic structures, interactions and transfers depend on several factors, such as habitats and ontogenetic changes. Size is one of the most important ecological attributes for an organism as it determines energy requirements (Werner and Gilliam, 1984). Ontogenesis influences biological interactions with other species and thus feeding competition. As fish grow, their

morphometric attributes and physical abilities change, such as larger mouth dimensions (Karpouzi and Stergiou, 2003; Keast and Webb, 1966) and improved swimming performance (Gibb et al., 2006). These ontogenetic changes allow fish to ingest a wider range of prey items, such as larger or faster prey (Karpouzi and Stergiou, 2003; Pinnegar et al., 2003). A change in diet as size changes is common and is often correlated with a change in habitat (Werner and Gilliam, 1984). Habitats can provide different prey depending on their environmental variables (depth, salinity, sediment type, etc.). Depth is an important factor as it regulates the benthic-pelagic connection, and it regulates the degree of interactions between the water column and the water near the bottom (Schindler and Scheuerell, 2002; Kopp et al., 2015; Giraldo et al., 2017).

Understanding trophic functioning requires holistic studies, especially through trophic modelling approaches, which have been developed in various parts of the world (Colleter et al., 2015). It also requires studying the feeding ecology of key component species to provide specific information on trophic processes, such as species' diet composition, intra- or inter-specific feeding competition, ontogenetic shifts and dependence on trophic pathways, all of which are essential for creating an overall picture. This information helps to delineate species' trophic niches historically investigated using gut content analysis (GCA) (Hyslop, 1980). GCA helps identify the fine taxonomic resolution of prey but depends greatly on the digestibility of prey taxon and their state of digestion when their predator is caught. GCA offers a snapshot of the diet, showing the most recently ingested prey. In contrast, stable isotope analysis (SIA), applied more recently to trophic ecology, integrates dietary information over time (Peterson and Fry, 1987; Layman et al., 2012). Nitrogen (N) isotope ratios serve as indicators of a consumer's trophic level (Post, 2002) and carbon (C) isotope

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ratios allow the origin of C sources to be traced back to a given environment (DeNiro and Epstein, 1978).

The present study focused on the Celtic Sea where demersal fish, large gadiform species such as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), hake (*Merluccius merluccius*) and whiting (*Merlangius merlangus*) represent approximately 25% of the biomass of the fish community in the central geographic range of this ecosystem (Martinez et al., 2013). These species are known as top predators on the continental shelf and upper slope (Froese and Pauly, 2018) and occupy a central position in trophic functioning of the ecosystem (Bentorcha et al., 2017; Moullec et al., 2017). The diets of these fish in the Celtic Sea were previously described by Du Buit (1982, 1995, 1996) and Du Buit and Merlinat (1985) and by Rault et al. (2017) based only GCA. Using integrated trophic tracers (SIA) combined with a snapshot view of the diet (GCA) we aimed to provide a new insight on their trophic ecology within this ecosystem.

More precisely, the present study investigated i) how the niches of cod, haddock, whiting and hake in the Celtic Sea depend on the pelagic vs. benthic trophic pathways, ii) how the patterns observed vary as a function of fish size and iii) how these patterns are influenced by habitat. For this purpose, GCA and SIA were combined to evaluate species' trophic niches and overlaps, and to estimate the partitioning of their prey between the two pathways. Accordingly, we considered two size classes of fish to investigate potential ontogenetic changes in trophic niche or position in the food web. We also examined two depths in the Celtic Sea to identify differences in trophic functioning resulting from contrasting habitats.

## 2　Materials and methods

### 2.1　Study area and sampling protocol

Fish were sampled on 67 sites (Fig.1) during the EVHOE survey ("EValuation des ressources Halieutique de l'Ouest de l'Europe", part of the International Bottom Trawl Survey performed, detailed in SM 1) using a GOV ("Grande Ouverture Verticale") demersal trawl with a cod-end of 20-mm stretched mesh, towed for 30 min at a speed of approximately 3.5 knots by R/V "Thalassa" during the day time in November 2014 and 2015. One tow was performed at each sampling sites and fish were identified to species and measured. The number of fish sampled for gut content and stable isotope are presented in the SM 2. To consider potential ontogenetic diet changes, size classes were determined according to the main modes observed in the size distribution of each species, obtained in the same season between 1998-2013 onto EVHOE samples (small/large size threshold at 60 cm for cod, 23 cm for haddock, 22 cm for whiting and 21 cm for hake, see SM 1).

Two zones were sampled: a shallow zone 70-120 m deep ("zone 1") and a deep zone 121-259 m deep ("zone 2", Fig. 1). These two zones were considered two distinct physical habitats. According to Pinot (1974), zone 1 has muddier sediments than zone 2. Zone 1 is located on the continental shelf itself, outside the direct influence of hydrological processes (tidal mixing and fronts) of the nearby coast, while zone 2 is influenced more by the edge of the shelf. During the sampling period (mid-autumn), stratification was assumed to be retreating (Pingree 1975), yielding a well-mixed water column in zone 1, while zone 2 remained thermally stratified (at a depth of 50 m). In zone 2, benthic photosynthesis was weak or absent, given the maximum critical depth of 130 m (in early summer) estimated by Pingree et al. (1976). The sampling design is summarised in SM 2.

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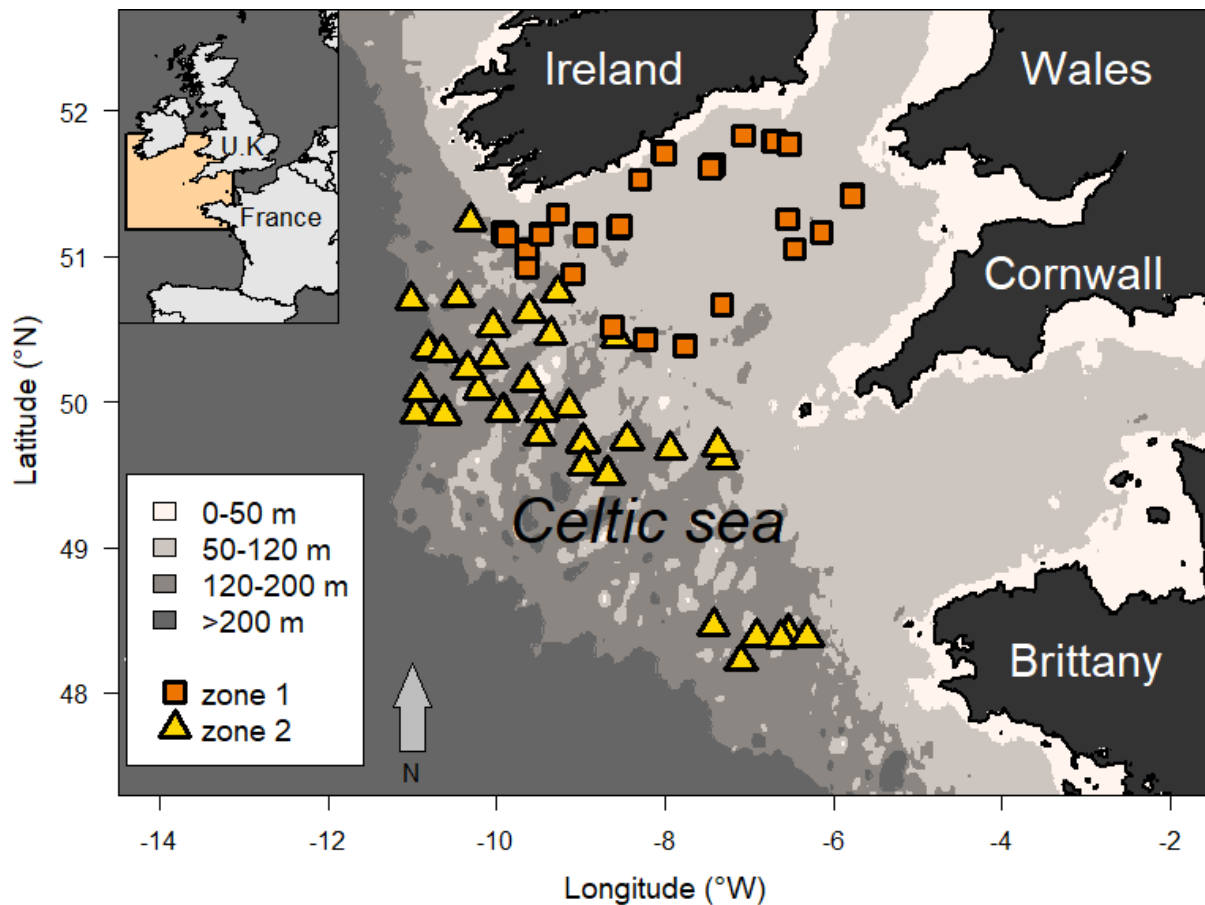
**Figure 1.** Location of sampling sites in the Celtic sea (zone 1: 70-120 m; zone 2: 121-259 m).

## 2.2   Stable isotope analysis

On board, a sample of muscle was dissected from the four gadiform species and their potential prey, and then frozen. Tissues were carefully dissected from the white dorsal muscle (fish), abdomen (shrimp), adductor muscle (bivalves), foot (gastropods) and mantle (cephalopods). In the laboratory, samples were oven dried at 60°C for 48 h and ground into a homogeneous powder using a mixer mill. Samples were sent to the Stable Isotopes in Nature Laboratory (University of New Brunswick, Canada), where they were analysed using a Carlo Erba NC2500 Elemental Analyser. Stable isotope values were converted into ratios (δ notation):

$$\delta X = \left[ \frac{R_{sample}}{R_{standard}} - 1 \right] \times 10^3 \ (in \ ‰)$$

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where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The international standard references are Pee Dee Belemite carbonate for $\delta^{13}C$ and atmospheric N for $\delta^{15}N$. Normalisation of $\delta^{13}C$ ratios for species with a C:N ratio greater than 3.5 (the value above which lipid normalisation is recommended; Post et al., 2007) was performed according to the following equation (Post et al., 2007):

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99\ C{:}N$$

The $\delta^{13}C$ and $\delta^{15}N$ compositions of a species provide information on its trophic level and pathway relative to a baseline. Studying higher-level consumers and comparing different zones require spatially adjusting their isotopic compositions depending on the baseline. Hence, compositions were rescaled to compare the trophic structure of each zone. Suspension-feeding bivalves, *Pecten maximus,* were chosen as the trophic baseline. This species is the most relevant one to use as a baseline for the entire food web (Chouvelon et al., 2012) as it feeds on suspended particulate organic material, which is a mixture of primary production (phytoplankton and micro-phytobenthos) and detrital material.

Hence, raw isotopic data for N and C were corrected with baseline isotopic compositions according to sampling depth, as it expressed spatial heterogeneity. First, a linear Gaussian regression was performed to investigate the relationship between isotopic values of *P. maximus* and depth. After checking the residuals (normality and homoscedasticity) graphically to validate the model's assumption, the regression coefficients were used to correct the raw data for each consumer by subtracting the predicted baseline at the sampling location (considering only depth) and by adding the mean of the baseline isotopic compositions for the given element in the entire zone:

$$\delta X_{corrected} = \delta X_{uncorrected} - [\alpha \times depth_{\delta X} + \beta] + mean(\delta X_{\text{P.maximus in Celtic Sea}})$$

### 2.3 Gut content analysis

Guts of the four gadiform species were dissected and frozen on board for subsequent analysis in the laboratory. In the laboratory, guts were thawed and then emptied to retrieve prey present in the stomach and the intestine. Gut contents were placed in a Petri dish, while prey were identified to the most precise taxonomic rank possible using a Leica stereo microscope outfitted with a Leica IC80 HD camera. Most cod and haddock guts contained prey (vacuity rates of 0-12%), while hake and whiting had high vacuity rates (13-54%). For individuals with guts, prey were grouped according to three factors – taxonomy, position in the water column, and trophic guild – resulting in 37 taxo-functional groups (SM 3). The main contributions to predators' diets were identified based on frequency of occurrence and relative abundance (SM 4a and 4b). Occurrence and abundance were chosen over bulk methods, which appear to have high uncertainty (Baker et al., 2014).

### 2.4 Data analysis

#### 2.4.1 Trophic interaction and dependence on pelagic and benthic pathways

#### 2.4.1.1 Relationships between gadiforms and prey groups

Relationships between the gadiform categories (species $\times$ size class) and the 37 prey groups found in digestive contents in the two zones were first examined using non-metric multi-dimensional scaling (nMDS) of occurrence data (Kruskal, 1964). Rare groups (occurrence < 5%) were excluded to avoid misinterpreting the nMDS (Manté et al., 2003). Then, a matrix of Bray-Curtis dissimilarities was calculated. Representations were considered valid if they had stress less than 0.3. Stress, which is minimised through the iterative process of the nMDS,

relates pairwise distances between objects in the reduced ordination space to their dissimilarities in the "real world" (the complete multidimensional space).

### 2.4.1.2 Trophic web through SIA and percentages of assimilated prey estimated by mixing models

To provide a simplified picture of the trophic web and reduce the number of potential sources in mixing models, each zone's community was clustered using hierarchical ascendant clustering via Euclidean distances and the Ward method on $\delta^{13}$C and $\delta^{15}$N data for gadiforms and their potential prey. The number of clusters was chosen according to an inertia criterion and taxonomy, position in the water column and trophic guild. Mixing models can estimate relative contributions of each prey or group of prey to the predator's diet. Bayesian approaches are well suited to address the multiple layers of uncertainty in the data, TEFs, etc. (Parnell et al., 2010; Phillips et al., 2014), as the mixing models estimate the probability distribution of multiple source contributions to a mixture.

Using the resulting clusters as sources and the predator category as the consumer, Bayesian mixing models (SIAR, Parnell et al., 2010) were built for each predator category using the R package 'siar' (Parnell and Jackson, 2013). Source contributions were estimated only for zone 1 and for cod, whiting and hake when the isotopic data composition was considered sufficient to encompass the spectrum of prey for gadiforms. Due to a low coverage of prey species in SIA in zone 2, it was not possible to build a mixing model in this zone.

Bond and Diamond (2011) found that outputs from mixing models were highly sensitive to, and thus significantly influenced by, the initial TEFs input in the model. They recommend using good estimates of TEFs to obtain a robust estimate of the relative contributions of prey items. Accordingly, in the lack of relevant laboratory experiments and data to estimate TEFs accurately on the species studied here, we set the TEFs to realistic compositions (Hussey et al., 2014; Zanden and Rasmussen, 2001): $0.5 \pm 1$ for $\delta^{13}$C for all clusters, and $3 \pm 1$ for $\delta^{15}$N

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of primary consumer clusters and $2 \pm 1$ for $\delta^{15}$N for other clusters. All prey clusters were chosen as potential assimilated prey, except for the cluster that included fish.

*2.4.2 Trophic niche breadth*

**2.4.2.1 Determining trophic niche breadth via taxonomic richness**

Trophic niche breadth was estimated from the taxonomic richness of gut content data. Precautions should be taken when comparing taxonomic richness from unbalanced sampling, such as predator categories containing different numbers of samples (Chao et al., 2014; Colwell et al., 2012). Taxonomic richness increased non-linearly as the number of units sampled increased. As our sampling was unbalanced (e.g. in zone 1, 41 guts from small cod and 15 from large cod), rarefaction curves were estimated for each predator category to increase robustness when comparing taxonomic richness using the R package 'INEXT' (Hsieh et al., 2016). Curves were constructed with unconditioned variance, and predators were compared using an estimate of taxonomic richness for n = 15 (the smallest number of gut contents in a predator category, except for small whiting in zone 2).

**2.4.2.2 Isotopic niche breadth**

Newsome et al. (2007) defined an isotopic niche as a zone in isotopic space where each axis is an element with isotopic composition coordinates ($\delta$X). To visualize species' isotopic niches, a sample-size-corrected standard ellipse area (SEAc) was plotted on $\delta^{15}$N/$\delta^{13}$C bi-plots (Jackson et al., 2011). To avoid underestimating the SEA when the sample size was less than 30, a corrective factor was applied, as follows:

$$SEAc = SEA \times (n-1)(n-2)^{-1} \ (in \ ‰^2).$$

The correction approaches 1 as n approaches infinity, which is a desired property.

To compare isotopic niches among species and size classes, a Bayesian approach was used to estimate the posterior distribution of the standard ellipse zone (SEAb). This method is based

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on Markov-Chain Monte Carlo draws in the posterior distribution combining the priors and likelihoods with the following parameters: 20 000 iterations, discarding of the first 1 000 values, a run with 2 chains, a thin posterior of 10, an Inverse Wishart prior on the covariance matrix $\begin{pmatrix} 2 & 0 \\ 0 & 2 \end{pmatrix}$ and a non-informative normal prior on the means ($10^3$). The likelihood is a multivariate normal distribution: $Y_i \sim MVN\big([\mu_x, \mu_y], \Sigma\big)$, with $\mu_x$ and $\mu_y$ the means and $\Sigma$ the covariance matrix. This procedure was performed using the R package 'SIBER' (Jackson et al., 2011).

### 2.4.3  *Trophic niche overlaps*

#### 2.4.3.1  **Diet overlaps**

The Renkonen similarity index (Renkonen, 1938), also known as the Schoener overlap index (Schoener, 1970), measures the degree of similarity between two predators' diets. It was used to identify niche overlaps between predators by constructing a similarity matrix. Similarity between predators i and j was determined as follows:

$$s_{i,j} = 100 \times \sum_{k=1}^{N} \min(p_{i,k}, p_{i,k})$$

where $p_{i,k}$ and $p_{j,k}$ are relative abundances of prey species k for predator i and predator j, respectively. The index ranges from 0 (no niche overlap) to 100 (full niche overlap).

#### 2.4.3.2  **Isotopic niche overlaps**

Niche overlaps were estimated and expressed as the mean of the percentage of the SEAc of niche 1 overlapped by that of niche 2 and the percentage of the SEAc of niche 2 overlapped by that of niche 1, using the R package 'siar' (Parnell and Jackson, 2013).

*2.4.4   Zone effect on isotopic compositions*

The effect of the zone (zone 1 or zone 2) on isotopic compositions ($\delta^{13}$C and $\delta^{15}$N ratios) of gadiforms was estimated using ANOVA based on Fisher's tests of $\delta^{13}$C compositions and then of $\delta^{15}$N compositions, followed by a linear model with an identity link. The models' assumptions (normality and variance homogeneity of the residuals) were verified graphically.

All analyses were performed using software R (R Core Team, 2015) with the significance threshold set at α = 0.05.

## 3   Results

### 3.1   Trophic interactions and gadiform dependence on pelagic and benthic pathways

*3.1.1   Gut content analysis*

From the 395 guts analysed, 155 taxa were identified. The digestive state of prey influenced the final taxonomic level. Approximately 56% of the prey were identified to the family level and 38% to the species level.

The two-dimensional nMDS plot, based on the occurrence data, shows links between prey groups and gadiforms. The first axis separates benthic from pelagic prey (Fig. 2), with pelagic crustaceans and fish to the right, groups of benthic invertebrates to the left and demersal fish in the middle. It illustrates the position of haddock in relation to benthic prey and, in contrast, the position of hake in relation to pelagic prey. Whiting lies between pelagic organisms and benthic crustaceans, while cod lies between benthic molluscs/crustaceans and demersal fish (Fig. 2). Dietary differences were influenced more by the species than their size or the zone in which they lived (Fig. 2). Nevertheless, GCA revealed differences in feeding preferences in the two zones by focusing more on prey taxonomy and occurrences of prey groups found in

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gut contents (SM 4a). In zone 2, polychaetes were nearly absent from the diet of whiting, cod and, to smaller extent, haddock, while molluscs and echinoderms occurred less often. Conversely, anomurans (mainly *Galathea* spp. and *Munida* spp. – SM 3) occurred much more frequently in the gut of cod in zone 2 than in zone 1. Haddock preyed mainly on *Echinocyamus pusillus* in zone 1 and on ophiuroids in zone 2. Hake showed greater preference for pelagic carideans (mainly Pasiphaeidae) in zone 1 than in zone 2.
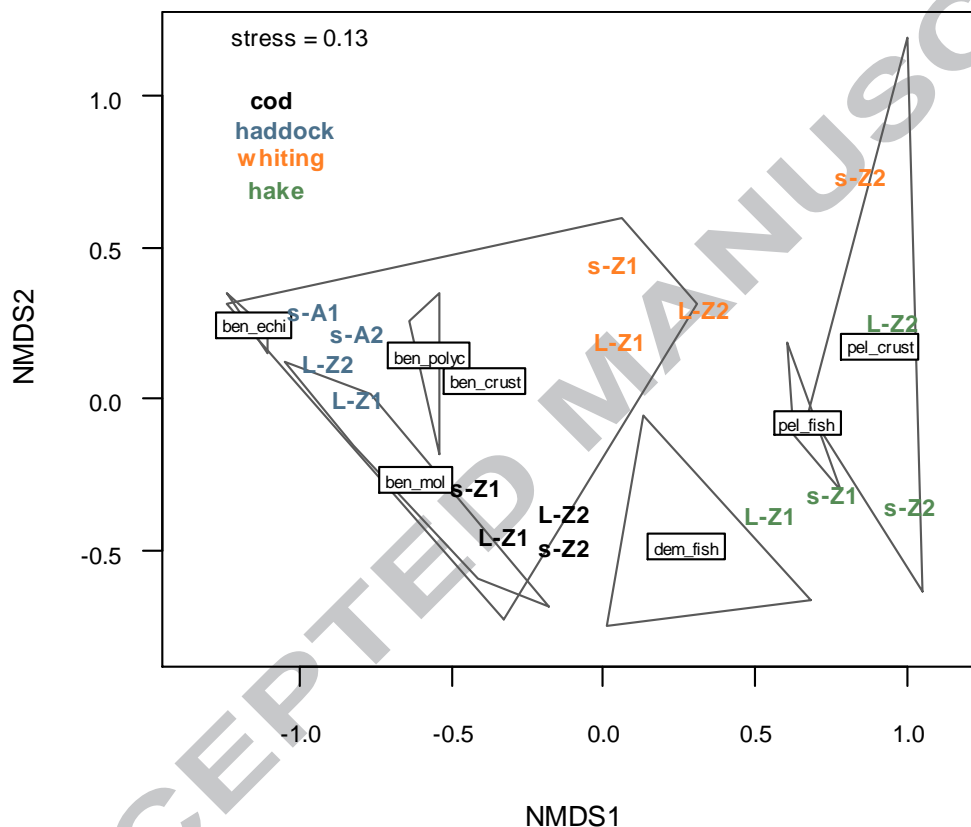


**Figure 2.** Two-dimensional ordination based on non-metric multidimensional scaling (nMDS) of fish predator categories (cod, haddock, whiting and hake) (coloured labels) and prey groups (grey polygons) from occurrence gut content data; ben_echi: benthic echinoderms; ben_polyc: benthic polychaetes; ben_crust: benthic crustaceans; ben_mol: benthic molluscs; dem_fish: demersal fish and cephalopods; pel_crust: pelagic crustaceans; pel_fish: pelagic fish. For predators, the color indicates the species detailed in the legend and

the label indicates the size class (s for small and L for Large), and the zone (ex: orange 's-Z1' is whiting, small size class in zone 1).

The relative abundance of benthic, demersal and pelagic groups of prey (SM 4b) helped to estimate the quantitative importance of the two food pathways (Fig. 3). Small and large haddock were benthic feeders, with 77-92% of prey being benthic, depending on size class and zone. Small and large cod also fed on benthic prey (53-71%) and to a smaller extent on pelagic and demersal prey. For these two benthic feeders, the percentages of benthic prey were smaller in zone 2 than in zone 1. Hake fed mainly on pelagic prey (41-57%) regardless of size class and zone. Small whiting fed mainly on benthic prey (50-65%), while large whiting fed on both benthic and pelagic prey, with greater dependence on pelagic prey ($\geq$ 35%) in zone 2.
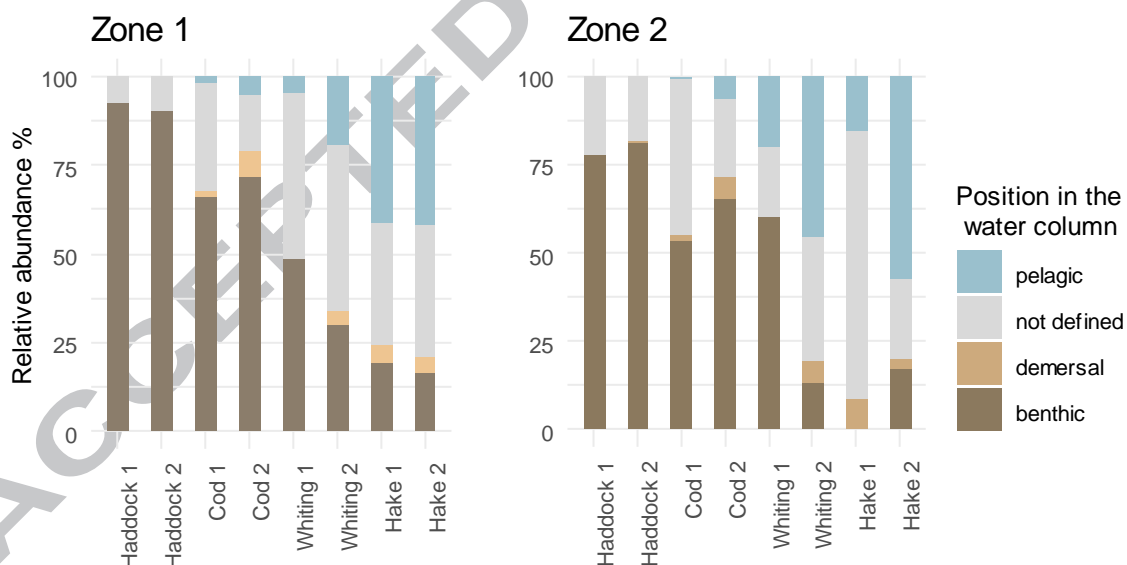


**Figure 3.** Relative abundance of prey groups in gut contents of fish predators by size class (1 = small, 2 = large) and zone (1 = shallow, 2 = deep).

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*3.1.2   Stable isotope analysis*

Separate clustering analyses of $\delta^{13}C$ and $\delta^{15}N$ compositions of the two zones distinguished several groups of consumers. They were identified to provide maximum correspondence between the two zones (SM 5) and are displayed on isospaces (Fig. 4) to show the trophic structure of each zone.
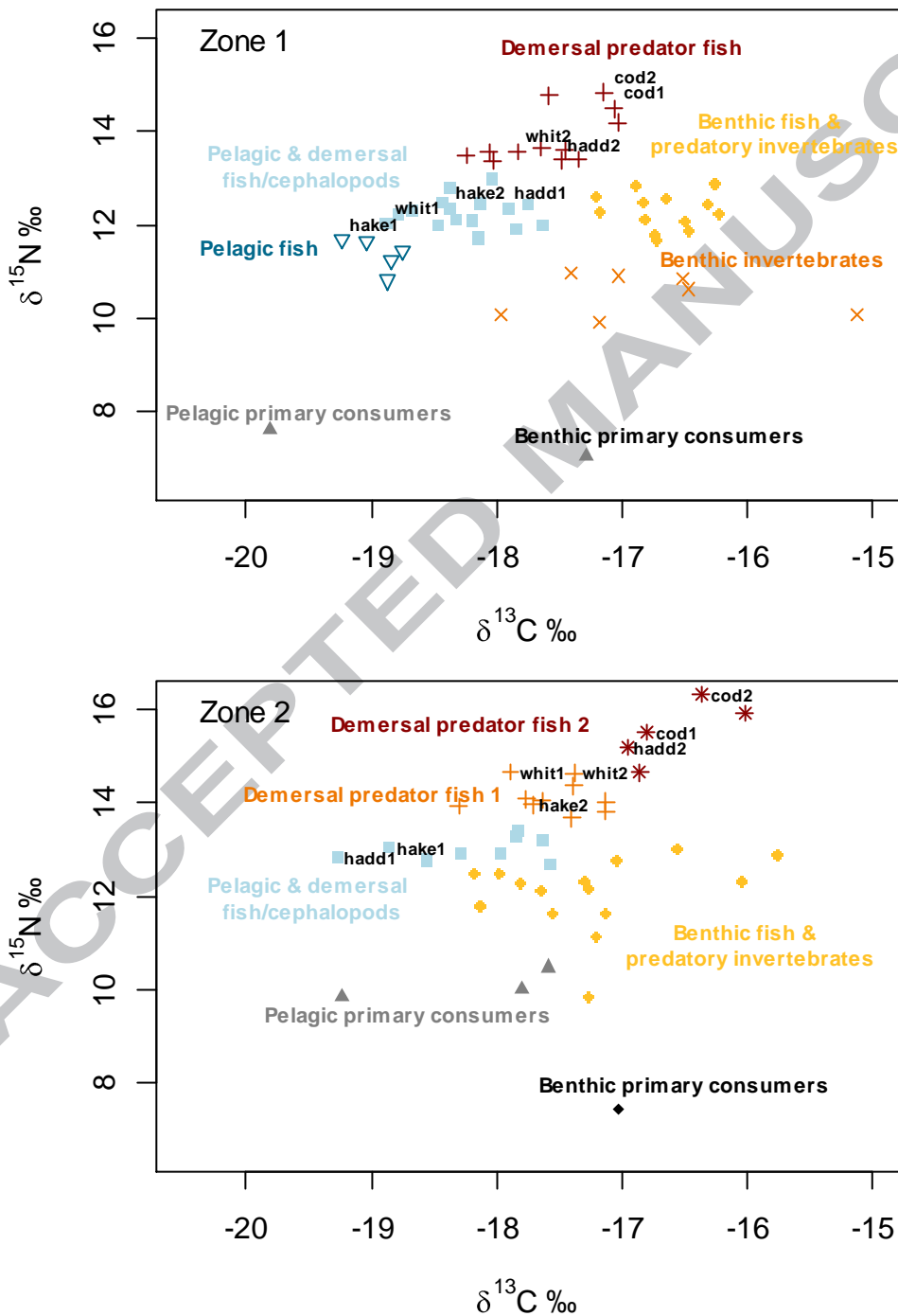
**Figure 4**. Isospace of the trophic web in zone 1 (shallow) and zone 2 (deep) showing groups of species from the clustering analysis (coloured symbols) and the four predator categories (cod, haddock, whiting and hake) (black text) by size class (1 = small, 2 = large). Each point represents the mean isotopic value for one species.

In zone 1, pelagic and benthic primary consumers were represented by pelagic copepods and the bivalve mollusc, *P. maximus,* respectively. Above these primary consumers on the $\delta^{15}$N axis, "pelagic fish" and, slightly higher, "pelagic and demersal fish/cephalopods" represented the pelagic pathway. To the right on the $\delta^{13}$C axis, "benthic invertebrates" and "benthic fish and predatory invertebrates" represented the benthic pathway. "Demersal predator fish" were located above these secondary consumers. In zone 2, we identified "pelagic and demersal fish/cephalopods" on the pelagic pathway and "benthic fish and predatory invertebrates" on the benthic pathway, while two groups of "demersal predator fish" were identified. Therefore, the food webs of both zones had a similar structure, with low $\delta^{13}$C compositions for the pelagic pathway and higher $\delta^{13}$C compositions for the benthic pathway.

The mixing models estimated prey proportions (in %) only for cod, whiting and hake sampled in zone 1 (Table 1). The estimates had wide 95% confidence intervals due to several factors, such as having more than three sources (number of isotopes used + 1) and highly variable isotopic compositions of predators (SM 2 and Fig. 5). Hence, the results should be interpreted as a trend in the predators' diets, with the mode of the distribution as the most likely composition.

**Table 1.** Estimated proportions (%) (mode [95% confidence interval]) of assimilated consumers' clusters in the diet of predator categories by size class (1 = small, 2 = large) in

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zone 1 from the stable isotope analysis mixing model. Numbers in bold correspond to proportion superior to 25%.

| Cluster no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| Name | **Pelagic primary consumers** | **Benthic primary consumers** | **Pelagic fish** | **Pelagic & demersal fish/ cephalopods** | **Benthic invertebrates** | **Benthic fish and predatory invertebrates** | **Demersal predator fish** |
| Cod 1 | 0.006 [0 - 0.7] | 0.007 [0 - 0.06] | 0.058 [0 - 0.25] | **0.38** [0.13 - 0.58] | 0.14 [0 - 0.17] | **0.44** [0.24 - 0.59] | |
| Cod 2 | 0.02 [0 - 0.2] | 0.02 [0 - 0.25] | 0.17 [0 - 0.33] | 0.23 [0.006 - 0.44] | 0.18 [0 - 0.33] | **0.25** [0.04 - 0.49] | |
| Whiting 1 | **0.44** [0.22 - 0.61] | 0.05 [0 - 0.24] | **0.28** [0.03 - 0.45] | | 0.02 [0 - 0.19] | 0.02 [0 - 0.21] | 0.01 [0 - 0.17] |
| Whiting 2 | 0.06 [0 - 0.22] | 0.01 [0 - 0.11] | **0.29** [0.06 - 0.53] | **0.32** [0.07 - 0.57] | 0.02 [0 - 0.21] | 0.12 [0.001 - 0.31] | |
| Hake 1 | **0.65** [0.36 - 0.79] | 0.02 [0 - 0.24] | | 0.05 [0 - 0.26] | 0.02 [0 - 0.17] | 0.01 [0 - 0.19] | 0.01 [0 - 0.16] |
| Hake 2 | **0.36** [0.2 - 0.53] | 0.04 [0 - 0.18] | **0.31** [0.05 - 0.53] | | 0.05 [0 - 0.24] | 0.02 [0 - 0.19] | 0.02 [0 - 0.18] |

The cod diet consisted mainly of benthic prey, with the largest proportions coming from benthic and demersal clusters (44% "benthic invertebrates", 14% "benthic fish and invertebrates"). Whiting fed more on pelagic prey, mainly "pelagic primary consumers" (copepods) for small whiting (44%) and "pelagic and demersal and fish/cephalopods" (32%) and "pelagic fish" (29%) for large whiting. Hake fed even more on pelagic prey, with small hake feeding on "pelagic primary consumers" (copepods) (65%) and large hake feeding on "pelagic primary consumers" (copepods) (36%) and "pelagic fish" (31%).

## 3.2 Gadiforms' trophic niches

### 3.2.1 Trophic niche breadth

Cod and haddock had the highest taxonomic richness (14.8-36.8 taxa), while whiting and hake had taxonomic richness of 5.0 -10.0 taxa (Fig. 5). The four fish categories occupied wide trophic niches in the isospace, with $\delta^{15}$N compositions (mean $\pm$ 1 standard deviation) ranging

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from $11.66 \pm 0.84‰$ for small hake in zone 1 to $16.29 \pm 0.28‰$ for large cod in zone 1, and $\delta^{13}C$ compositions ranging from $-19.33 \pm 0.28‰$ for small haddock in zone 2 to $-16.44 \pm 0.4‰$ for large cod in zone 2 (SM 2). Large cod and small haddock had the widest isotopic niches, with modes of the distributions of ca. $1.0‰^2$ and $1.6‰^2$, respectively, in zone 1 (Fig. 5). In zone 1, large hake had a much narrower isotopic niche than small hake (Fig. 5). In zone 2, cod and haddock had narrow isotopic niches (ca. $0.3‰^2$ and $0.1‰^2$, respectively), while small whiting and small hake had wider isotopic niches than large whiting and large hake, respectively. Isotopic niches in zone 2 were also wider than those in zone 1 for the same fish category.

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Zone 1                    Zone 2
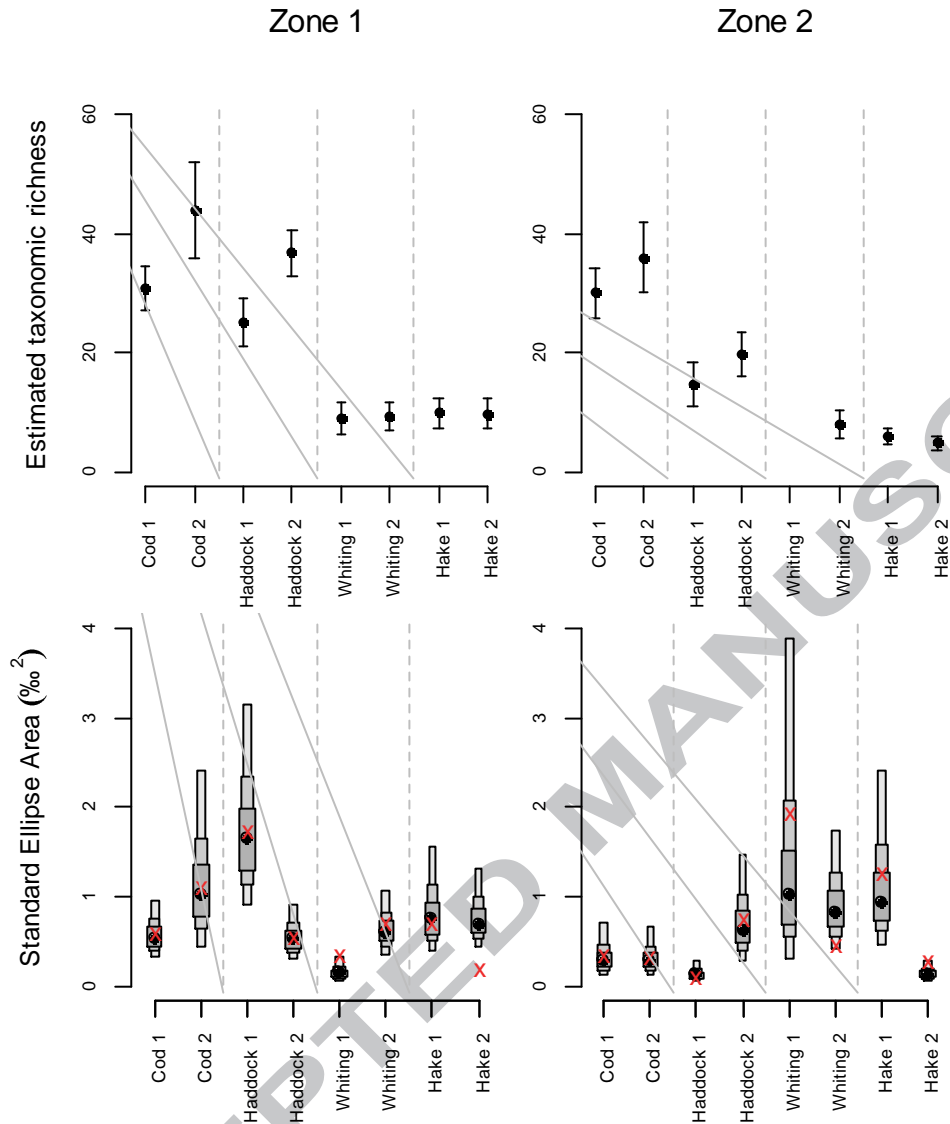


**Figure 5.** Estimated taxonomic richness (top) from the rarefaction curve with n = 15 (lowest common number of guts), and posterior Bayesian distributions of the standard ellipse zone (SEAb; grey boxplots) and sample size-corrected standard ellipse zone (SEAc; red crosses) (bottom) for each fish category by size class (1 = small, 2 = large) and zone (1 = shallow, 2 = deep).

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### 3.2.2 Trophic niche overlaps

In zone 1, the Schoener overlap index was high (> 60%) between size classes of cod, haddock and whiting, and slightly lower (53%) between size classes of hake (Table 2). In zone 2, only cod and haddock followed this pattern, while size classes of whiting and hake showed no substantial overlap. In zone 1, while haddock and large cod were separated from other fish, both size classes of hake and whiting overlapped (43-58%). Small cod overlapped with small and large whiting and small hake. Overlaps in zone 1 occurred twice as often as in zone 2, where large cod, small and large haddock and small whiting were clearly separated from other fish. The only substantial interspecific overlaps in zone 2 were between small cod and small hake and between large whiting and large hake (Table 2).

**Table 2.** Overlap (%) between trophic niches of the four predator categories by size class (1 = small, 2 = large) and zone (1 = shallow, 2 = deep). Schoener's overlap index (top right triangle); light and dark shaded cells indicate a Schoener overlap index greater than 40% and 60%, respectively. Standard Ellipse Area overlaps (bottom left triangle); light and dark shaded and hatched cells, indicate an overlap greater than 0% and 20%, respectively.

| Zone 1 | Cod 1 | Cod 2 | Haddock 1 | Haddock 2 | Whiting 1 | Whiting 2 | Hake 1 | Hake 2 |
|---|---|---|---|---|---|---|---|---|
| Cod 1 | | 62 | 11 | 17 | 58 | 54 | 40 | 30 |
| Cod 2 | 45 | | 9 | 15 | 29 | 37 | 27 | 37 |
| Haddock 1 | 0 | 0 | | 61 | 10 | 12 | 4 | 6 |
| Haddock 2 | 0 | 0 | 8 | | 13 | 16 | 7 | 10 |
| Whiting 1 | 0 | 0 | 3 | 0 | | 71 | 48 | 37 |
| Whiting 2 | 8 | 14 | 10 | 19 | 0 | | 43 | 40 |
| Hake 1 | 0 | 0 | 0 | 0 | 36 | 0 | | 53 |
| Hake 2 | 0 | 0 | 39 | 0 | 11 | 10 | 0 | |

| Zone 2 | Cod 1 | Cod 2 | Haddock 1 | Haddock 2 | Whiting 1 | Whiting 2 | Hake 1 | Hake 2 |
|---|---|---|---|---|---|---|---|---|
| Cod 1 | | 68 | 21 | 13 | 26 | 29 | 45 | 14 |
| Cod 2 | 0 | | 19 | 15 | 36 | 37 | 28 | 30 |
| Haddock 1 | 0 | 0 | | 60 | 12 | 23 | 5 | 7 |
| Haddock 2 | 59 | 0 | 0 | | 4 | 17 | 3 | 3 |
| Whiting 1 | 0 | 0 | 0 | 12 | | 33 | 19 | 24 |
| Whiting 2 | 2 | 0 | 0 | 40 | 42 | | 33 | 48 |
| Hake 1 | 0 | 0 | 49 | 0 | 0 | 0 | | 7 |
| Hake 2 | 0 | 0 | 0 | 0 | 27 | 15 | 0 | |

SEAc of small and large individuals of the same species overlapped only for cod in zone 1 (45%) and whiting in zone 2 (42%) (Table 2 and Fig. 6). In zone 1, substantial interspecific overlaps were observed only between small haddock and large hake (39%) and between small whiting and small hake (36%). In zone 2, substantial overlaps occurred between small cod and large haddock (59%), small haddock and small hake (49%), large haddock and large whiting (40%) and small whiting and large hake (27%) (Table 2 and Fig. 6).
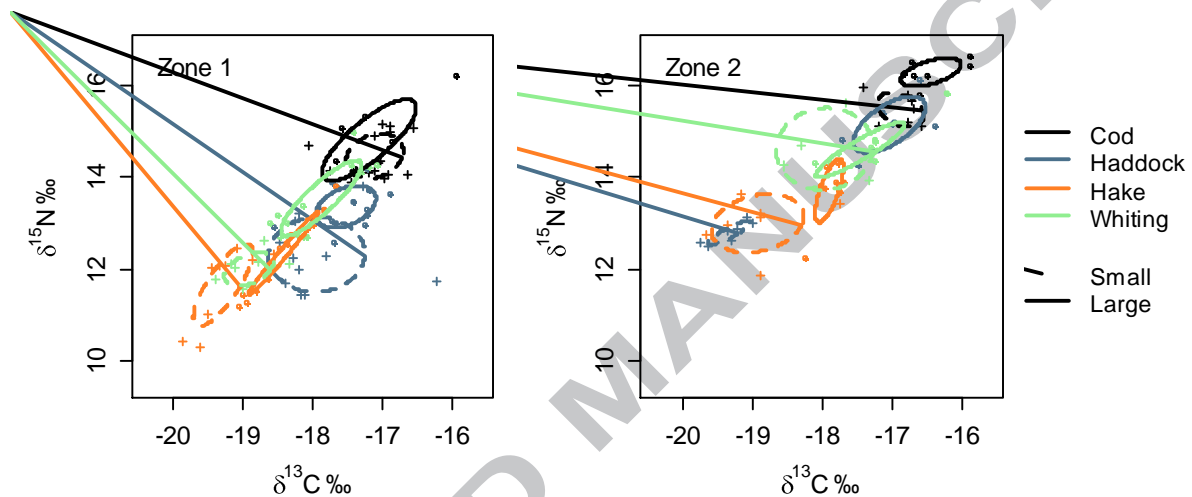


**Figure 6.** Sample-size-corrected standard ellipses (SEAc) from $\delta^{15}$N and $\delta^{13}$C values for each predator category by size class and zone (1 = shallow, 2 = deep). Crosses and points represent the raw isotopic data, while lines represent the SEAc.

### 3.3 Zone effect on isotopic compositions

ANOVA of the isotopic compositions of gadiforms showed that the factor 'zone' had a significant positive effect on mean $\delta^{15}$N compositions (p < 0.001), explaining ca. 22% of variance in the data, with higher $\delta^{15}$N compositions in zone 2. As raw isotopic data had been corrected with isotopic compositions of a primary benthic consumer (*P. maximus*) as a function of depth, this positive effect of zone on mean $\delta^{15}$N compositions reflects a larger

difference between the $\delta^{15}$N compositions of *P. maximus* and those of the four gadiforms in the zone 2 than in zone 1. The factor 'zone', however, had no significant effect on mean $\delta^{13}$C compositions (SM 6).

## 4    Discussion

Stable isotopes and gut contents both depict trophic niches, trophic pathways, interactions as well as potential ontogenetic and spatial changes. GCA has been used for many decades and provides concrete information on prey-predator interactions (Hyslop, 1980). It has been associated with sometime substituted by SIA, which is developing rapidly (Phillips et al., 2014). Most studies that use SIA, including the present study, are only based on $^{15}$N and $^{13}$C. These two tracers are sometimes insufficient to distinguish prey species as prey species can have the same isotopic composition. In this study, we emphasis on the gain of information enabled by the combination of this two complementary methods.

We characterised trophic niches of four large gadiforms to determine the species' links to the trophic pelagic and benthic pathways that structure the food web of this ecosystem. Cod, haddock, whiting and hake have different strategies and can even display ontogenetic changes from small to large individuals. As they are key species in the ecosystem, analysing their ecology in shallow vs. deep zones provides information on the trophic functioning of the Celtic Sea.

### 4.1    Cod and haddock: strong dependence on the benthic trophic pathway

Percentages of benthic prey of large cod estimated from GCA and SIA (Fig. 1, Table 3) showed that large cod depends mainly on the benthic pathway. They consumed a large percentage of crustaceans, such as brachyurans and anomurans. Du Buit (1995) concluded that cod was an opportunistic feeder with a diet evenly split between decapods and fish in the

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Celtic Sea. They preyed on demersal fish, which explains its higher $\delta^{15}$N composition and trophic position than that of haddock. Cod have also been observed feeding on benthic epifauna and infauna in the adjacent Irish Sea (Nagabushanam, 1965). Its wide prey spectrum, from benthic invertebrates to fish, might explain its wider isotopic niche than those of other gadiforms in the shallow zone. Its narrower isotopic niche in the deep zone (zone 2), indicates more piscivorous feeding and/or that fish are probably more easily digested and assimilated than benthic invertebrates. The lack of niche overlap (diet or SEAc) with other gadiforms suggests low interspecific competition for food in either zone.

Percentages of benthic prey for small cod were similar to those observed for large ones, indicating a main dependence on the benthic pathway. The trophic niche breadth of small cod was lower than that of large cod, which feed on a wider spectrum of prey, including fish. This difference might explain the narrower isotopic niche of small cod, at least in the shallow zone, because it preyed more on benthic invertebrates. Despite this difference between size classes, the high values of diet overlap in both zones and SEAc overlap in the shallow zone indicated close interactions between small and large cod and thus, likely no ontogenetic shift. In the deep zone, however, small individual's trophic position was clearly lower than the large one and showed no SEAc overlap, indicating a probable ontogenetic shift. Ramsvatn and Pedersen (2012) found a gradual change in cod's isotopic composition with size. Similarly, Du Buit (1995) found an increase in fish items in the diet of cod as cod size increased in the Celtic Sea, as did Hüssy et al. (2016) for the North Sea.

$\delta^{15}$N composition and trophic position of haddock in the food web were just below those of cod. GCA showed that haddock was strongly linked to the benthic pathway (80%), specialising on benthic echinoderms and molluscs. Some of its prey were primary consumers, which lowered haddock's trophic level below that of cod. Indeed, benthic echinoderms are

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common prey for several haddock populations in the Atlantic Ocean (Tam et al., 2016). Thus, its trophic niche is segregated from those of the other gadiforms studied. The percentage of fish in its diet, however, depends greatly on the ecosystem considered (e.g. North Sea, Barrents Sea, Rockall Bank) (Tam et al., 2016). Hence, haddock has pronounced trophic plasticity depending on the biotic environmental conditions. This could explain its overlap with large whiting and small cod in the deep zone, suggesting probable interspecific competition with them (Høines and Bergstad, 1999). The breadth of its trophic niche suggests that large haddock may have to feed on more numerous and diverse small benthic prey to obtain the same amount of energy as that obtained by preying on fewer but larger demersal or pelagic fish, which contain 2-3 times as much energy as echinoderms (Brawn et al. 1968). Although diverse, the prey could have similar isotopic compositions, resulting in a narrow isotopic niche.

Based on the breadth of trophic niches, small haddock have a less diverse diet than large one. Benthic prey, indicating a clear dependence on the benthic pathway, mainly composes it. Even if their trophic niche was narrower than that of large haddock, their overlap may indicate no clear ontogenetic shift. Small haddock had lower $\delta^{15}$N composition than large individuals, particularly in the deep zone, probably because they fed on prey from lower trophic levels. Isotopic niche breadth of small haddock was wide in the shallow zone, partly due to the wide range of $\delta^{13}$C compositions, indicating some pelagic prey. In the deep zone, small haddock had lower $\delta^{13}$C composition, indicating also that they fed on pelagic prey, which were not observed in the diet. Albert (1995) observed that small haddock fed also on pelagic prey in the North Sea off southwestern Norway. Ramsvatn and Pedersen (2012) also found a significant difference in $\delta^{13}$C and $\delta^{15}$N compositions between small and large haddock in the Norwegian Sea off northern Norway.

**4.2    From whiting to hake: increasing dependence on the pelagic trophic pathway**

Large whiting depended more on the pelagic than on the benthic pathway (Fig. 1, Table 3), with preferential feeding on pelagic and demersal fish as identified previously (Du Buit and Merlinat 1985; Pinnegar et al., 2003; Rault et al., 2017). The narrowness of its trophic and isotopic niches suggests that whiting's prey spectrum is permanently restricted to a few prey species regardless of the zone. As the small diet overlap indicates, whiting is well separated from more benthic invertebrate consumers such as cod and haddock but shows feeding interaction with large hake, which consumes more pelagic prey in both zones. This feeding interaction is nearly absent when considering the isotopic niche overlaps of whiting and hake, probably due to whiting consuming a larger percentage of demersal fish.

Small and large whiting had similar diets in the shallow zone, but not in the deep zone (albeit with only three guts analysed), where large whiting consumed fish and cephalopods, while small individuals consumed more crustaceans as observed by Hamerlynk and Hostens (1993) and Demain et al. (2011) in the North Sea. This pattern seems to be related to depth. In the Irish Sea, whiting diet was mainly benthic in nursery zones and pelagic in the open sea (Nagabhushanam 1965). In our study, whiting's low $\delta^{13}$C composition and diet proportion indicated the importance of pelagic prey in the shallow zone and the dependence of small whiting on the pelagic pathway. The trophic position of small whiting, clearly below that of large whiting in the shallow zone, increased to the same level as that of large whiting in the deep zone. Similarly, the SEAc overlap between small and large whiting absent in the shallow zone clearly occurred in the deep zone, where the large individuals' isotopic niche was much wider with a more pelagic feeding. Therefore, GCA and SIA appear to show ontogenetic shift from small to large individuals in the deep and shallow zone, respectively. This shift with

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increasing size from mainly invertivory to mainly piscivory was also observed in the Irish Sea (Nagabhushanam, 1965) and in the North Sea (Hislop et al., 1991).

Large hake depended on the pelagic pathway (Fig. 1, Table 3). In the Celtic Sea and other northern European waters, hake feeds mainly on *Trachurus trachurus, Micromesistius poutassou* and *Trisopterus* sp., with a particular preference for *M. poutassou* (Du Buit, 1996; Mahé et al., 2007). The hake's feeding preference changes in the Mediterranean Sea, where it targets *Sardina pilchardus* and *Engraulis encrasicolus* (Carpentieri et al., 2005). Hake is known to inhabit sea bottoms (Belloc, 1929) but feeds on fast moving and swimming pelagic species. In the Irish Sea, hake is a nekton and epibenthic feeder (Nagabushanam, 1965). Its trophic and isotopic niche breadth was the narrowest of the four gadiforms. Its prey spectrum seemed narrower than that of whiting. It also had the lowest $\delta^{15}$N composition and thus the lowest trophic position of the four gadiforms. As large hake are a top predator, mainly on the pelagic food web, its lower trophic level than that of the other three gadiforms could reflect a shorter pelagic trophic web than those of benthic feeders (e.g. cod or haddock).

Small hakes were mainly pelagic feeders preying on pelagic carideans, amphipods and clupeiforms, as observed in the Celtic Sea (Mahé et al., 2007), Portugal (Cabral and Murta, 2002) and in the Mediterranean Sea (Cartes et al., 2009). The diet of small and large hake overlapped only in the shallow zone, thus ontogenetic shift probably occurred in the deep zone. More than 60% of assimilated prey of small hake were pelagic invertebrates and small hake had a lower $\delta^{13}$C composition than large hake. For large hake in the Bay of Biscay, $\delta^{13}$C and $\delta^{15}$N compositions increase as size increased, indicating $\delta^{13}$C enrichment and increasing trophic level (Le Loc'h and Hily, 2005). As hake grew from ca. 16 cm to 40 cm, Mahé et al. (2007) in the Celtic Sea and Carpentieri et al. (2005) in the Mediterranean Sea observed a gradual change towards an entirely piscivorous diet. Thus, the shift in diet occurred with sexual maturity. This change occurred at the same time as ontogenetic development of mouth

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size and mobility (Mahé et al., 2007). Indeed, mouth size and fish length are positively correlated in many fish species (Karpouzi and Stergiou, 2003). The visual (Mas-Riera, 1991) and hearing (Lombarte and Popper, 1994) acuity of hake are known to increase with growth, which enables it to catch more mobile prey.

### 4.3 Contrasting habitats in the Celtic Sea influence the feeding ecology of gadiforms

Within the limitations of the data available, the overall architecture of the food web provided by SIA was similar for both zones for the four species. Nevertheless, some differences between the two zones were identified. The difference between $\delta^{15}N$ compositions of primary benthic consumers and the gadiforms was larger in the deep zone than in the shallow zone, suggesting a longer food chain in the deep zone. This could be due to differences between coastal and deeper zones in the main source of organic matter sustaining benthic food webs and/or to differences in the trophic level or feeding strategies of the organisms (Chouvelon et al., 2015). A scarcity of potential prey on the deep continental shelf led consumers to feed at a higher trophic level than in shallower water (Schaal et al., 2016). This could be related to a difference on the low trophic levels generated by the thermal stratification still present in the deep zone in autumn (Pingree, 1975) corresponding to the permanently cold deep layer ("cold pool") described in the north bay of Biscay. In this layer, at the difference of shallower zone, benthic trophic functioning is based on a microbial food web that included significant contribution from heterotrophic planktonic organisms and/or sediment organic matter (Chouvelon et al., 2015).

Like depth, substrate type is an important factor that influences the spatial distribution of benthic communities in the Celtic Sea (Ellis et al., 2013). As the map by Pinot (1974) and the study of Bouysse et al. (1979) suggest, the sediment becomes less muddy and/or coarser in the deep zone. Epibenthic communities of the "shelf edge" and "southern Celtic Sea"

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(corresponding to our deep zone) differed from the ones of the "outer shelf" (corresponding to our shallow zone - Ellis et al., 2013). One main feature was the greater dominance and diversity of crustaceans in the shallow zone than in the deep zone. Thus, the deep zone seems to have little to offer to fish that feed on benthic crustaceans. It is also uncertain whether it can provide enough specific prey, such as small crustaceans and especially benthic copepods (harpacticoids), which small haddock feed on more frequently than cod or whiting do once they settle (Demain et al., 2011). A decrease in the diet spectra of haddock and cod from shallow to deep zones could be related to changes in hydrological and sedimentary habitats, as well as to changes in the availability of benthic prey.

Finally, we observed a wider isotopic niche for small whiting and small hake in the deep zone, perhaps due to feeding on prey with variable isotopic composition. Pelagic copepods and euphausiids species, two main zooplanktonic prey, vary from one side of the thermocline to the other, and have varied diet of phytoplankton, particulate detritus and faecal material (Williams, 1985; Williams and Fragopoulu, 1985). It most likely results in variable isotopic compositions. Evidence suggests that juvenile whiting and hake move vertically when foraging at night (Bozzano et al., 2005), allowing them to prey on a variety of zooplankton populations that differ isotopically on each side of the thermocline. This may result in a wider isotopic niche in the deep zone than in the shallow zone, where the water column is not stratified during this period of the year.

# 5    Conclusion

Gadiforms present distinct feeding strategies in the Celtic Sea resulting in limited interspecific competition, despite some feeding interactions. Cod and haddock depend mainly on the benthic trophic pathway, but differ in favouring piscivory and invertivory, respectively. Hake

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was positioned mainly on the pelagic trophic pathway, while whiting seemed to feed on both pathways. This study resulted from an autumnal survey. The dependence on trophic pathways may varies with season as showed for cod (Trenkel et al., 2005) but seem to remain stable for whiting and hake (Patterson, 1985; Guichet, 1995; Cartes et al. 2009). Several ontogenetic shifts from invertivory to piscivory were observed in one or both of the zones studied (whiting in both zones, and hake and cod in the deep zone). Isotopic data showed an unexpected shift from the pelagic to the benthic trophic pathway between small and large haddock in the deep zone. As the benthic pathway turns over more slowly than the pelagic pathway, the use of these two pathways has a stabilizing effect on consumer populations. Thus, whiting populations in the Celtic Sea could be more stable than the other three species studied. However, literature on adjacent ecosystems, seasons or years illustrate that their trophic plasticity is closely related to their trophic opportunism for the more abundant prey in either trophic pathway. The shallow and deep zones displayed differences in trophic ecology related to benthic and pelagic prey characteristics, which we assumed were driven by differences in hydrological and sedimentary contexts. Improving understanding and modelling of ecosystem functioning requires specific studies on pelagic and benthic habitats (e.g. sedimentary characteristics) and communities (e.g. species composition, biomass and isotopic compositions), specially for the Celtic Sea. Based on our study, future trophic models of this ecosystem must consider separate size classes for top predators that experience ontogenetic diet shifts and distinguish habitats as a function of depth. Further research could benefit from using others biochemical tracers such as DNA-based tools or fatty acid analysis (Pethybridge et al., 2018) that can help to get a more comprehensive and complete picture of the trophic functioning of such ecosystems.

# 6 Acknowledgements

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## Supplementary material

**Supplementary Material 1.** Detailed description of the EVHOE survey and size distribution of each species obtained during EVHOE surveys (1998-2013).

The EVHOE survey is part of part of the International Bottom Trawl Survey founded by the European Data Collection Framework, which aim at assessing fish stock dynamics and recruitment of the main commercial fish species. The survey is performed every year since 1998 between October and December on board R/V Thalassa in the Bay of Biscay and Celtic se (43,50°N-52,00°N ; 01,00°O-11,00°O). The sampling gear is a GOV ("Grande Ouverture Verticale") demersal trawl with a cod-end of 20-mm stretched mesh, towed for 30 min at a speed of approximately 3.5 knots during the daytime. Three to five tows are performed every day following a stratified sampling scheme, where strata were defined according depth and geographical sub-region. All fish and mega fauna are identified and numbered to produce abundance indices. Biological parameters such as length and otoliths are collected on a subset of species.
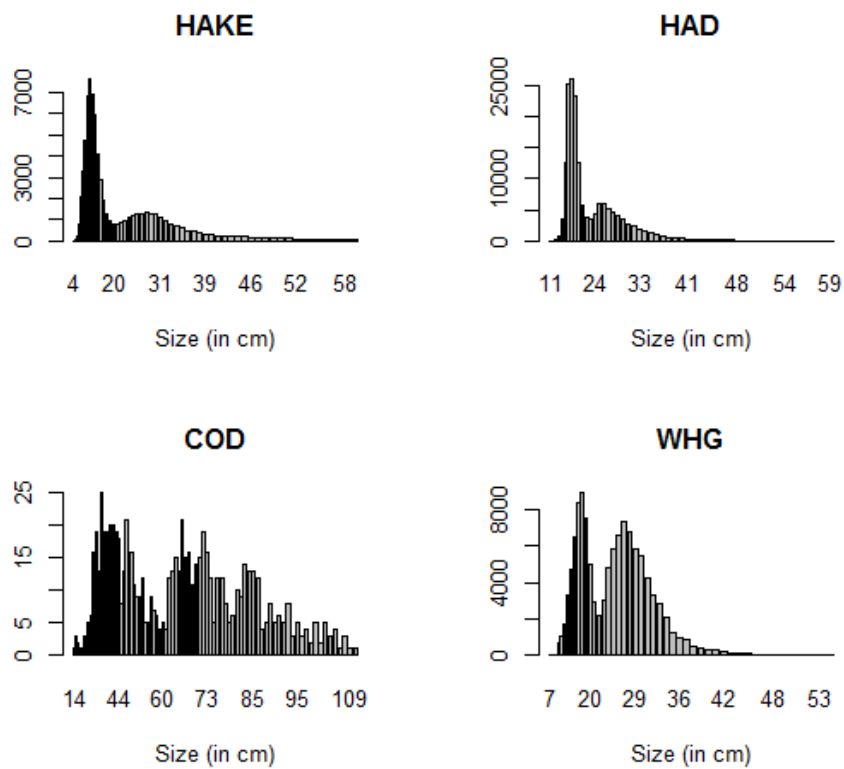
**Figure S1.** Size distribution of each species obtained during EVHOE surveys (1998-2013).

**Supplementary Material 2.** Sampling design and $\delta^{15}$N and $\delta^{13}$C composition of the four predator categories by zone (1 = shallow, 2 = deep) and size class (1 = small, 2 = large).

| Zone | Fish | Gut contents | | | Stable isotopes | | | |
|------|------|------|------|------|------|------|------|------|
| | | Size ranges (min – max in cm) | Number of samples dissected | Number samples containing prey | Size ranges (min – max in cm) | Number of samples | $\delta^{15}$N (‰) Mean ± SD | $\delta^{13}$C (‰) Mean ± SD |
| 1 | Cod 1 | 27-59 | 44 | 41 | 30-53 | 15 | 14.46 ± 0.47 | -17.11 ± 0.39 |
| | Cod 2 | 64-100 | 15 | 15 | 68-100 | 7 | 14.81 ± 0.81 | -17.19 ± 0.62 |
| | Haddock 1 | 15-21 | 30 | 30 | 15-21 | 11 | 12.32 ± 0.77 | -17.95 ± 0.66 |
| | Haddock 2 | 24-41 | 37 | 37 | 25-32 | 14 | 13.36 ± 0.44 | -17.53 ± 0.42 |
| | Whiting 1 | 13-21 | 33 | 21 | 15-18 | 8 | 12 ± 0.34 | -18.92 ± 0.33 |
| | Whiting 2 | 23-41 | 43 | 26 | 23-37 | 14 | 13.55 ± 0.79 | -17.88 ± 0.55 |
| | Hake 1 | 8-18 | 27 | 23 | 10-13 | 9 | 11.66 ± 0.84 | -19.29 ± 0.4 |
| | Hake 2 | 22-52 | 45 | 30 | 23-43 | 14 | 12.34 ± 0.86 | -18.42 ± 0.48 |
| 2 | Cod 1 | 39-58 | 28 | 28 | 39-50 | 7 | 15.47 ± 0.34 | -16.87 ± 0.31 |
| | Cod 2 | 63-104 | 20 | 20 | 67-104 | 7 | 16.29 ± 0.28 | -16.44 ± 0.4 |
| | Haddock 1 | 14-21 | 25 | 22 | 15-21 | 7 | 12.79 ± 0.23 | -19.33 ± 0.28 |
| | Haddock 2 | 27-45 | 30 | 30 | 27-45 | 7 | 15.15 ± 0.56 | -17.03 ± 0.47 |
| | Whiting 1 | 15-17 | 3 | 3 | 15-20 | 4 | 14.62 ± 0.73 | -17.96 ± 0.57 |
| | Whiting 2 | 26-42 | 33 | 19 | 24-42 | 9 | 14.6 ± 0.56 | -17.45 ± 0.6 |
| | Hake 1 | 7-21 | 37 | 23 | 9-21 | 7 | 13 ± 0.58 | -18.93 ± 0.6 |
| | Hake 2 | 22-121 | 59 | 27 | 27-69 | 8 | 13.72 ± 0.64 | -17.89 ± 0.19 |

**Supplementary Material 3.** Composition of the taxo-functional prey groups (UND.: undetermined) from gut contents.

| Group | Taxa |
|---|---|
| Polychaeta-carnivore-benthic | *Hyalinoecia bilineata*, *Aphrodita aculeata*, *Glycera* sp., Glyceridae, Nephtyidae, Nereididae |
| Polychaeta-deposivore-benthic | *Lagis koreni*, *Notomastus sp.*, *Ophelina* sp. |
| Polychaeta-UND.-benthic | Polychaeta |
| Amphipoda-deposivore-benthic | *Ampelisca brevicornis*, *Ampelisca spinipes*, *Hippomedon denticulatus*, *Maera othonis*, *Maerella tenuimana*, *Harpinia antennaria*, *Urothoe marina*, *Ampelisca* sp., Melitidae, |
| Amphipoda-carnivore-benthic | *Socarnes crenulatus*, *Monoculodes carinatus*, *Anonyx sarsi*, Oedicerotidae, Caprellidea |
| Amphipoda-UND.-UND. | Gammaridea, Amphipoda |
| Amphipoda-carnivore-pelagic | Hyperiidea |
| Cumacea-deposivore-benthic | Cumacea |
| Brachyura-carnivore-benthic | *Atelecyclus rotundatus*, Atelecyclidae, *Goneplax rhomboides*, *Macropodia tenuirostris*, *Ebalia nux*, *Ebalia tuberosa*, *Eurynome aspera*, *Liocarcinus depurator*, *Liocarcinus holsatus*, *Liocarcinus marmoreus*, *Liocarcinus pusillus*, *Liocarcinus vernalis*, *Macropipus tuberculatus*, *Liocarcinus sp.*, *Macropodia sp.*, *Inachus sp.*, *Ebalia sp.*, *Eurynome sp.*, Xanthidae, Portunoidea, Brachyura. |
| Caridea-carnivore-benthic | *Crangon allmanni*, *Crangon crangon*, *Philocheras bispinosus*, *Caridion gordoni*, *Chlorotocus crassicornis*, *Processa canaliculata*, *Processa edulis*, *Processa nouveli*, *Spirontocaris lilljeborgi*, *Processa sp.*, Crangonidae, Pandalidae, Processidae, Crangonoidea, Caridea |
| Anomura-carnivore-benthic | *Galathea dispersa*, *Galathea intermedia*, *Munida intermedia*, *Munida rugosa*, *Galathea sp.*, *Munida* sp., Galatheidae, Paguridae, Anomura |
| Astacidea-carnivore-benthic | *Nephrops norvegicus* |
| Caridea-carnivore-pelagic | *Pasiphaea sivado*, Pasiphaeidae |
| Eumalacostraca-UND.-UND. | Pleocymata, Eumalacostraca, Eucarida, Crustacea |
| Isopoda-UND.-benthic | Isopoda |
| Mysida-carnivore-benthic | Mysida |
| Copepoda-suspensivore-pelagic | Copepoda |
| Clupeiforms-carnivore-pelagic | *Clupea harengus*, *Engraulis encrasicolus*, Clupeiforme |
| Gadiforms-carnivore-pelagic | *Micromesistius poutassou*, *Trisopterus esmarkii* |
| Gadiforms-carnivore-UND. | *Trisopterus minutus*, *Trisopterus sp.*, *Merluccius merluccius*, Merlucciidae, Gadiforms |
| Actinopteri other-carnivore-demersal | *Argentina silus*, *Lepidorhombus whiffiagonis*, *Sebastes viviparous*, Pleuronectiformes |
| Perciforms-carnivore-demersal | *Callionymus lyra*, *Capros aper*, Gobiidae |
| Perciforms-carnivore-pelagic | *Trachurus trachurus*, Scombridae |
| Actinopteri other-carnivore-pelagic | *Maurolicus muelleri* |
| Actinopteri other-UND.-UND. | Actinopteri |
| Actinaria-carnivore-benthic | Actiniaria |
| Echninodermata other-UND.-benthic | Asteriidae, Holothuroidea, Echinozoa |
| Echinoidea-omnivore-benthic | *Gracilechinus acutus*, *Psammechinus miliaris*, *Echinocyamus pusillus*, *Echinocardium cordatum*, *Spatangus purpureus*, Spatangoida, Echinoidea |
| Ophiuridea-carnivore-benthic | *Ophiura affinis*, *Ophiura albida*, *Ophiura ophiura*, *Ophiura sp.*, Ophiurida, Ophiuroidea |
| Bivalvia-suspensivore-benthic | *Astarte sulcata*, *Palliolum tigerinum*, *Spisula elliptica*, *Gari costulata*, *Venus casina*, Pectinidae, Cardiidae |
| Bivalvia-deposivore-benthic | *Nucula nucleus*, *Abra prismatica*, *Abra sp.*, *Nucula sp.*, Nuculidae, Tellinidae |
| Bivalvia-UND.-benthic | Bivalvia |
| Cephalopoda-carnivore-demersal | *Illex coindetii, Rossia macrosoma, Sepiola atlantica, Alloteuthis sp.*, Loliginidae, |

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| | |
|---|---|
| | Cephalopoda |
| Gastropoda-carnivore-benthic | *Philine scabra, Scaphander lignarius, Euspira montagui, Euspira pulchella, Euspira sp.*, Epitoniidae, Naticidae, Thecosomata |
| Gastropoda-suspensivore-benthic | *Turritella communis* |
| Gastropoda-UND.-benthic | Gastropoda |
| Mollusca other-UND.-benthic | *Antalis entalis*, Dentaliidae, Polyplacophora |

**Supplementary Material 4a.** Occurrence (%) of prey groups (UND.: undetermined) in gut contents of the gadiform categories by size class (1 = small, 2 = large) and zone (1 = shallow, 2 = deep).

| Gadiform category | Zone 1 | | | | | | | | Zone 2 | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Cod 1 | Cod 2 | Haddock 1 | Haddock 2 | Whiting 1 | Whiting 2 | Hake 1 | Hake 2 | Cod 1 | Cod 2 | Haddock 1 | Haddock 2 | Whiting 1 | Whiting 2 | Hake 1 | Hake 2 |
| Polychaeta-carnivore-benthic | 4.9 | **13.3** | 3.3 | **13.5** | 0 | 3.8 | 0 | 0 | 0 | **5.0** | 0 | 0 | 0 | 0 | 0 | 0 |
| Polychaeta-deposivore-benthic | **7.3** | **6.7** | **33.3** | 8.1 | **19.0** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Polychaeta-UND.-benthic | **12.2** | 0 | **30** | **40.5** | **9.5** | **7.7** | 0 | 3.3 | 0 | 0 | **22.7** | **16.7** | 0 | 0 | 0 | 0 |
| Amphipoda-deposivore-benthic | 0 | 0 | **23.3** | **13.5** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **6.7** | 0 | 0 | 0 | 0 |
| Amphipoda-carnivore-benthic | 2.4 | 0 | 0 | **8.1** | 0 | 0 | 0 | 0 | 3.6 | 0 | 4.5 | 0 | 0 | 0 | 0 | 0 |
| Amphipoda-UND.-UND. | 2.4 | 0 | **40** | **70.3** | 4.8 | **7.7** | 0 | 0 | **7.1** | **5.0** | 22.7 | **43.3** | 0 | **15.8** | 0 | 0 |
| Amphipoda-carnivore-pelagic | 0 | 0 | 0 | 0 | 0 | 3.8 | 0 | 0 | 0 | **5.0** | 0 | 0 | 0 | **10.5** | **8.7** | 0 |
| Cumacea-deposivore-benthic | 0 | 0 | **10** | 0 | 0 | 0 | 4.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Brachyura-carnivore-benthic | **61.0** | **86.7** | 3.3 | **45.9** | 4.8 | 3.8 | 0 | 0 | **89.3** | **70** | 9.1 | **30** | 0 | 0 | 0 | 0 |
| Caridea-carnivore-benthic | **39.0** | **40** | **40** | **40.5** | **19.0** | **23.1** | **26.1** | **16.7** | **42.9** | **40** | **18.2** | 3.3 | **100** | **10.5** | 0 | **14.8** |
| Anomura-carnivore-benthic | **24.4** | **33.3** | 0 | **21.6** | 0 | 0 | 0 | 0 | **67.9** | **50** | 4.5 | 0 | 0 | 0 | 0 | 0 |
| Astacidea-carnivore-benthic | 4.9 | **6.7** | 0 | 0 | 0 | 0 | 0 | 0 | 3.6 | **15.0** | 0 | 0 | 0 | 0 | 0 | 0 |
| Caridea-carnivore-pelagic | 0 | 0 | 0 | 0 | 0 | 0 | **13.0** | **10** | 0 | 0 | 0 | 0 | 0 | 0 | 4.3 | 0 |
| Eumalacostraca-UND.-UND. | **48.8** | **13.3** | **20** | **40.5** | **47.6** | **38.5** | **26.1** | **6.7** | **60.7** | **55.0** | **13.6** | **10** | **66.7** | **26.3** | **73.9** | 0 |
| Isopoda-UND.-benthic | 0 | 0 | 0 | **21.6** | 0 | 0 | 0 | 0 | **21.4** | 0 | 4.5 | **26.7** | 0 | **5.3** | 0 | 0 |
| Mysida-carnivore-benthic | 0 | 0 | 0 | 0 | 4.8 | **7.7** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Copepoda-suspensivore-pelagic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **33.3** | **5.3** | 0 | 0 |
| Clupeiforms-carnivore-pelagic | 0 | 0 | 0 | 0 | 4.8 | 0 | **8.7** | 3.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gadiforms-carnivore-pelagic | **9.8** | **20** | 0 | 0 | 4.8 | **15.4** | 0 | **13.3** | 3.6 | **15.0** | 0 | 0 | 0 | **31.6** | 0 | **59.3** |
| Gadiforms-carnivore-UND. | 0 | **26.7** | 0 | 0 | 0 | 0 | 0 | **13.3** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Actinopteri other-carnivore-demersal | 2.4 | **20** | 0 | 0 | 0 | 0 | 0 | **6.7** | 3.6 | **5.0** | 0 | 0 | 0 | 0 | 0 | 0 |
| Perciforms-carnivore-demersal | 4.9 | **6.7** | 0 | 0 | 0 | 0 | **8.7** | 0 | 3.6 | **10** | 0 | 0 | 0 | 0 | **17.4** | 0 |
| Perciforms-carnivore-pelagic | 0 | **6.7** | 0 | 0 | 0 | 3.8 | **13.0** | **16.7** | 3.6 | **10** | 0 | 0 | 0 | 0 | 4.3 | **7.4** |
| Actinopteri other-carnivore-pelagic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Actinopteri other-UND.-UND. | **24.4** | **26.7** | 0 | 8.1 | **19.0** | 7.7 | **26.1** | **33.3** | **10.7** | **40** | 0 | 6.7 | **33.3** | **15.8** | **13.0** | **29.6** |
| Actinaria-carnivore-benthic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **6.7** | 0 | 0 | 0 | 0 |
| Echninodermata other-UND.-benthic | 0 | 0 | **10** | **5.4** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Echinoidea-omnivore-benthic | 4.9 | **13.3** | **90** | **94.6** | 0 | 0 | 0 | 0 | 0 | 0 | **9.1** | **43.3** | 0 | 0 | 0 | 0 |
| Ophiuridea-carnivore-benthic | 2.4 | 0 | **53.3** | **48.6** | 0 | 0 | 0 | 0 | 0 | **10** | **63.6** | **66.7** | 0 | 0 | 0 | 0 |
| Bivalvia-suspensivore-benthic | **12.2** | **13.3** | **10** | **45.9** | 0 | 0 | 0 | 3.3 | 0 | **5.0** | 0 | **13.3** | 0 | 0 | 0 | 0 |
| Bivalvia-deposivore-benthic | 2.4 | **6.7** | **76.7** | **40.5** | 0 | 0 | 0 | 0 | 3.6 | 0 | **13.6** | **13.3** | 0 | 0 | 0 | 0 |
| Bivalvia-UND.-benthic | **9.8** | **13.3** | 3.3 | 2.7 | 0 | 0 | 0 | 0 | 0 | **15.0** | 4.5 | **10** | 0 | 0 | 0 | 0 |

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| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cephalopoda-carnivore-demersal | 4.9 | **33.3** | 0 | 0 | 0 | **7.7** | 0 | 0 | **14.3** | **20** | 0 | 3.3 | 0 | **10.5** | 0 | 3.7 |
| Gastropoda-carnivore-benthic | **7.3** | **26.7** | **23.3** | **13.5** | 0 | 3.8 | 0 | 0 | 0 | 0 | 4.5 | 0 | 0 | 0 | 0 | 0 |
| Gastropoda-suspensivore-benthic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **5.0** | 0 | 0 | 0 | 0 | 0 | 0 |
| Gastropoda-UND.-benthic | **7.3** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **5.0** | 0 | 0 | 0 | 0 | 0 | 0 |
| Mollusca other-UND.-benthic | 2.4 | 0 | 0 | 2.7 | 0 | 0 | 0 | 0 | **35.7** | 0 | 4.5 | 0 | 0 | 0 | 0 | 0 |

**Supplementary Material 4b.** Relative abundance (%) of prey groups (UND.: undetermined) in gut contents of the gadiform categories by size class (1 = small, 2 = large) and zone (1 = shallow, 2 = deep).

| Gadiform category | Zone 1 | | | | | | | | Zone 2 | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Cod 1 | Cod 2 | Haddock 1 | Haddock 2 | Whiting 1 | Whiting 2 | Hake 1 | Hake 2 | Cod 1 | Cod 2 | Haddock 1 | Haddock 2 | Whiting 1 | Whiting 2 | Hake 1 | Hake 2 |
| Polychaeta-carnivore-benthic | 0.6 | 1.3 | 0.2 | 0.5 | 0 | 2.1 | 0 | 0 | 0 | 0.3 | 0 | 0 | 0 | 0 | 0 | 0 |
| Polychaeta-deposivore-benthic | 0.9 | 0.7 | 2.3 | 0.3 | **9.3** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Polychaeta-UND.-benthic | 1.9 | 0 | 1.7 | 1.6 | 4.7 | 4.3 | 0 | 2.1 | 0 | 0 | **8.5** | 3.2 | 0 | 0 | 0 | 0 |
| Amphipoda-deposivore-benthic | 0 | 0 | 4.4 | 0.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2.6 | 0 | 0 | 0 | 0 |
| Amphipoda-carnivore-benthic | 0.3 | 0 | 0 | 1.6 | 0 | 0 | 0 | 0 | 0.5 | 0 | 3.4 | 0 | 0 | 0 | 0 | 0 |
| Amphipoda-UND.-UND. | 0.3 | 0 | **5.9** | **6.6** | 2.3 | 4.3 | 0 | 0 | 0.5 | 0.3 | **16.9** | **14.8** | 0 | 9.7 | 0 | 0 |
| Amphipoda-carnivore-pelagic | 0 | 0 | 0 | 0 | 0 | 8.5 | 0 | 0 | 0 | 0.3 | 0 | 0 | 0 | 16.1 | 12.1 | 0 |
| Cumacea-deposivore-benthic | 0 | 0 | 0.6 | 0 | 0 | 0 | 2.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Brachyura-carnivore-benthic | **25.8** | **42.3** | 0.2 | 1.9 | 2.3 | 2.1 | 0 | 0 | **19.0** | **19.8** | 3.4 | **7.1** | 0 | 0 | 0 | 0 |
| Caridea-carnivore-benthic | **22.0** | **12.8** | 2.5 | 3.8 | **20.9** | **14.9** | **17.1** | **12.5** | **12.2** | **18.8** | 6.8 | 0.6 | **60** | 9.7 | 0 | **17.1** |
| Anomura-carnivore-benthic | **5.3** | **5.4** | 0 | 1.1 | 0 | 0 | 0 | 0 | **15.9** | **19.5** | 1.7 | 0 | 0 | 0 | 0 | 0 |
| Astacidea-carnivore-benthic | 1.6 | 2.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 3.4 | 0 | 0 | 0 | 0 | 0 | 0 |
| Caridea-carnivore-pelagic | 0 | 0 | 0 | 0 | 0 | 0 | **29.3** | **8.3** | 0 | 0 | 0 | 0 | 0 | 0 | 1.7 | 0 |
| Eumalacostraca-UND.-UND. | **27.4** | 4.0 | 1.3 | 2.6 | **34.9** | **36.2** | **19.5** | **8.3** | **43.1** | **17.8** | 5.1 | 1.9 | **13.3** | **16.1** | **70.7** | 0 |
| Isopoda-UND.-benthic | 0 | 0 | 0 | 1.6 | 0 | 0 | 0 | 0 | 1.4 | 0 | 1.7 | **9.7** | 0 | 3.2 | 0 | 0 |
| Mysida-carnivore-benthic | 0 | 0 | 0 | 0 | **11.6** | 4.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Copepoda-suspensivore-pelagic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **20** | 3.2 | 0 | 0 |
| Clupeiforms-carnivore-pelagic | 0 | 0 | 0 | 0 | 2.3 | 0 | 4.9 | 2.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gadiforms-carnivore-pelagic | 1.6 | 4.7 | 0 | 0 | 2.3 | **8.5** | 0 | **8.3** | 0.2 | 3.7 | 0 | 0 | 0 | **25.8** | 0 | **51.4** |
| Gadiforms-carnivore-UND. | 0 | 4.0 | 0 | 0 | 0 | 0 | 0 | **8.3** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Actinopteri other-carnivore-demersal | 0.3 | 2.0 | 0 | 0 | 0 | 0 | 0 | 4.2 | 0.2 | 0.3 | 0 | 0 | 0 | 0 | 0 | 0 |
| Perciforms-carnivore- | 0.6 | 2.0 | 0 | 0 | 0 | 0 | 4.9 | 0 | 0.6 | 3.7 | 0 | 0 | 0 | 0 | **8.6** | 0 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| demersal | | | | | | | | | | | | | | | | |
| Perciforms-carnivore-pelagic | 0 | 0.7 | 0 | 0 | 0 | 2.1 | **7.3** | **18.8** | 0.5 | 2.3 | 0 | 0 | 0 | 0 | 1.7 | **5.7** |
| Actinopteri other-carnivore-pelagic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Actinopteri other-UND.-UND. | 3.1 | **7.4** | 0 | 0.3 | **9.3** | **6.4** | **14.6** | **20.8** | 0.8 | 4.0 | 0 | 1.3 | **6.7** | **9.7** | 5.2 | **22.9** |
| Actinaria-carnivore-benthic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.3 | 0 | 0 | 0 | 0 |
| Echninodermata other-UND.-benthic | 0 | 0 | 0.6 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Echinoidea-omn-benthic | 0.9 | 1.3 | **40.1** | **66.3** | 0 | 0 | 0 | 0 | 0 | 0 | 3.4 | **21.3** | 0 | 0 | 0 | 0 |
| Ophiuridea-carnivore-benthic | 0.3 | 0 | 3.2 | 2.4 | 0 | 0 | 0 | 0 | 0 | 0.7 | **30.5** | **24.5** | 0 | 0 | 0 | 0 |
| Bivalvia-suspensivore-benthic | 1.9 | 1.3 | 0.6 | 3.5 | 0 | 0 | 0 | 2.1 | 0 | 1.0 | 0 | 3.9 | 0 | 0 | 0 | 0 |
| Bivalvia-deposivore-benthic | 0.3 | 0.7 | **34.7** | 3.9 | 0 | 0 | 0 | 0 | 0.2 | 0 | **13.6** | 4.5 | 0 | 0 | 0 | 0 |
| Bivalvia-UND.-benthic | 1.3 | 1.3 | 0.2 | 0.1 | 0 | 0 | 0 | 0 | 0 | 1.0 | 1.7 | 2.6 | 0 | 0 | 0 | 0 |
| Cephalopoda-carnivore-demersal | 0.6 | 3.4 | 0 | 0 | 0 | 4.3 | 0 | 0 | 0.6 | 2.3 | 0 | 0.6 | 0 | **6.5** | 0 | 2.9 |
| Gastropoda-carnivore-benthic | 1.3 | 2.7 | 1.5 | 0.8 | 0 | 2.1 | 0 | 0 | 0 | 0 | 1.7 | 0 | 0 | 0 | 0 | 0 |
| Gastropoda-suspensivore-benthic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gastropoda-UND.-benthic | 0.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mollusca other-UND.-benthic | 0.6 | 0 | 0 | 0.1 | 0 | 0 | 0 | 0 | 4.5 | 0 | 1.7 | 0 | 0 | 0 | 0 | 0 |

**Supplementary Material 5.** Cluster analysis (Euclidian distance) of isotopic compositions of prey by zone (1 = shallow, 2 = deep). Clusters were named based on the main taxonomic group (e.g. fish, invertebrate) in the cluster, its position in relation to the bottom (benthic/demersal/pelagic) and its position in the trophic web. Names of the four gadiform categories are identified by size class (1 = small, 2 = large).

| Zone 1 | | | Zone 2 | | |
|---|---|---|---|---|---|
| Cluster number | Name | Taxon | Cluster number | Name | Taxon |
| **1** | "Pelagic primary consumers" | Copepoda | **1** | « Pelagic primary consumers » | Copepoda, Hyperiidea, Caridea |
| **2** | "Benthic primary consumers" | *Pecten maximus* | **2** | « Benthic primary consumers » | *Pecten maximus* |
| **3** | « Pelagic fish » | *Scomber scombrus, Micromesistius poutassou,* **Merluccius merluccius 1**, *Capros aper, Sepiola* sp. | **3** | « Pelagic & demersal fish/ cephalopods » | *Trachurus trachurus, Scomber scombrus, Micromesistius poutassou, Sardina pilchardus,* **Melanogrammus aeglefinus 1, Merluccius merluccius 1**, *Sepiola* sp., *Todaropsis eblanae, Macropipus tuberculatus* |
| **4** | « Pelagic & demersal fish/ cephalopods » | *Engraulis encrasicolus, Trachurus trachurus, Clupea harengus, Sprattus sprattus, Lepidorhombus whiffiagonis, Glyptocephalus cynoglossus, Eutrigla gurnardus, Mullus surmuletus,* **Merluccius merluccius 2, Merlangius merlangus 1, Melanogrammus aeglefinus 1**, *Illex coindetii, Loligo forbesi, Rossia macrosoma, Todaropsis eblanae, Alloteuthis* sp. | | | |
| **5** | « Benthic invertebrates » | *Scaphender lignarus, Pagurus prideaux, Aequipecten opercularis, Pallium tigrinum, Hyalinoecia tubicola, Pasiphae sivado, Processa* sp., Hyperiidea | **4** | « Benthic fish & predatory invertebrates » | *Callionymus lyra, Aspitrigla cuculus, Capros aper, Gadiculus argenteus argenteus, Lepidorhombus whiffiagonis, Microstomus kitt, Pleuronectes platessa, Microchirus variegatus, Eledone cirrhosa, Scaphender lignarus, Crangon allmanni, Processa* sp., *Nephrops norvegicus, Pagurus prideaux, Cancer pagurus* |
| **6** | « Benthic fish & predatory invertebrates » | *Hippoglossoides platessoides, Limanda limanda, Microstomus kitt, Pleuronectes platessa, Solea solea, Microchirus variegatus, Callionymus lyra, Eledone cirrhosa, Crangon allmanni, Pontophilus spinosus, Dichelopandalus bonnieri, Macropipus tuberculatus, Nephrops norvegicus* | | | |

| | | | | |
|---|---|---|---|---|
| **7** | « Demersal predator fish » | *Dicentrarchus labrax,* **Melanogrammus aeglefinus 2**, *Aspitrigla cuculus, Molva molva,* **Merlangius merlangus 2, Gadus morhua 1, Gadus morhua 2**, *Trisopterus minutus, Argentina sphyraena, Phycis blennoides, Zeus faber, Scophthalmus maximus* | **5** | « Demersal predator fish 1 » | *Molva macrophthalma,* **Merlangius merlangus 1, Merlangius merlangus 2, Merluccius merluccius 2,** *Trisopterus minutus, Argentina sphyraena, Phycis blennoides, Solea solea, Illex coindetii, Loligo forbesi* |
| | | | **6** | « Demersal predator fish 2 » | **Gadus morhua 1, Gadus morhua 2, Melanogrammus aeglefinus 2,** *Molva molva, Zeux faber* |

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**Supplementary Material 6.** Results of ANOVAs for $\delta^{15}$N and $\delta^{13}$C compositions of gadiforms.

| | $\delta^{15}$N | | | | | $\delta^{13}$C | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Sum Sq | Df | F value | Pr(>F) | | Sum Sq | Df | F value | Pr(>F) | |
| (Intercept) | 15822.4 | 1 | 10469.3 | < 2.2e-16 | *** | 29701.6 | 1 | 35386.3 | < 2.2e-16 | *** |
| **zone** | 61.0 | 1 | 40.376 | **2.514e-09** | *** | 2.2 | 1 | 2.6 | 0.109 | |
| Residuals | 220.7 | 146 | | | | 122.5 | 146 | | | |

## Highlights

- Cod and haddock relied mainly on the benthic trophic pathway

- Hake relied mainly on the pelagic trophic pathway

- Whiting feed on both pathways

- Shifts with size for whiting in both zones and for hake and cod in the deepest one