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Investigating the trophic ecology of five species of Gadiformes in the Celtic Sea combining stable isotopes and gut contents

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Résumé étendu en français

Etude compare de l'écologie trophique de cinq espèces de Gadiformes en mer Celtique à partir de deux approches : les isotopes stables et les contenus digestifs

Contexte

Il est bien connu que dans un écosystème marin, les espèces présentes interagissent de plusieurs manières. On compte parmi ces multiples interactions celles d'ordre trophique : prédation inter et intra espèce ou encore compétition pour une même ressource alimentaire. De plus, pratiquement toutes les pêcheries sont multi spécifiques de par le fait que les engins utilisés peuvent difficilement ne cibler qu'une seule espèce. Partant de ces deux constats, la communauté scientifique recommande d'opter pour une vision écosystémique des systèmes marins et de baser les outils de gestion sur cette approche. Cette dernière reconnaît les interactions trophiques et techniques entre les espèces commerciales ou non, et permettant ainsi une meilleure gestion des ressources marines. La mise en place d'une telle gestion nécessite de collecter des informations locales et récentes sur la nature des interactions entre espèces et notamment : qui mange qui ou quoi ? Ces données servent alors à alimenter des modèles écosystémiques qui à leur tour permettent de diagnostiquer l'état d'un système et de prédire ses réactions face à des changements de gestion ou globaux. L'étude en amont de l'écologie trophique des espèces est donc essentielle à la robustesse de ces modèles.

L'écologie trophique est une science ancienne qui s'intéresse donc aux niches trophiques des espèces, aux facteurs qui les influencent (avec entre autre l'ontogénie et l'habitat) et aux interactions entre ces espèces. Historiquement, ces études étaient menées via l'analyse de contenus stomacaux et l'observation des comportements alimentaires. Aujourd'hui, les scientifiques ont également recours à l'analyse des isotopes stables, un outil qui permet de déterminer la position trophique d'un individu et les sources consommées par ce dernier.

La mer Celtique est située entre l'Irlande, la Bretagne et le Pays de Galles. C'est une zone d'importance majeure pour les pêcheries européennes. Le présent travail vise à étudier l'écologie trophique de cinq espèces de gadiformes (la morue, l'églefin, le merlan, le merlu et le merlan bleu), toutes exploitées en mer Celtique par des pêcheries mixtes.

Objectifs

L'objectif de cette étude est donc de déterminer les différences et les similarités dans la niche trophique de ces cinq espèces, qui partagent des caractères physiques du fait de leur appartenance à un même groupe taxonomique. On cherche alors à étudier la compétition entre ces espèces, mais aussi des potentielles différences ontogénétiques (via deux classes de taille) et spatiales (via deux zones – une profonde et une moins profonde) dans les niches trophiques

de ces espèces. Cette étude s'appuie sur une double approche méthodologique : analyse des contenus digestifs et analyse des signatures isotopiques.

Matériel et Méthodes

Pour réaliser cette analyse, deux types de données ont été utilisées : des contenus digestifs et des signatures isotopiques pour chacune des espèces dans les deux zones et pour les deux classes de taille. Tout d'abord, la composition des régimes alimentaires a été décrite pour chaque espèce, chaque classe de taille et chaque zone. En parallèle, les effets de l'espèce, de la taille et de la zone sur les signatures isotopiques ont été analysés à l'aide de régressions linéaires. Ensuite, les niches trophiques ont été décrites à l'aide de leur largeur estimée via la richesse taxonomique pour les contenus digestifs et via l'aire du nuage isotopique. Cette aire, représentant 40% de la variance des données, a été estimée avec une approche bayésienne afin de mesurer l'incertitude associée. Ensuite, les recouvrements de niches ont été abordés à partir d'un indice mesurant le taux de similarité entre les contenus digestifs et le pourcentage de recouvrement des aires de niches isotopiques. Enfin, des modèles de mélange bayésiens ont été construits afin d'estimer, à partir des signatures isotopiques du réseau trophique, les contributions relatives des différents groupes préalablement identifiés.

Résultats et discussion

Cette étude a confirmé le caractère généraliste de ces cinq espèces avec une importante diversité de proies à l'échelle des populations. Ces espèces se situent globalement en haut du réseau trophique de mer Celtique. Cependant, leurs niches trophiques présentent chacune des particularités les séparant les unes des autres. L'églefin consomme exclusivement des proies benthiques (échinodermes et mollusques). La morue se nourrit pour une grande partie sur des décapodes (crabes, anomoures ou langoustines) nécrophages et présente ainsi un très haut niveau trophique. La part de poissons dans son alimentation reste faible et contredit les études précédentes. Cependant, les contenus digestifs sont le reflet d'un aperçu instantané et peuvent biaiser notre vision. L'églefin et la morue sont les espèces avec la diversité de proies la plus élevée, cependant, leur niche isotopique ne reflète pas cette étendue. Le merlan possède une large niche trophique s'alimentant sur les voies pélagique et benthique, de crustacés et poissons faisant de lui un top-prédateur du système. Le merlu est une espèce presque exclusivement piscivore et présente un niveau trophique inférieur aux trois autres prédateurs. Son alimentation est en partie pélagique, ce qui impliquerait une alternance entre chasse dans la colonne d'eau et repos sur le fond. Enfin, le merlan bleu est un zooplanctonophage et constitue une proie pour la morue, le merlu et le merlan.

Des shifts ontogénétiques ont été mis en évidence pour le merlu et dans une moindre mesure, pour le merlan et l'églefin. Le merlu passe d'un régime composé de crustacés et de poissons à un régime largement dominé par les poissons, ceci est confirmé par les signatures isotopiques. Les signatures isotopiques de l'églefin montrent un changement brutal entre les deux classes de taille, cependant les contenus digestifs révèlent une relative constance du régime. La morue ne semble pas changer radicalement d'alimentation entre le stade juvénile et le stade adulte,

contrairement à des études plus anciennes ou dans des écosystèmes voisins. Ces changements de régime et de niveau trophique observés ici peuvent être reliés à l'arrivée de la maturité et donc à une demande énergétique supplémentaire, le tout étant permis par la modification des caractères biologiques tels que la largeur de la bouche ou la vitesse de nage.

Les contenus digestifs révèlent une plus grande diversité de proies dans la zone peu profonde, confirmé par une niche isotopique plus large à l'échelle de la communauté. Cependant, les ressources présentes, et donc disponibles dans ces zones, ne sont pas connues et ne permettent pas de conclure quant à une telle différence. De plus, il semblerait que le couplage entre les compartiments pélagique et benthique soit plus faible en zone profonde à cause d'une stratification plus forte des masses d'eau. Toutefois les contenus digestifs ne nous permettent pas de confirmer ce résultat, puisque ce dernier dépend également d'une correction appliquée aux données isotopiques.

Conclusion

Finalement, cette étude montre que ces cinq espèces très proches dans la classification possèdent des comportements et préférences alimentaires assez différents. Dans l'établissement de modèles, ces spécificités sont à intégrer, de même que le shift ontogénétique du merlu. Des indices tendent à montrer une différence de structure trophique entre les deux zones. Cependant, une enquête plus approfondie des ressources disponibles ou en analysant un plus grand nombre d'espèces serait appropriée. Une des perspectives majeures de ce travail est l'étude des variations saisonnières et annuelles des niches trophiques pour avoir une image plus complète et plus proche de la réalité.

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1 INTRODUCTION

1.1 Towards an ecosystem-based fisheries management approach

Fisheries management science and stock evaluations have been realized using a single-stock approach for decades. Exploited European species are generally evaluated independently of other populations and proposals of quotas by the International Council for the Exploration of the Sea (ICES) are stock-specific. Yet, virtually all fisheries are multi-specific as fishing gears cannot target a single species. In order to reach the goal of sustainability in fisheries, the scientific community recommends to switch to an ecosystem-based fishery management (Botsford et al., 1997; Pikitch et al., 2004). Ecosystem-based management is a holistic approach which acknowledges that exploited species interact with other species and the environment.

Technically, this approach requires the development of multi-species and ecosystemic models. Several scientific teams have developed such models. For example, *Multi-Species Virtual Population Analysis* MSVPA (Helgason and Gislason, 1979; Pope, 1979) or the more recent *Stochastic Multi-Species model* SMS (Lewy and Vinther, 2004) are operational models in terms of management. On the other hand, models such as *Ecopath-With-Ecosim* Ewe (Christensen and Pauly, 1992; Christensen and Walters, 2004; Polovina, 1984), *Object-oriented Simulator of Marine ecosystem Exploitation* OSMOSE (Shin and Cury, 2004) allow a better understanding of the functioning and the trophic interactions within a given ecosystem. They also are comprehensive tools to predict the future trophic functioning under different fishing scenarios. All these models acknowledge that species interact, notably predation and competition interactions. Then, models rely on trophic data and information in order to estimate predation between the species or trophic compartments. Fisheries management can be greatly improved by relying on an ecosystemic approach as trophic interactions are crucial in understanding resource dynamics. Pope (1991) explained that in the North Sea, the multi-species model revealed a fresh point of view of the trophic functioning and in terms of fishing impacts compared to single-species models. Indeed, the multi-species model resulted in a decrease of the overall yield when reducing the fishing mortality because of an increase of the predation. Additionally, ecosystemic models allow taking into consideration technical interactions between fleets: a given species could be captured by several fishing gears and so several fleets.

To get robust estimations, models should be based on local trophic data (Heymans et al., 2016). As this resource is scarce, they often use data from similar close supposed ecosystems. Therefore, one major drawback of these models is the need of accurate and local diet information (Moullec et al., 2017). Indeed, fish diet may vary according to numerous factors, including depth (Kopp et al., 2015) and local prey availability (Pinnegar et al., 2003). Thus, studying and understanding the trophic ecology of all the species within a given ecosystem, with a particular attention for commercial species, is essential in the implementation of an ecosystem approach to fisheries.

1.2 Influence of biotic and abiotic environment on the trophic niche

The concept of ecological niche has several definitions and modifications through time as some ecologists defined it as a reference to an environment and some others to species (Pulliam, 2000). This concept of niche is fundamental as it is the base of how species use resources (Bearhop et al., 2004). Hutchinson (1957) described the ecological niche as an 'n dimensional space' which axes represent environmental variables. Among these variables, the food resources constitute the trophic niche.

Trophic niche could vary according to several factors, such as ontogeny (especially the development stage or size), habitat, sex, season, geographical position, depth, local prey availability and, more generally, on various abiotic and biotic environmental factors.

The size is one of the most important attribute for an organism in terms of ecology as it determines the needs in energy (Werner and Gilliam, 1984). Ontogenetic shifts influence the biologic interactions with others species and so predation interactions. As fish grow, their morphometric attributes and physical abilities evolve such as increase in mouth dimension (Karpouzi and Stergiou, 2003; Keast and Webb, 1966) or improvement in swimming performance (Gibb et al., 2006). These ontogenetic changes allow fish to ingest a larger range of prey items larger or faster prey for example (Karpouzi and Stergiou, 2003; Pinnegar et al., 2003). Hence, diet composition and trophic position within the ecosystem of a given species is likely to evolve with ontogenesis. In an ecosystem modelling approach, such information on species could lead to make pertinent choices. For example, in Ewe models, it is possible to separate size classes in different trophic compartments (*i.e.* to create "stanzas").

Among fish, change of diet with the size is very common and is often correlated with a change of habitats (Werner and Gilliam, 1984). Indeed, habitats could have different prey offers according to environmental variables (depth, salinity, sediment type, etc.). In aquatic systems, depth is an important factor in regulation of the benthic-pelagic coupling. Depth is a regulator of the degree of interactions between the water column and the water close to the bottom (Schindler and Scheuerell, 2002). Indeed, with depth occurs the phenomenon of stratification of the water mass stratification. Stratification results from differences in the density of the water column caused mainly by temperature (and so solar radiation) and differential in salinity (Baustian et al., 2014). Benthic-pelagic coupling is the interactions between the two environments, mainly driven by organism movements, biogeochemical cycling and trophic interactions (Baustian et al., 2014). For example, Lassalle et al. (2011) concluded from a Ewe model set in the Bay of Biscay that demersal fish species, and in particular suprabenthivorous species, are an important link between the pelagic and the benthic layers as they feed on benthic organisms and are preyed by large pelagic consumers. In the Channel Sea, the benthic-pelagic coupling was investigated as a function of depth and it appeared that the coupling is stronger in shallow waters and weakens with depth increasing (Giraldo et al., 2017; Kopp et al., 2015). For example, with increasing depth, demersal species have a more and more benthic diet whereas pelagic predators concentrate their foraging effort on pelagic prey (Giraldo et al., 2017).

1.3 Studying feeding ecology

Feeding ecology of marine organisms is a key component to understand their roles and importance in the food web. Trophic studies allow answering to important ecological issues such as predation, position within the food web or competition.

Historically, investigating the trophic niche of marine species relied on gut contents analysis GCA (Hyslop, 1980). This approach is essential as it allows fine resolution in taxonomic prey identification. However, GCA has several limits. First, the prey identification is extremely time-consuming and requires good knowledge on consumed species. Then, it provides only a snapshot of the diet, showing the last ingested prey. Moreover, stomach content analysis is biased toward prey items which are not readily digested (Jackson et al., 1987).

Stable isotopes analysis SIA is a useful and contemporary tool for studying the trophic ecology and niche in estuarine and marine systems (Peterson and Fry, 1987; Layman et al., 2012; Fry 2007). Isotopes are chemical elements which occupy the same place in the periodic table as they have the same proton number but differ in neutron number. Isotopes can be natural or artificial and stable or unstable. In ecological and trophic studies, the most commonly used naturally occurring stable isotope ratios are carbon (^{13}C : ^{12}C expressed as $\delta^{13}\text{C}$ in ‰ units) and nitrogen (^{15}N : ^{14}N expressed as $\delta^{15}\text{N}$). SIA are based on two useful properties of isotopes: isotope fractionation and natural variations of their abundance. DeNiro and Epstein (1978) stated: “You are what you eat... plus a few per mil”. Fractionation represents the fact that $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are transformed from dietary sources to consumers. Consumer’s composition is generally higher than its prey; this is referred to enrichment (Phillips et al., 2014). This is due to phenomena of isotopes’ discrimination according to their atomic mass during assimilation and excretion. Indeed, early lab studied demonstrated that lighter isotopes are preferentially used by metabolism, resulting in enrichment in heavier isotopes (DeNiro and Epstein, 1978). The trophic enrichment factor (TEF or Δ) depends on multiple factors such as the given element, tissue and organism (Phillips, 2012). So far, it has been accepted by the scientific community that the average values for $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ range between 0 and 1‰ and between 3 and 4‰, respectively (DeNiro and Epstein, 1978; Minagawa and Wada, 1984; Peterson and Fry, 1987). Consequently $\delta^{15}\text{N}$ measurements serve as indicators of a consumer’s trophic level as a result of bioaccumulation of heavy isotopes ^{15}N (Post, 2002). Oppositely, carbon isotope ratios are rather stable through trophic levels and enable to trace back the origin of the carbon sources in a given environment (DeNiro and Epstein, 1978). For example, (France, 1995) showed that benthic sources were ^{13}C enriched compared to pelagic algae. As $\delta^{13}\text{C}$ present also natural gradient, they can be used to trace habitats and organisms migrations. Comparing $\delta^{13}\text{C}$ latitude variations and $\delta^{13}\text{C}$ measurement from fur seals’ whiskers, Kernaléguen et al. (2012) demonstrated a spatial foraging gradient between species and sex.

SIA is increasingly used thanks to the numerous benefits it provides. The development of effective technologic tool (mass spectrometry) allows us to obtain data with automated process and easy quantification of the proportions from each prey eaten by a predator. Stable isotopes are data with a time-integration of several weeks of the assimilated diet and time-integration depends on the tissue sampled (Phillips et al., 2014).

Newsome et al. (2007) provided a review on the use of stable isotopes in order to investigating the trophic niches. They discussed the concept of isotopic niche as “an area (in with isotopic values as coordinates”. The isotopic niche is often represented as bivariate plots with $\delta^{13}\text{C}$ values on the x-axis, $\delta^{15}\text{N}$ values on the y-axis and variance estimates.

However, SIA should be interpreted with caution as two predators with the same isotopic compositions have not necessarily the same prey and stable isotopes cannot allow identification of specific prey. Hence, guts and isotopic approaches are complementary in the study of diet and trophic niche as their association allows a better understanding of the

feeding ecology and processes. Many studies today combine the two methods, on various species and places as seals in Arctic (Dehn et al., 2007), snow crab *Chionoecetes opilio* (Divine et al., 2017) or elasmobranchs in the Gulf of Mexico (Churchill et al., 2015).

1.4 Study case: 5 species of Gadiformes in the Celtic Sea

The Celtic Sea (Divisions VIIe-k according to the classification of ICES) is a major fishing area in Europe, mainly exploited by Ireland, France, the United Kingdom, Spain and Belgium. This is a large continental shelf with a sandy bottom. Most of the area is shallower than 200 m and is bounded to the west by a steep and rocky slope. In order to better understand the trophic functioning of the Celtic sea and develop a multi-species model for fisheries management, the EATME program was started in 2014 by IFREMER with the mission of collecting data on local fish diet. Isotopic data and stomach contents of 10 commercial species were sampled. Among those species, five belong to the Gadiformes family: the Atlantic cod *Gadus morhua* (Linnaeus 1758), the haddock *Melanogrammus aeglefinus* (Linnaeus 1758), the whiting *Merlangius merlangus* (Linnaeus 1758), the European hake *Merluccius merluccius* (Linnaeus 1758) and the blue whiting *Micromesistius poutassou* (Risso 1827).

These five species present an important commercial interest. As an order of magnitude, in 2009 around 30,000 t were caught. The demersal fisheries catches were estimated to 120,000 tons in 2008 in both the Celtic Sea and the Bay of Biscay (Guénette and Gascuel, 2012). About three quarters of the catches can be attribute to the Celtic Sea only (Moullec, 2015). With a rough estimation, we estimated the demersal catches in the Celtic Sea around 90,000 t in 2009. Hence, the 5 species represented about one third of the demersal catches in tons in 2009. The other two third were composed by large crustaceans, monkfish and species of flatfish (Guénette and Gascuel, 2012).

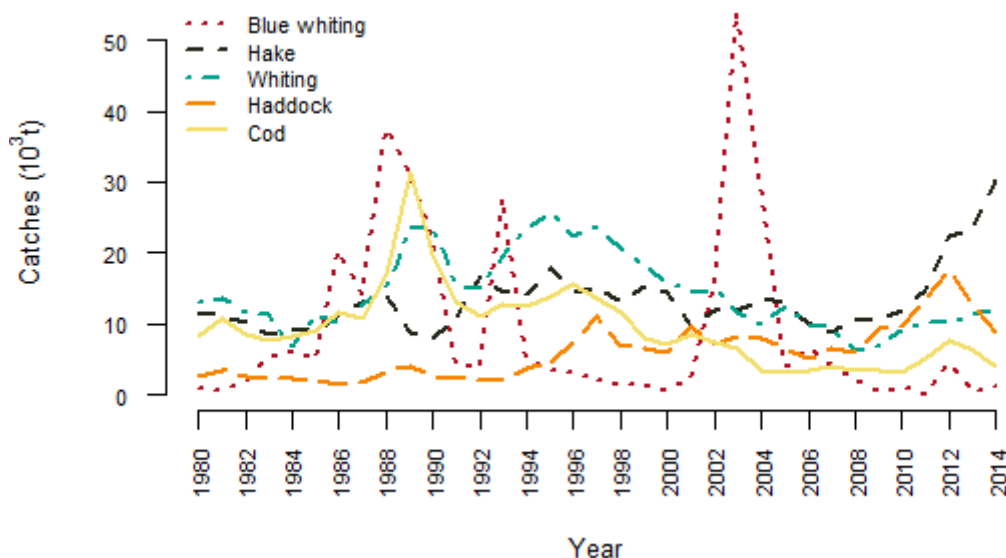


Figure 1: Catches of the five species studied in the Celtic Sea from 1980 to 2014 (Statland database <http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx> compiled by ICES).

Figure 1 shows the temporal evolution of the catches of the five species. *G. morhua* and *M. merlangus* have experienced high capture level in tons in the 1980's and the 1990's, with between 2 and 3 times today's level (Figure 1). In contrast, haddock's catches are increasing since the 1980's. Hake's catches raise recently due to an amelioration of the stock status with

a decrease of fishing mortality and an increase of the spawning biomass (ICES, 2016a). Blue whiting's catches are highly variable due to the variations of the recruitment¹ (ICES, 2016b). Fisheries in the Celtic Sea are highly mixed and are targeting a range of species with different gears. Among them, the mixed gadoid fishery (cod, haddock and whiting) using beam trawls is responsible of more than 75% of the landings for these species in the ICES areas 7.f and 7.g (ICES, 2016c). Hake is captured by gillnetters, beam trawlers and pelagic trawlers (ICES, 2016a). Blue whiting is caught by large pelagic trawlers (ICES, 2016b) and is the by-catch of demersal fisheries.

These five species of gadiformes present morphological similarities as they come from a common ancestor. They have an elongated body with three dorsal fins and one or two anal fins (Muus et al., 1998). Among these species *M. merluccius* belongs to the family Merlucciidae and the four others to the Gadidae family. Members of Gadidae are demersal or benthopelagic species inhabiting circumpolar and temperate waters. They usually have a chin barbel. Merlucciidae species do not have barbel but a large and terminal mouth with pointed teeth in most species. They are known as top predators present on continental shelf and upper slope (Froese and Pauly, 2017).

The **European hake** is a demersal species widely distributed in the European waters at depths from 30 to 1,000 meters (Belloc, 1929). Its mouth is filled with sharp teeth.



Source: European Commission - FISHERIES

The **Atlantic cod** is also a demersal species widely distributed in the Atlantic Ocean (off the European and American coasts). It is an omnivorous predator feeding on fish, molluscs, crustaceans, annelids (Muus et al., 1998).



Source: European Commission - FISHERIES

The **haddock** is a demersal species present in European and American waters, presents at depths from 10 to 200 meters. It has a downward directed, protrusible mouth which enables it to feed on benthic prey (Muus et al., 1998).



Source: fisheries.no the official Norwegian site

The **whiting** is a voracious predator present along the European coasts. Juveniles have a small barbell and adults don't (Muus et al., 1998).



Source: Iceland Quality Seafood

The **blue whiting** is a bathy-pelagic fish widely distributed throughout the North Atlantic at depths from 100 to 400 meters, near the continental slope (Muus et al., 1998; Sorbe, 1980).



Source: fisheries.no the official Norwegian site

It is therefore of interest to study the diversity of the trophic niches and the feeding strategies within one taxonomic group presenting common biological traits and being often fished simultaneously in the same areas. It is essential to gain insight on their trophic interactions notably the competition and the predation existing between these species in order to understand their population co-dynamics. To this end, emphasis will be laid on the comparison between species and size classes as we explained that size is a key factor in determining of diet. Additionally, as depth could create disparities in trophic niche, we will explore the effects of two areas in the Celtic Sea on the feeding ecology of these species.

¹ Recruitment : number of fish entering in the exploited part of a fish population every year

Global problematic

Are there differences in trophic ecology of these five commercial gadiformes with taking into account two areas (proxy of a depth gradient) and two size classes (proxy of ontogeny) in the highly exploited Celtic Sea?

This work will seek to answer to two aims:

- a. Investigate the trophic structure between the two zones for the 5 species and potential ontogenetic shifts in trophic niche and diet
- b. Compare the two methodologic approaches: are they complementary or do they suggest two different views of the trophic functioning?

Hypotheses

(1) Interspecific variability

Diets observed in this study will be compared to the scientific literature on one side and to the diet matrix of a Ewe model in the Celtic Sea recently published. Moullec et al. (2017) built an Ecopath models in order to understand trophic functioning of the Celtic Sea and the Bay of Biscay. They used a diet matrix as an input of the model and they obtained trophic level among outputs for the 2013 model. The diet matrix was based on a review of literature on diet in similar ecosystems. Thus, we assumed from these data that *G. morhua* and *M. merluccius* are top predators in this ecosystem, feeding mainly on small demersal fish, shrimps, sardine and carnivorous invertebrates for cod and boarfish, horse mackerel, mackerel, pouts, shrimps and zooplankton for hake. *M. aeglefinus* feeds mainly on surface suspension and deposit feeders, demersal fish and sub-surface deposit feeders invertebrates. *M. merlangus* is considered as an omnivorous species feeding on a numerous number of preys including many fish species, pelagic and benthic and macrozooplankton. Finally, *M. poutassou* is a planktivorous species preying on macro/mesozooplankton and shrimps.

(2) Size influence on diet and trophic niche

Larger individuals consume larger bodied prey although they keep consuming smaller ones (Pinnegar et al., 2003). Hence, we hypothesize that larger predators have wider trophic niches than small ones. Moreover, we hypothesize that larger predators feed on a higher proportion of fish as demonstrated for *M. merluccius* in the bay of Biscay and the Celtic Sea by Mahe et al. (2007) and for *G. morhua* in the Celtic Sea by Du Buit (1995); which could lead to higher trophic level for larger predators.

(3) Local feeding strategies

We hypothesize that the weakening of the coupling between the pelagic and the benthic compartments with a depth-gradient (Giraldo et al., 2017; Kopp et al., 2015) accentuates with a deeper depth-gradient. Benthic sources increases in demersal feeders' diet with increasing depth (*i.e.* from zone 1 to 2) whereas pelagic feeders feed on more important part of pelagic sources.

2 MATERIEL AND METHODS

2.1 Data collection

2.1.1 Sampling design: definition of size classes and areas

Fish were collected in November 2014 and 2015 during EVHOE campaigns (Evaluation des ressources *halieutiques* de l'ouest européen) on board R/V “Thalassa” in the Celtic Sea. Fishing operations were realized using a GOV (*Grande Ouverture Verticale*) 36/47 demersal trawl, towed for 30 min at a speed of approximately 3.5 knots. It has an opening of 20 m horizontally and 4 m vertically. The net is fitted with a 20 mm cod end liner stretched mesh. As part of the IBTS (International Bottom Trawl Survey) protocol, all fishing operations were carried out during daytime.

To evaluate the potential ontogenetic shifts within trophic niches, size classes were established. To optimize the sampling effort, size classes were chosen before collecting data according to the main modes observed in the size distribution of each species obtained during previous EVHOE campaigns 1998-2013. For *M. aeglefinus*, *M. merlangus*, *M. merluccius* and *G. morhua*, 2 modes were distinguishable, hence two size classes were considered. For *M. poutassou*, only one mode could be observed on the histogram, hence all individuals were considered from the same size class. The limits between the two size classes for each species are summarized in Table 1.

Table 1: Size classes of the five species based on size measures taken during EVHOE campaigns from 1998 to 2013.

Species	Size class 1 (cm)	Size class 2 (cm)
<i>G. morhua</i> (cod)	< 60	≥ 60
<i>M. aeglefinus</i> (haddock)	< 23	≥ 23
<i>M. merlangus</i> (whiting)	< 22	≥ 22
<i>M. merluccius</i> (hake)	< 21	≥ 21
<i>M. poutassou</i> (blue whiting)	No size class	

The size classes chosen were consistent with a well-known meaningful biological parameter: the length at maturity. *G. morhua* matures around 50-70 cm in the Celtic Sea (Brander, 2005). *M. aeglefinus* reaches maturity between 20 and 25 cm in the North Sea in 2005 (Wright et al., 2011). *M. merlangus* matures around 19-22 cm in the Irish Sea (Gerritsen et al., 2003). A study in the Bay of Biscay and the Galician coast showed that length at maturity for *M. merluccius* is between 40 and 50 cm (Domínguez-Petit et al., 2008).

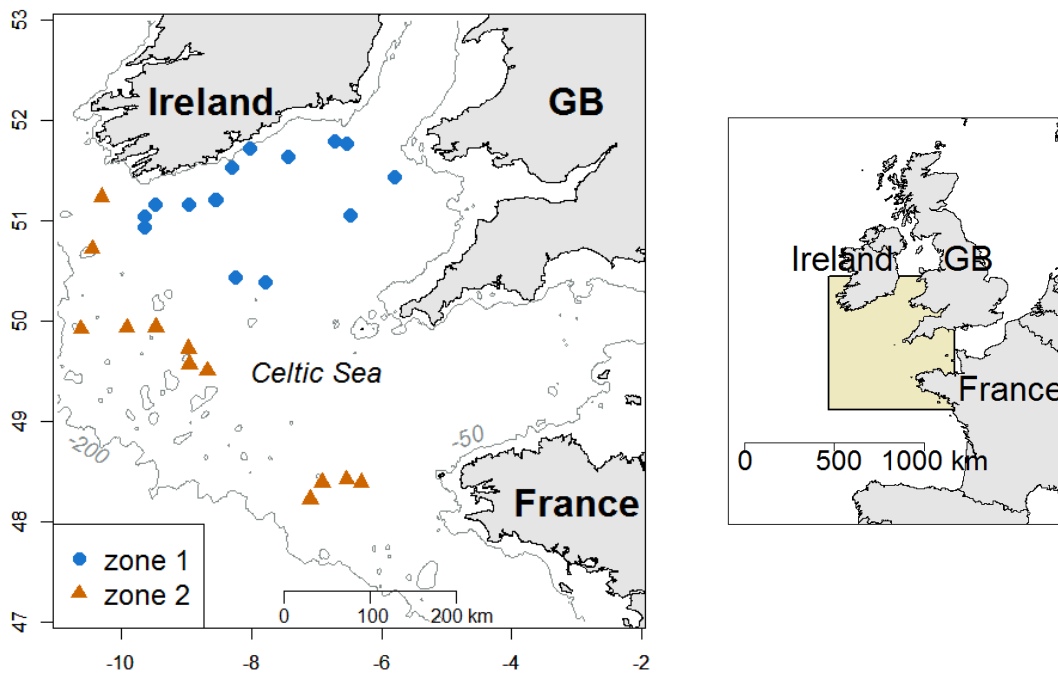


Figure 2 : Map of EVHOE stations where Gadiformes were sampled during the campaigns 2014 and 2015 for the EATME program.

In order to explore the potential effect of the geographical location on trophic niches and diet preferences, samples we collected in two zones. EVHOE survey design is based on strata based on depth and location (south, central, north part of the Celtic Sea and Bay of Biscay). To optimize the sampling effort, EVHOE strata were grouped by performing clustering analysis on annual abundances of species sampled during EVHOE since 1998. Two zones were identified, gathering different EVHOE stratas, based on homogeneous specific composition (Figure 2): a shallow inshore one from 71 m to 119 m deep in the central Celtic Sea (zone 1) and a deeper offshore one from 121 m to 158 m (zone 2) on the continental shelf.

The sampling design is summarized in Appendix I.

2.1.2 Gut contents

Sample preparation

On-board, all fishes were measured. Guts of the five species of Gadiformes were dissected and frozen for subsequent analyses back in the laboratory.

At the laboratory, guts were thawed and then emptied to retrieve prey that were in the stomach and the intestine. Gut contents were placed in a Petri dish and prey were identified at the most precise taxonomic level using a binocular stereoscopic magnifier Leica outfitted with a Leica IC80 HD camera (Figure 3). A total of 593 guts were analysed. Most of the guts were full for cod and haddock with vacuity rates between 0 and 12%. Blue whiting had an intermediate vacuity rate with 18 and 13% in zone 1 and 2 respectively. Hake and whiting had high vacuity rates between 13 and 54% (Appendix I). Only individuals with non-empty guts have been considered for further analysis.

The largest part of the laboratory work has been made by Margaux Denamiel and I realised the 5 % left during 3 weeks of this internship in Agrocampus laboratory with the help of Hervé Le Bris.

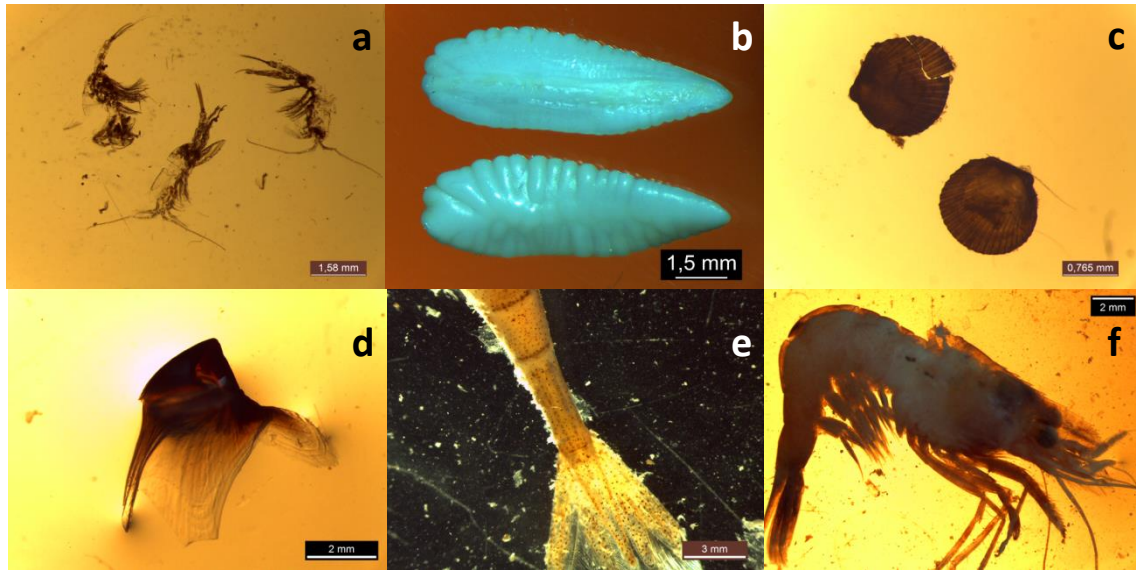


Figure 3: Photographs taken during gut contents identification a: pelagic Copepoda (scale = 1.6 mm), b: blue whiting *Micromesistius poutassou* otoliths (1.5 mm), c: bivalve *Cardiidae* (0.8 mm), d: cephalopod beak (2 mm), e: shrimp *Crangon allmanni* telson (3 mm), f: shrimp *Spirontocaris liljeborgii* (2 mm).

Prey grouping

Prey were grouped to ease interpretation of the results. The grouping was chosen according to 3 factors: the taxonomy (crustaceans, echinoderms...), the position in the water column (pelagic, demersal, and benthic) and the trophic guild (carnivore, omnivore, deposit feeder, suspension feeder...). Hence, from 156 different taxa identified we end up with 37 functional groups. The composition of each prey group is detailed in Appendix II. Main contributions to predators' diet were highlight using the frequency of occurrence and relative abundance (Appendices IV and V). Occurrence and abundance were chosen over bulk methods as they are more robust (Baker et al., 2014). Bulk methods appeared to have a high level of uncertainty because digested material cannot easily be separated.

2.1.3 Stable isotopes

Samples preparation

On-board, a sample of white dorsal muscle was dissected (Pinnegar and Polunin, 1999) and frozen on a subset of individuals. At the laboratory, samples were oven dried 60°C during 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 Analyzer. Stable isotopes values were converted into ratio (δ notation):

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

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

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

2.2 Data analyses

2.2.1 Gut contents analysis

Taxonomic richness

Precautions should be taken when comparing taxonomic richness from unbalanced sampling as predator categories containing different numbers of samples (Chao et al., 2014; Colwell et al., 2012). The taxonomic richness increases with the number of units sampled in a non-linear way. As our sampling was unbalanced (in zone 1, 41 guts were dissected for small cod and 15 for larger ones), rarefaction curves were estimated for each predator category in order to gain robustness in comparing taxonomic richness using the R package “INEXT” (Hsieh et al., 2016). Curves were constructed with unconditioned variance and predators were compared using an estimation of taxonomic richness for $n = 15$ (the lowest number of guts for a predator category – except small *M. merlangus* in zone 2).

Niche breadth

Pielou index, also known as the normalized Shannon’s index, was used to evaluate the trophic niche breadth. This index is equal to 0 when the considered predator is fully specialist and prey only upon one prey type and it is equal to 1 when the predator is generalist and consumes all possible prey types equally:

$$Pielou_i = -\frac{1}{\ln N} \sum_{k=1}^N p_{i,k} \ln p_{i,k}$$

where N is the total number of prey taxon groups and $p_{i,k}$ is the relative abundance of prey taxon k in the diet of predator species i .

Feeding strategy

Tokeshi (Tokeshi, 1991) is a graphical method to evaluate the feeding strategy of a predator by using the mean individual feeding diversity (DI) plotted against the population feeding diversity (DP) defined by the following formulas:

$$DI = -\frac{1}{N} \sum_{i,k} p_{i,k} \ln p_{i,k}$$

$$DP = -\sum_i p_i \ln p_i$$

where N is the total number of predators, $p_{i,k}$ the proportion of prey item i in the k th predator and p_i the proportion of prey i in the entire population.

Links between prey community and predators

To visualise differences in community structure and predator categories/prey groups relationships between the two areas, an unconstrained ordination method: the non-metric multi-dimensional scaling (MDS) was carried out (Kruskal, 1964). A selection of prey groups was preliminarily made to exclude scarce groups which could lead to difficulties in MDS interpretation (Manté et al., 2003). Prey groups were thus selected for these MDS analyses when the frequency of occurrence was superior to 5% for at least one predator category. In order to perform this analysis, we formed a matrix of dissimilarities using the Bray-Curtis

dissimilarity calculation. Non-metric MDS is a rank-based approach i.e. it is based on rank orders instead of original distance. The quality of the representation was validated with a stress under 0.3. Stress relates pairwise distances between objects in the reduced ordination space to their dissimilarities in the “real world”, the complete multidimensional space. nMDS is an iterative process which optimizes the stress by minimizing it.

Diet overlaps

The Renkonen similarity index (Renkonen, 1938) also known as the Schoener overlap index (Schoener, 1970) was used to assess niche overlaps between predators by constructing a similarity matrix. The similarity between the predators i and j was given by:

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

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 feeding overlap), to 1 (same distribution of prey).

2.2.2 Stable isotopes analysis

Baseline correction

Isotopic values of the baseline of a trophic web might vary along environmental gradients such as the inshore-offshore gradient or depth gradient (Chouvelon et al., 2012; Nerot et al., 2012; Schaal et al., 2016). In the study of higher consumers and comparison between different areas, there is a need to spatially adjust their isotopic values. Indeed, without baseline correction, it is impossible to distinguish variations in the isotopes ratios due to spatial variations of the base of the food chain or due to changes in the food web structure. Hence, an artificial rescaling allowed us to compare trophic structure between areas. Ideally, this correction should be done using the primary producers of the ecosystem as the base, but they have highly variable isotopes ratios (Jennings and Warr, 2003). Thus, Cabana and Rasmussen (1996) suggested to use primary consumers as bivalves as they have more stable signatures and are supposed to mainly feed on primary producers. Suspension feeding bivalves, *Pecten maximus* were chosen as the trophic baseline for this study.

Hence, raw isotopic data for both nitrogen and carbon were corrected with baseline isotopic values. We decided to correct the raw data according to the depth of the collection as it expressed spatial heterogeneity. First, a linear Gaussian regression was realised to investigate the relationship between the isotopic values of *P. maximus* and the depth (Appendix III):

$$\delta X_{P.maximus}(depth, i) = \alpha * depth + \beta + \varepsilon_i \sim N(0, \sigma^2)$$

After checking graphically the residuals (normality and homoscedasticity) in order to validate the model's hypothesis, we used the coefficients of the regression in order to correct the raw data of each consumer sample by subtracting the predicted baseline at the sampling location (considering only depth) and by adding the mean of the baseline isotopic values for the given element in the whole zone:

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

Isotopic values or ratios hereafter will refer to corrected values.

Trophic level (TL)

Trophic level was estimated using Post equation (Post, 2002):

$$TL_i = \frac{\delta^{15}N_i - \delta^{15}N_{base}}{3.4} + 2$$

where $\delta^{15}N_i$ is the corrected $\delta^{15}N$ value for the individual i and $\delta^{15}N_{base}$ is the mean of all *P. maximus* $\delta^{15}N$ values. TL for a predator category was then calculated by averaging the individual TLs.

Stable isotopes compositions

The effects of the categorical variables: predator category (9 levels, combination of species and size classes), zone (2 levels) and their two-way interactions on isotopic compositions ($\delta^{13}C$ and then $\delta^{15}N$ ratios) were assessed through Linear Model with an identity link. A preliminary variable selection was performed, using an ANOVA procedure based on Fisher's tests on $\delta^{13}C$ values and then on $\delta^{15}N$ values:

$$(M_N) \quad \delta^{15}N_{p,z,i} = \mu + \alpha_p + \beta_z + \gamma_{p,z} + \varepsilon_i \sim N(0, \sigma^2)$$

$$(M_C) \quad \delta^{13}C_{p,z,i} = \mu' + \alpha'_p + \beta'_z + \gamma'_{p,z} + \varepsilon_i \sim N(0, \sigma'^2)$$

where i is the individual, p the predator category and z the zone. Models' hypotheses, normality and variance homogeneity of the residuals, were validated graphically (Appendix VIII). Tukey post hoc tests were performed to evaluate potential shifts between size classes.

Isotopic niche

Isotopic niche is defined by Newsome et al. (2007) as an area in the isotopic space where each axe is an element with isotopic values coordinates (δX). To visualize isotopic niches, sample size-corrected standard ellipse area (SEAc) were plotted on bi-plots $\delta^{15}N/\delta^{13}C$ (Jackson et al., 2011). These ellipses represent the trophic niche of a group by integrating 40% of the sample variance. To avoid a problem of underestimation of the SEA when the sample size is inferior to 30, a corrective factor is applied as following:

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

The correction approaches 1 when n tends to infinity, which is a desired property here.

For the purpose of comparing isotopic niches between species and size classes, a Bayesian approach was set up to estimate the posterior distribution of the standard ellipse area (SEAb) and then uncertainty was incorporated to SEAc. This method is based on Markov-Chain Monte Carlo (MCMC) draws in the posterior distribution combining the priors and the likelihoods with the followings parameters: 20000 iterations, a discard of the 1000 first values, a run with 2 chains and a thin posterior of 10; and the following priors: an Inverse Wishart prior on the covariance matrix $\begin{pmatrix} 2 & 0 \\ 0 & 2 \end{pmatrix}$ and a vague normal prior on the means (10^3). The likelihood is a multivariate normal distribution: $Y_i \sim MVN([\mu_x, \mu_y], \Sigma)$, with μ_x and μ_y the means and Σ , the covariance matrix. This procedure was realised using R package 'SIBER' (Jackson et al., 2011).

Isotopic overlaps

Niches overlaps were estimated and expressed as the percentage of the ellipse area (SEAc) of the niche 1 overlapped by the niche 2 using the R package 'SIAR' (Parnell et al., 2010).

Mixing model and assimilated prey proportions estimation

Mixing models allow estimating relative contributions of each prey or group of prey from isotopic signatures of the prey (the sources) and the predator (the consumer) and the TEF between the consumer and its sources. However, the sources of uncertainty are numerous with this type of analysis: uncertainty on the data, on the TEF, on the concentration of carbon and nitrogen within an individual, etc. (Phillips et al., 2014). Hence, a Bayesian approach is well suited to deal with the different layers of uncertainty (Parnell et al., 2010) as this approach allows estimation of probability distribution of multiple source contributions to a mixture. When the isotopic signatures of different sources are too close *i.e.* sources overlap in the isotopic space, mixing model can encounter difficulties in estimating their relative contributions (Phillips et al., 2005).

The EATME program sampled other species than the five gadiformes analysed in this study: many fish species, some large crustaceans and some other invertebrates. In order to reduce the number of potential sources in the mixing model, clustering was performed on each zone community using a Hierarchical ascendant clustering (HAC). The result gives a simplified picture of the species community within each zone. Additionally, it eases the comparison between areas and creates distinct sources for the mixing model. Euclidean distances and Ward method (which minimising the total within-cluster variance) were used. The number of clusters was chosen according to inertia criterion and also to ecological interpretation.

Using clusters established beforehand as sources and predator category as consumer, Bayesian mixing models SIAR (Parnell et al., 2010) were built for each predator categories. Sources' contributions were not estimated for haddock as we considered that available prey from EVHOE did not reflect its diet. Moreover, the same decision was made for small hake in zone 2 as applying a positive enrichment on carbon led to no potential sources (Figure 12).

TEFs were chosen as the more realistic choice according to the suggestions made by Hussey et al., (2014) and Zanden and Rasmussen (2001). TEFs are decreasing as the trophic level increase (Hussey et al., 2014) and Zanden and Rasmussen (2001) gave an order of magnitude for marine fractionation factors. Hence, TEFs between resources and the consumers were chosen at 0.5 ± 1 for $\delta^{13}\text{C}$, 3 ± 1 for $\delta^{15}\text{N}$ of primary consumers clusters and 2 ± 1 for $\delta^{15}\text{N}$ of other clusters.

In order to reduce the number of possible sources, prey clusters were selected prior to each mixing models according to the predator considered. The selection was made according to biological consideration (for example *G. morhua* does not feed on pelagic primary consumer) and mixing model constraints (consumer ratio is supposed to be surrounded by the sources adjusted by TEFs). All mixing models were conducted using the R package 'SIAR' (Parnell et al., 2010) with no a priori on contributions, 500000 iterations, a burning of 50000 and a thinby of 15.

All analyses were conducted using the software R (R Core Team, 2015) and significant threshold was taken at $p \leq 0.05$.

3 RESULTS

3.1 Gut contents analyses

Among the 1349 prey found in the 466 non-empty guts dissected, 156 different taxa were identified. The digestive state of prey influenced the final taxonomic level identified. Approximately 50% of the prey were identified at a family level and 35% at a species level.

3.1.1 Diet description

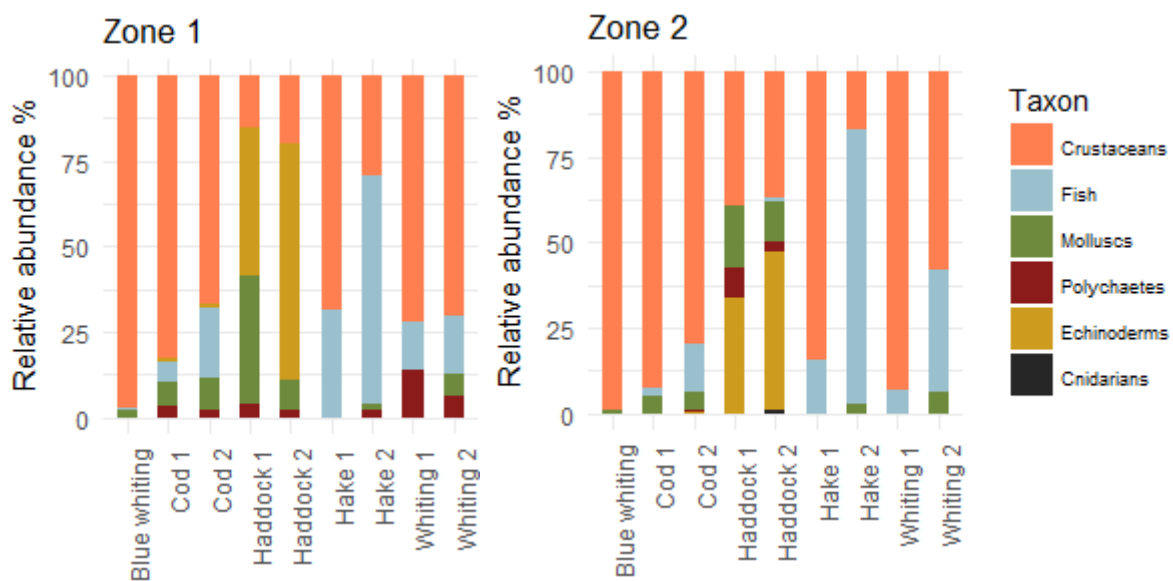


Figure 4: Relative abundance of prey phyla in the digestive content of each predator categories for both zones.

Different feeding preferences between the five species were identified (Figure 4). *G. morhua* mainly fed on benthic crustaceans (brachyurans, anomurans and carideans) and to a lesser extent on fish and molluscs (Figure 4, Appendices IV and V). Cod was the only species feeding on Norway lobster *Nephrops norvegicus*, especially second size class. Large individuals had a larger proportion of fish (*Trisopterus esmarkii*, *Callionymus lyra*, Gobiidae and other Gadiformes) than smaller ones in their diet in both zones. Anomurans (*Galathea* sp. and *Munida* sp.) had higher occurrences and relative abundances in the diet in zone 2 than in zone 1 with *Munida rugosa* an important prey in occurrence and abundance. Cod foraged on carnivore and deposit feeder polychaetes in zone 1.

M. aeglefinus largely fed on benthic prey. It was also the only species feeding on echinoderms, particularly sea urchins (*Echinocyamus pusillus*) in zone 1 and ophiuroids in zone 2 (Figure 4, Appendices IV and V). Large and small individuals had similar diet, with a sensitive larger proportion of molluscs for large haddock than for small one. Haddock also consumed molluscs (as deposit feeder bivalves, essentially *Abra* spp.), crustaceans (mainly amphipods in zone 2) and to a lesser extend polychaetes with high occurrence frequencies in zone 1 with 40.5% of the small haddock's guts containing "benthic polychaetes" (Appendix IV). It can be noted that the proportion of echinoderms and molluscs decreased from zone 1 to 2 in favour of crustaceans (Figure 4).

M. merlangus had a diversified diet, feeding both on pelagic and benthic prey, both on fish and crustaceans (Figure 4). In zone 1, it mainly fed on crustaceans and especially carideans as *Crangon allmanni*, amphipods and mysids (Appendices IV and V). A minor part of its diet was composed by fish and polychaetes, such as *Lagis koreni*. There were few differences between size classes, except that large whiting included cephalopods like *Rossia macrosoma* or *Illex coindetii* in their diet. In zone 2, whiting did not consume polychaetes. An increase of the part of the fish in the diet was observed from small to large individuals, with a particular affinity for gadiforms (*Micromesistius poutassou*, *Trachurus trachurus* or *Trisopterus esmarkii*).

M. merluccius was the most piscivorous species. It fed on fish and crustaceans (Figure 4). There was a shift between small and large hakes regarding fish proportion on their diets. Fish represented 66% and 80% of the large hake diet respectively in zone 1 and 2 against 31% and 15% for small hake (Appendix V). Fish prey of large hake was more diversified in zone 1 (pelagic perciforms, gadiforms and clupeiforms) whereas it fed mainly on pelagic gadiforms in zone 2 (Appendices IV and V). Small hake fed mainly on crustaceans as pelagic and benthic carideans (*Pasiphaea sivado* and *Crangon allmanni*) in zone 1 and eumalacostraca and pelagic amphipods (Hyperiiidea) in zone 2.

M. poutassou fed on pelagic crustaceans. No differences are observed in the relative proportion of prey type between the two areas however, its main prey were pelagic carideans (*Pasiphaea sivado*) and amphipods (Hyperiiidea) in zone 1 and copepods in zone 2 (Figure 4, Appendices IV and V).

Finally, as a large part of the prey items was identified at an imprecise taxonomic level (as order or class), it was not possible to conclude about the proportions of pelagic and benthic prey in the predators' diet (Appendix VII).

3.1.2 Taxonomic prey richness and feeding strategy

Rarefaction curves showed that the sampling of all predator categories didn't reach an asymptote (Appendix VI). To access the absolute prey diversity, sampling should be greater. However, using rarefaction curves, it was possible to compare relative taxonomic richness of prey between predator categories.

Taxonomic richness was the highest for cod and haddock with estimated richness (for $n = 15$) between 14.8 and 36.8 taxa respectively whereas other predators' estimations were between 5 and 10 taxa (Figure 5a, Table 2). These species had also the highest number of different taxa per fish and number of prey per fish, meaning that they had numerous and diverse prey in their guts. Piélou's index was 0.49 and 0.59 for both size classes of haddock in zone 1 (Table 2). Thus, despite a high taxonomic richness reflecting an opportunist feeding strategy, haddock in zone 1 had preference for some prey items (as *E. pusillus*). Whiting and hake had close feeding strategies. They had a low number of prey per fish (means between 1.6 and 2.5 preys per individuals) as well as a low diversity of prey (means between 1.1 and 2.3 different taxa per individuals; Table 2). They didn't show a marked preference for a prey type as they had high Piélou's index values (except for hake 1 in zone 2: its index is low because of a large part of its diet in the "Eumalacostraca" prey category). Finally, blue whiting had a great number of prey per individual with a mean of 8.4 preys in zone 1 and 6.7 in zone 2 and a low diversity of taxa. Its Piélou's index was relatively low which confirmed a strong preference for some prey items (Table 2).

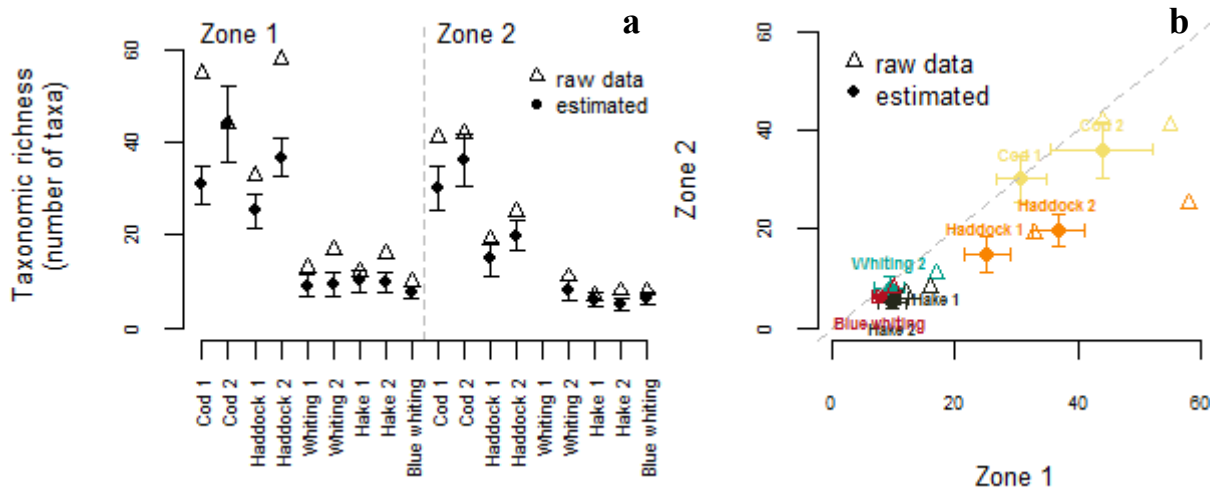


Figure 5: Taxonomic richness (a) comparison between raw taxonomic richness and estimated taxonomic richness from the rarefaction curve with $n = 15$ (lowest common denominator) for each predator category (b) comparison between zones; triangles represent raw counts of richness and error bars are the estimated richness.

The global taxonomic richness appeared to be higher in zone 1 since 133 taxa were identified in this zone compared to 83 in zone 2. It was particularly marked for both class sizes of haddock (Figure 5 b) with estimated taxonomic richness of 25.2 and 36.8 for small and large fish in zone 1 and 14.8 and 19.8 in zone 2 respectively (Table 2). However, this pattern was not confirmed at an individual scale as there was no clear difference between zones regarding the mean number of different taxa per fish (Table 2).

Table 2: Characteristics on feeding strategy: taxonomic richness, estimated taxonomic richness (for $n=15$), number of different taxa per fish and number of preys per fish for each predator category.

Taxonomic richness was not estimated for Whiting 1 in zone 2 as there were only 3 guts dissected.

Zone	Predator	Taxonomic richness	Estimated taxonomic richness (for $n=15$)		Number of different taxa per fish		Number of prey per fish		Pielou index
			mean	min-max	mean \pm sd	min-max	mean \pm sd	min-max	
1	Cod 1	55	30.8	(27.1-34.6)	3.6 \pm 2.3	(1-11)	7.8 \pm 8.7	(1-44)	0.65
	Cod 2	44	44	(35.9-52.1)	5.1 \pm 2.2	(2-9)	9.9 \pm 5.7	(2-23)	0.73
	Haddock 1	33	25.2	(21-29.3)	5 \pm 1.6	(2-9)	17.5 \pm 12.4	(2-57)	0.59
	Haddock 2	58	36.8	(32.8-40.8)	6.5 \pm 2.6	(2-12)	28.7 \pm 22.4	(2-100)	0.49
	Whiting 1	13	9	(6.5-11.6)	1.4 \pm 0.6	(1-3)	2 \pm 1.4	(1-7)	0.82
	Whiting 2	17	9.4	(6.9-11.9)	1.3 \pm 0.6	(1-3)	1.8 \pm 1.5	(1-7)	0.82
	Hake 1	12	10	(7.5-12.5)	1.3 \pm 0.6	(1-3)	1.8 \pm 1.4	(1-7)	0.88
	Hake 2	16	9.8	(7.4-12.3)	1.3 \pm 0.6	(1-3)	1.6 \pm 1	(1-5)	0.9
	Blue whiting	10	7.8	(6.4-9.2)	1.7 \pm 0.8	(1-4)	8.4 \pm 19	(1-114)	0.57
2	Cod 1	41	30.1	(25.8-34.4)	5.3 \pm 2.8	(1-12)	23.1 \pm 24.9	(2-96)	0.59
	Cod 2	42	36.1	(30.1-42)	5.3 \pm 2.7	(2-12)	14.9 \pm 12	(2-50)	0.73
	Haddock 1	19	14.8	(11.2-18.5)	2 \pm 0.9	(1-4)	2.7 \pm 2	(1-9)	0.82
	Haddock 2	25	19.8	(16.2-23.4)	3.1 \pm 1.7	(1-8)	5.2 \pm 3	(1-12)	0.81
	Whiting 1	7			2.3 \pm 1.5	(1-4)	5 \pm 2.6	(2-7)	0.78
	Whiting 2	11	8.1	(5.8-10.4)	1.3 \pm 0.6	(1-3)	1.6 \pm 1	(1-4)	0.92
	Hake 1	7	6	(4.6-7.3)	1.3 \pm 0.6	(1-3)	2.5 \pm 3.1	(1-14)	0.56
	Hake 2	8	5	(3.8-6.2)	1.1 \pm 0.4	(1-2)	1.3 \pm 0.7	(1-4)	0.77
	Blue whiting	8	6.4	(5.1-7.7)	1.6 \pm 0.7	(1-3)	6.7 \pm 7.4	(1-32)	0.54

Estimated taxonomic richness showed a slightly different pattern compared to the raw taxonomic richness (Figure 5 a). Estimated prey diversity was systematically higher for large cod and haddock in both zones and seemed to be constant for the other categories within each zone.

Tokeshi graphical representation summaries differences in the feeding strategies of the 9 predator categories in both zones (Figure 6). As shown in Figure 6-a, the higher the population diversity gets, the more generalist the species is. Generalist species with a lower mean individual diversity are heterogeneous feeding species. Indeed, they have a low diversity taken one by one but the whole population has a high diversity Shannon index.

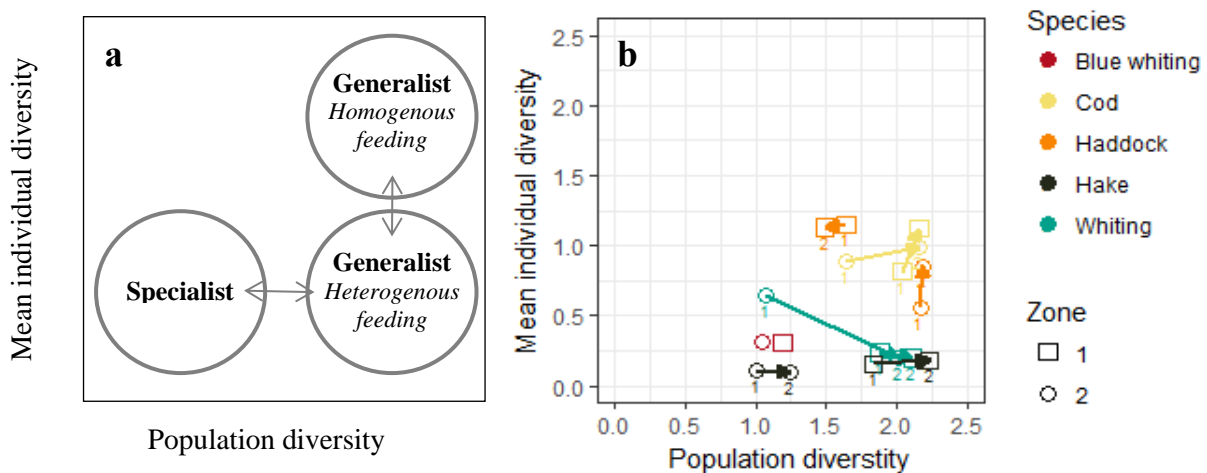


Figure 6: Tokeshi graphical representation of population diversity (Shannon index) against mean individual diversity (a) explanatory diagram for interpretation of feeding strategy according to Tokeshi (1991) and (b) diagram for the 5 species, 2 size classes (indicated by the numbers 1 and 2 linked by arrows) in both zones. The arrows represent ontogenetic shifts.

Thus, the predators studied presented a generalist feeding behaviour (Figure 6-b). Hake, whiting and blue whiting showed a more heterogeneous feeding strategy than haddock and cod an individual scale. The long arrow linking small and large whittings in zone 2 should be analysed with caution as the small category contained 3 guts. Finally, hake seemed more specialist in zone 2 and haddock adopted a more heterogeneous feeding behaviour in zone 2 compared to zone 1. For other species, no clear difference can be noted between zones.

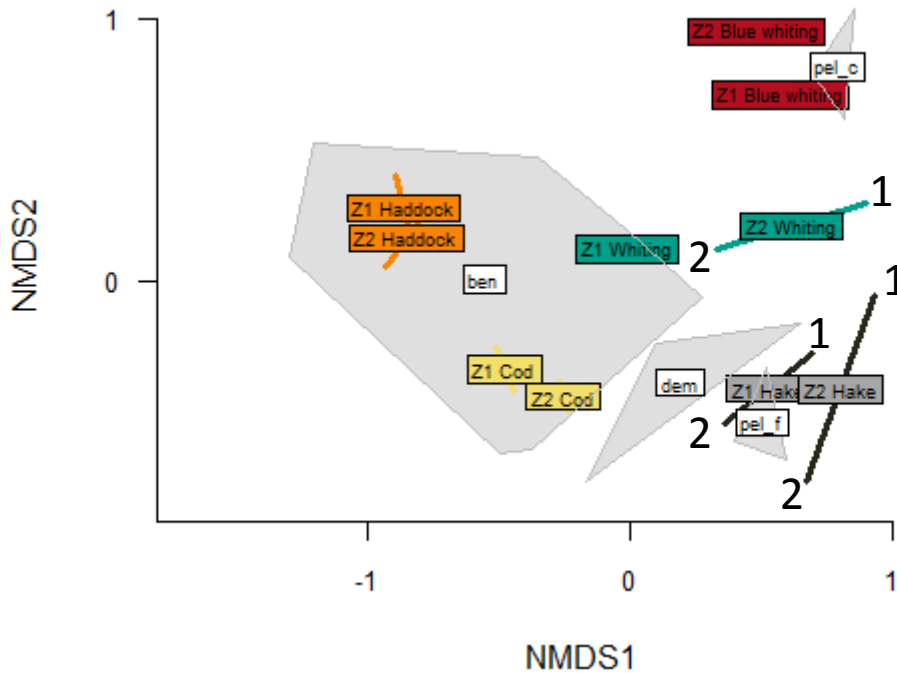


Figure 7: Two-dimensional ordination from non-metric multidimensional scaling on predator categories (coloured labels) and prey groups (grey polygons) from %FO tab - ben: benthic invertebrates, dem: demersal fish, pel_c: pelagic crustaceans and pel_f: pelagic fish. Numbers (1 and 2) indicate position of the two size classes for a predator category (stress = 0.13).

The two-dimensional nMDS plot clearly separates benthic from pelagic prey (grey polygons, Figure 7). Hence, it revealed that blue whiting, small hake and small whiting had a preference on pelagic prey. On the contrary, haddock was a strict benthic feeder. Large whiting and both size classes of cod had an intermediate position between benthic and pelagic paths. Then, diets of hake in both zones and whiting in zone 2 exhibited important changes between size classes (as shown by the line between small and large individuals in Figure 7). Finally, it seemed that hake and whiting in zone 2 exhibited a more pelagic diet than in zone 1.

3.1.3 Diet overlap

Schoener index was used to analyse diet overlaps. It was always strictly positive due to the prey group “Eumalacostraca” which was found in guts of each predator category. Small cod had high index with many other predator categories *i.e.* it shared prey with these categories especially with large cod and both whiting categories (Table 3).

In zone 1, Schoener index was superior to 50% between all small and large predators which suggest no size class shift in this area. In zone 2, only small and large cods and haddocks had a high index (superior to 50%) which suggests an ontogenetic shift in diet for whiting and hake in this area (Table 3).

Overlaps which are maintained between the two zones are between small and large cod, small and large haddock suggesting an absence of ontogenetic shift and between large hake and large whiting and between small cod and small hake supporting competition for food in both zones.

Considering the number of realized overlaps (*i.e.* a Schoener index superior to 50%) over the number of possible overlaps, there were more overlaps in zone 1 than in zone 2. This finding could suggest more competition in zone 1.

Table 3: Schoener's overlap index between predator categories in both zones. The shaded cells indicate a Schoener index superior to 50%.

	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	
	Zone 1								Zone 2								
Cod 2	0.62								0.68								
Haddock 1	0.11	0.09							0.21	0.19							
Haddock 2	0.17	0.15	0.61						0.13	0.15	0.60						
Whiting 1	0.58	0.29	0.10	0.13					0.26	0.36	0.12	0.04					
Whiting 2	0.54	0.37	0.12	0.16	0.71				0.29	0.37	0.23	0.17	0.33				
Hake 1	0.40	0.27	0.04	0.07	0.48	0.43			0.45	0.28	0.05	0.03	0.19	0.33			
Hake 2	0.30	0.37	0.06	0.10	0.37	0.40	0.53		0.14	0.30	0.07	0.03	0.24	0.48	0.07		
Blue whiting	0.07	0.07	0.04	0.04	0.05	0.16	0.34	0.13	0.11	0.11	0.07	0.02	0.30	0.29	0.23	0.00	

Gut contents analyses in a nutshell

Despite an overall generalist feeding strategy for all predators, gut contents revealed an interspecies diversity in terms of prey consumed and feeding strategies. Haddock was a strictly benthic feeder with food preferences for echinoderms and molluscs. Cod preyed on demersal prey and to a lesser extent pelagic fish, as well as whiting. However, cod prey were much higher diversified than those of whiting. Hake was the most piscivorous species, feeding on both demersal and pelagic species. Finally, blue whiting was a zooplanktivorous species targeting small and numerous preys.

Strong size class shift was observed for hake with small individuals feeding on crustaceans and large ones on fish. A shift was also noted for whiting essentially in zone 2. Large whiting preyed on fish and cephalopods whereas small ones consumed crustaceans. Generally speaking, second size class consumed more fish than first one except for haddock.

Finally, viewed through the gut contents, it seemed that the benthic community was richer in zone 1 along with the near disappearance of polychaetes and the decreased proportion of molluscs and echinoderms in guts from zone 2. A change of species composition could be depicted with the example of haddock and echinoderms which showed a high preference for *E. pusillus* in zone 1 and consumed mainly ophiuroids in zone 2. However, a clear change in feeding strategy was not brought to light in this study. Moreover, it was difficult to conclude about a potential change in the benthic-pelagic coupling between zones as many prey taxa could not be identified as a precise enough level and so could not be attribute to the pelagic or the benthic compartment (Appendix VII). However, the two-dimensional MDS plot tended to indicate a more pelagic diet for hake and whiting in zone 2.

3.2 Stable isotopes analyses

3.2.1 Predators stable isotope signatures

Isotopic signatures of the nine predator categories showed a quite broad range of variation with $\delta^{15}\text{N}$ values (mean \pm sd) ranging from $11.42 \pm 0.89\%$ for blue whiting in zone 1 to $16.29 \pm 0.28\%$ for large cod in zone 2 and $\delta^{13}\text{C}$ values 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 (Table 5). At a community scale

and despite baseline correction, we observed that δN range (the difference between the highest $\delta^{15}N$ values and the lowest one; Layman et al., 2007) was greater in zone 1 than in zone 2 as it was 6.5 ‰ in zone 1 and 4.8 ‰ in zone 2. In the same way, δC range was 4.1 ‰ in zone 1 and 3.9 ‰ in zone 2.

Table 4: Results of ANOVAs procedures prior to M_N and M_C selecting the variables to explain the variability of isotopic signature $\delta^{13}C$ and $\delta^{15}N$.

	$\delta^{15}N$					$\delta^{13}C$				
	Sum Sq	Df	F value	P value		Sum Sq	Df	F value	P value	
(Intercept)	1564.69	1	3731.99	7.14E-109	***	4282.28	1	18972.05	1.71E-161	***
predator category	125.86	8	37.52	2.45E-32	***	52.84	8	29.26	3.08E-27	***
zone	20.71	1	49.39	6.62E-11	***	5.23	1	23.19	3.52E-06	***
predator category *zone	11.41	8	3.40	0.001	**	16.91	8	9.37	1.82E-10	***
Residuals	63.73	152				34.31	152			

The procedures of selection based on ANOVAs kept the two variables (predator categories and zones) and their interaction for both models, M_N and M_C (Table 4). Both models' hypothesis (normality and homoscedasticity of the residuals) were graphically validated (Appendix VIII). Moreover, M_N and M_C explained respectively 71% and 69% of the variance contained in the data (Table 4). The predator category was the main factor influencing the isotopic compositions as it explained around the half of the variance in the data (57% and 48% respectively). The factor *zone* explained around 9% and 5% respectively of the variance. The interaction was significant for both models meaning that the effect of the predator category depends on the zone (Appendix IX).

Table 5: Isotopic characteristics: $\delta^{15}N$ and $\delta^{13}C$ composition, standard ellipse area corrected (SEAc).

zone	predator	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	SEAc (‰ ²)
1	Cod 1	14.46 ± 0.47	-17.11 ± 0.39	0.61
	Cod 2	14.81 ± 0.81	-17.19 ± 0.62	1.13
	Haddock 1	12.32 ± 0.77	-17.95 ± 0.66	1.77
	Haddock 2	13.36 ± 0.44	-17.53 ± 0.42	0.58
	Whiting 1	12 ± 0.34	-18.92 ± 0.33	0.37
	Whiting 2	13.55 ± 0.79	-17.88 ± 0.55	0.74
	Hake 1	11.66 ± 0.84	-19.29 ± 0.4	0.73
	Hake 2	12.34 ± 0.86	-18.42 ± 0.48	0.22
	Blue whiting	11.42 ± 0.89	-18.89 ± 0.6	1.8
2	Cod 1	15.47 ± 0.34	-16.87 ± 0.31	0.37
	Cod 2	16.29 ± 0.28	-16.44 ± 0.4	0.35
	Haddock 1	12.79 ± 0.23	-19.33 ± 0.28	0.12
	Haddock 2	15.15 ± 0.56	-17.03 ± 0.47	0.78
	Whiting 1	14.62 ± 0.73	-17.96 ± 0.57	1.95
	Whiting 2	14.6 ± 0.56	-17.45 ± 0.6	0.49
	Hake 1	13 ± 0.58	-18.93 ± 0.6	1.28
	Hake 2	13.72 ± 0.64	-17.89 ± 0.19	0.31
	Blue whiting	13.37 ± 0.55	-17.91 ± 0.31	0.52

The interaction between the two factors was essentially driven by small haddock and to a lesser extent, by small cod in M_C and by large whiting in M_N . The factor *zone* had a positive effect on mean isotopic values (+1.95 for nitrogen and +0.98 for carbon in zone 2 Appendix IX). This effect was reduced for small haddock and large whiting in M_N and for small haddock and small cod in M_C (significant interaction). For example, the mean $\delta^{15}N$ estimated value for small haddock in zone 2 was: 11.42 (intercept) + 0.9 (effect of the *predator category* the reference being *M. poutassou*) + 1.95 (effect of the *zone*) – 1.47 (effect of the interaction *zone*predator category*).

Cod, large haddock and large whiting had higher isotopic compositions than hake, blue whiting, small whiting and small haddock (Table 5, Figure 8 and Appendix IX). There was a significant difference in $\delta^{13}C$ between size classes for hake in both zones (Tukey p-value = 0.004 and 0.006 for zone 1 and 2). Small hake were $\delta^{13}C$ -depleted compared to large ones. There were significant differences in $\delta^{13}C$ and $\delta^{15}N$ values between size classes for whiting in zone 1, haddock in zone 2 and to a lesser extent haddock in zone 1 (Tukey p-value < 0.01 for all comparisons) with large individuals being C and N-enriched. There were not significant shift between size classes for cod in both zones and whiting in zone 2 (Tukey p-value > 0.63 for all comparisons).

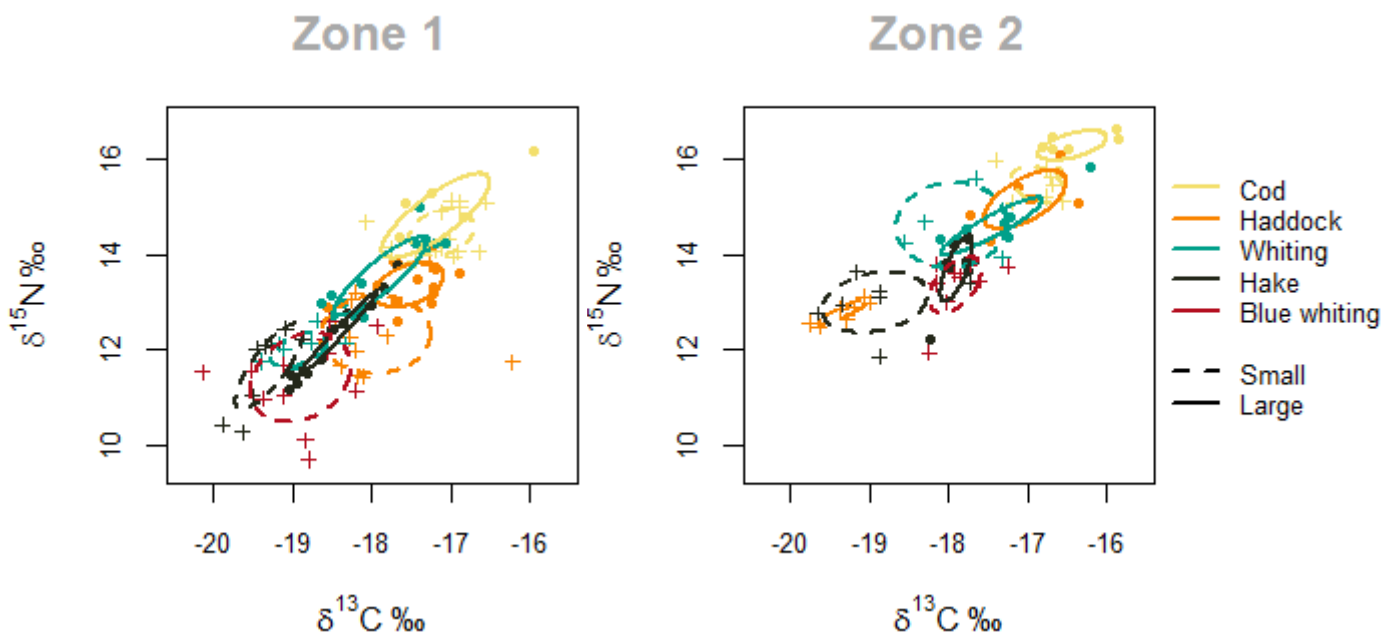


Figure 8: Sample size-corrected standard ellipse (SEAc) from $\delta^{15}N$ and $\delta^{13}C$ values for each prey category in both zones. The crosses and points represent the raw isotopic data and lines the SEAc.

Overall, $\delta^{13}C$ and $\delta^{15}N$ were higher in zone 2 (except for $\delta^{13}C$ of small haddock which were all sampled at a station at 121 m depth in zone 2, very close to zone 1 depth range).

Thus, the two models demonstrated a predator category effect in carbon and nitrogen isotopic signatures, as well as a spatial difference. This could suggest niches distinction between some species and a difference of trophic structure between the two zones.

3.2.2 Trophic level

The highest TL was observed for large cod up to 4.7 in zone 2 and lowest TL for blue whiting and small hake in zone 1 and small haddock in zone 2 (Figure 9). Moreover, we noted a

global increase of the TL between small and large individuals in each predator category. There was a clear shift between size classes for haddock in both zones and whiting in zone 1 (*cf* Tuckey tests on $\delta^{15}\text{N}$).

TLs were higher in zone 2 than in zone 1. Mean trophic levels ranged from 3.3 for blue whiting and 4.3 for large cod in zone 1 and from 3.7 for small haddock to 4.7 for large cod in zone 2.

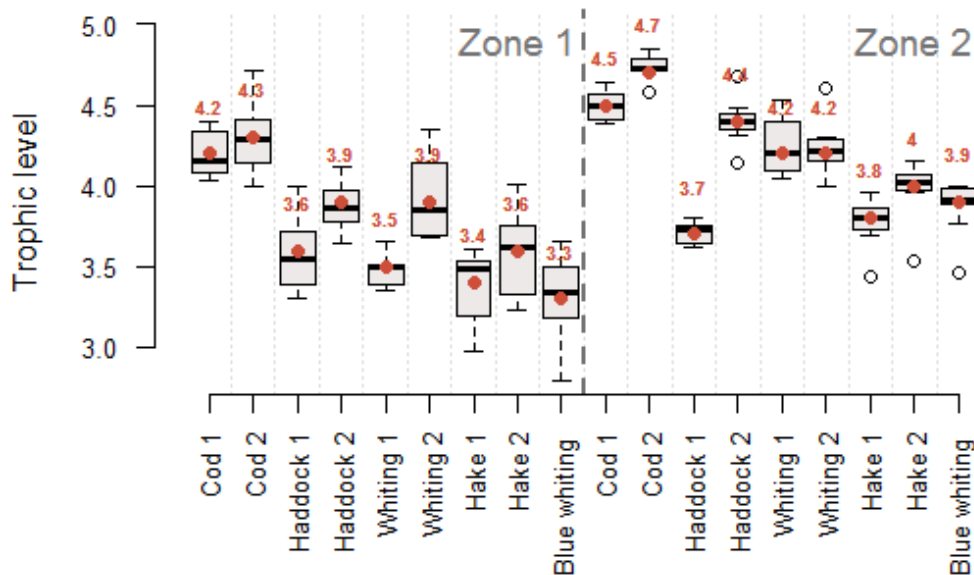


Figure 9: Trophic level calculated from Post’s equation (2002) for each predator categories in both zones. Boxplots represent the median and quantiles; red point with the value is the mean.

3.2.3 Isotopic niche breadth

The isotopic niche breadth was evaluated through the Surface Ellipse Area distributions estimated with a Bayesian method (SEAb).

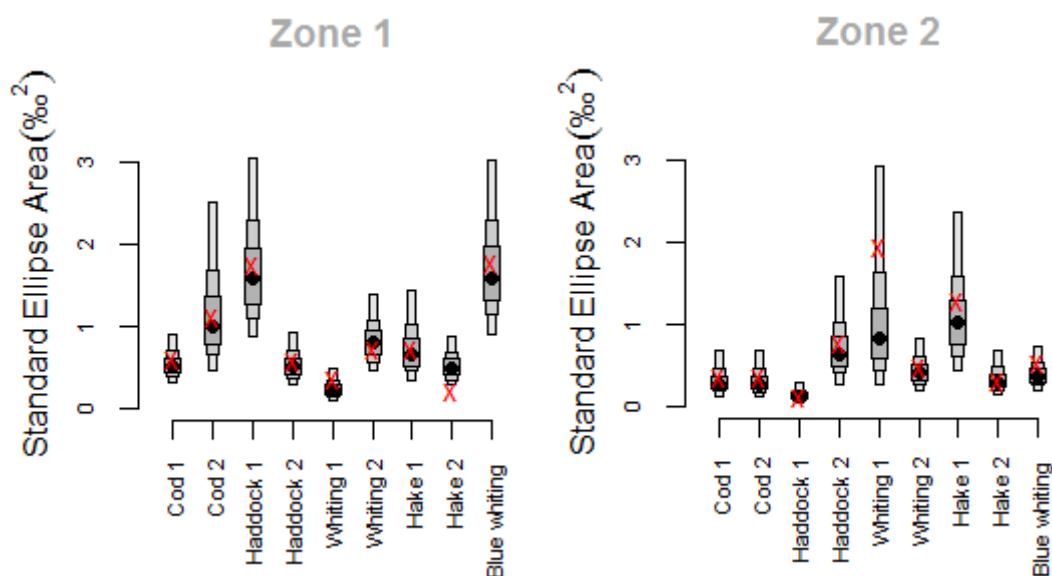


Figure 10: Posterior Bayesian estimates of the standard ellipse area (SEAb in grey) and sample size-corrected standard ellipse area (SEAc red crosses) for each prey category in both zones.

Large cod, small haddock and blue whiting had large isotopic niches with SEAc of 1.13, 1.77 and 1.8 in zone 1 respectively (Table 5 and Figure 10), whereas SEAc are much lower in area 2. Reversly, SEAc value were higher for small whiting and small hake in zone 1 than in zone 2. Moreover, small whiting showed a high incertitude on SEAb and a great difference between SEAb mode and SEAc value. This category had only 4 samples for stable isotopes which could lead to incertitude on SEA estimations. In zone 2, cod and haddock had small isotopic niches. Finally, in both zones, large hake had smaller isotopic niche than small one (Table 5 and Figure 10).

3.2.4 Isotopic niche overlaps

In zone 1, 99% of the small whiting ellipse overlapped with the one of the blue whiting (Figure 8). Both categories fed on pelagic crustaceans in zone 1. Blue whiting and both size classes of hake isotopic areas overlapped. Moreover, 69% of the large hake ellipse was included in the small haddock ones (Figure 8, Appendix X-A). Ellipses of small and large cods (and to a lesser extent small and large haddocks) overlapped whereas small and large whittings and hakes ellipses did not overlap. This finding tends to indicate an ontogenetic shift for whiting and hake in zone 1.

In zone 2, 80% of the small cod's ellipse is overlapped by large haddock's one. Other inter-species overlaps were hard to explain as overlapping species did not prey on the same prey groups as small hake and small haddock (Appendix X-B). Ellipses of small and large whittings overlapped whereas small and large cods, haddocks and hakes ellipses did not overlap (Figure 8). This finding tends to indicate an ontogenetic shift for cod, haddock and hake in zone 2.

Moreover, ellipses overlapped more in zone 1 than in zone 2 as there were globally more positive overlaps (Appendices X-A and X-B).

3.2.5 Predators' location in the food web

In both zones, two distinct feeding paths could easily be identified: pelagic with lower $\delta^{13}\text{C}$ values and benthic higher $\delta^{13}\text{C}$ values (Figures 11 and 12).

Clustering analysis of prey in zone 1 results in seven groups, two of which resulting of a manual separation: pelagic and benthic primary consumers were initially associated in the same group by the clustering process, we decided to separate them into two groups. Benthic primary consumers were represented by great scallop and pelagic ones by copepods. Pelagic fish was a small group composed by mackerel, blue whiting, small hake and boarfish. The cluster just above was a mixture between fish and cephalopods, as well as pelagic and demersal species. Nevertheless, demersal species (like small haddock, grey gunard, stout bobtail) had globally higher $\delta^{13}\text{C}$ values compared to pelagic ones (like small whiting, horse mackerel, herring and large hake). On the right part of the isospace, there were two benthic clusters. The lower one was named benthic invertebrates represented by polychaetes, molluscs, two species of *Caridea*, one of *Pagurus* and two species of scallops species. Benthic fish and predatory invertebrates were mainly composed by flatfish (like common sole, european plaice, common dab) and benthic feeding invertebrates (portunid crab, 3 species of caridea). Finally, at the top of the foodweb, there were the demersal predators composed by cod, large whiting, as well as European seabass or john dory fish with high $\delta^{15}\text{N}$ values (Figure 11).

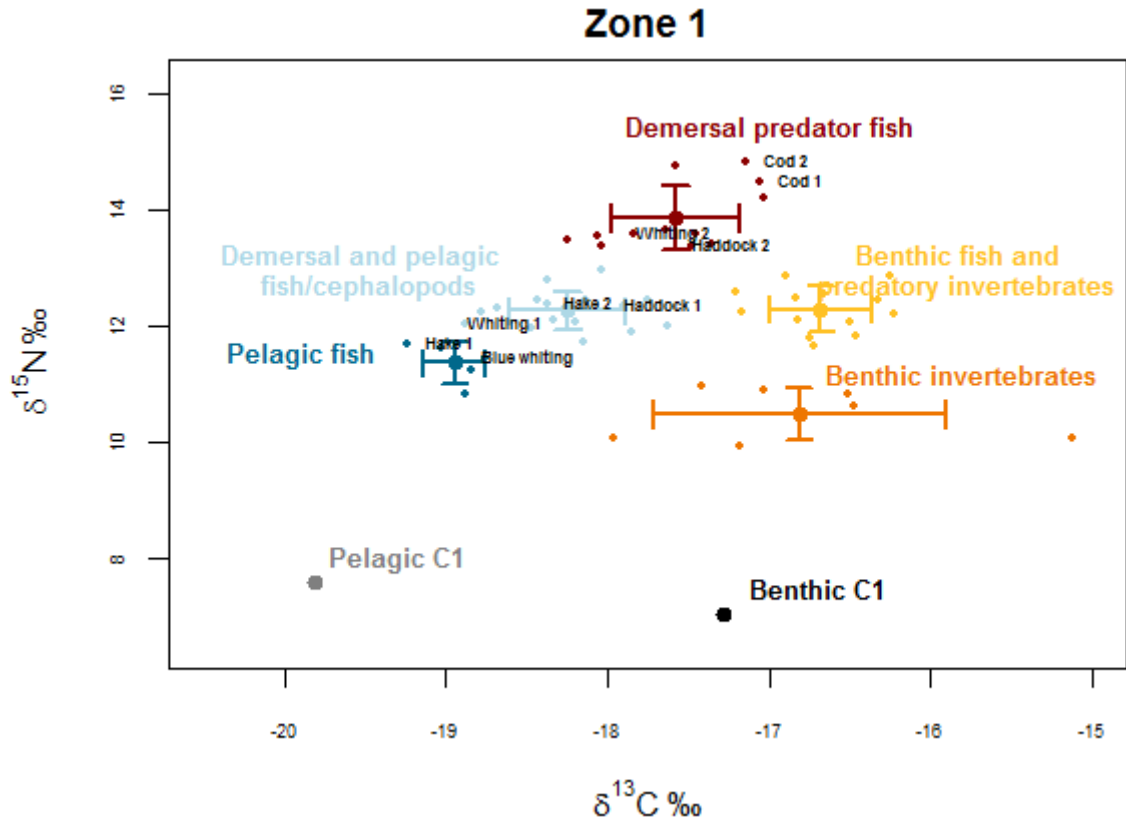


Figure 11: Isospace of the trophic web in zone 1 displaying species average stable isotopes values (colored dots) and the sources average stable isotopes values (colored crosses).

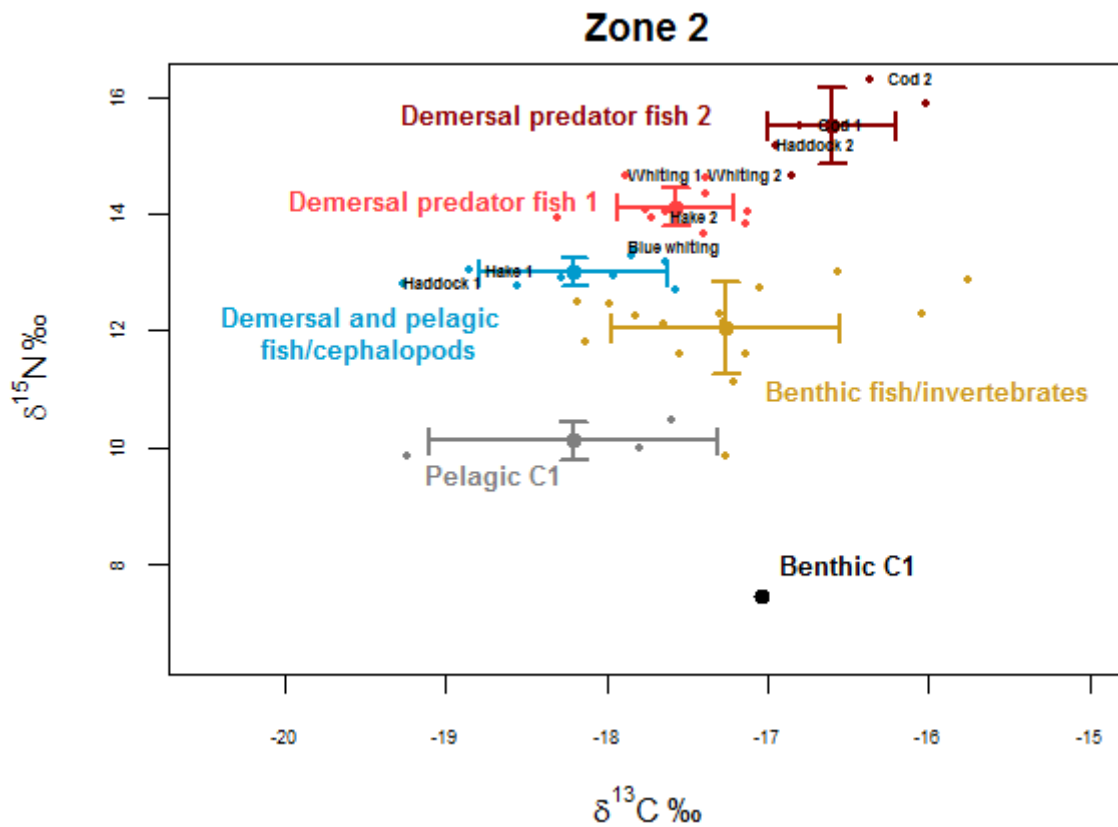


Figure 12 : Isospace of the trophic web in zone 2 displaying species average stable isotopes values (colored dots) and the sources average stable isotopes values (colored crosses).

Six groups were identified in Zone 2. Benthic primary consumers were represented by great scallop as in zone 1; pelagic primary consumers were composed by copepods, pelagic carideans and hyperids. “Pelagic fish” and “Benthic fish and predator invertebrates” were combined in one cluster named “Demersal and pelagic fish and cephalopods”. It was composed by species as small haddock, small hake, common dragonet, red gurnard (demersal fish) and blue whiting, sardine horse maquerel or boarfish (pelagic fish). Once again, demersal species had globally higher $\delta^{13}\text{C}$ values compared to pelagic ones. Demersal predator fish were split into 2 clusters compared to zone 1. The first cluster was mainly composed by gadiforms (as whiting, large hake and Spanish ling) and the second cluster was composed by top predators (cod, large haddock, European pollack or john dory fish). The benthic path was grouped into one cluster compared to zone 1. It contained flatfish and benthic crustaceans as *C. allmanni*, *C. pagurus* or *N. norvegicus* (Figure 12).

3.2.6 Estimated proportions of assimilated prey

The estimated relative contributions of the prey clusters to the diet of the predator categories differed using different TEFs. The models were quite sensitive to those parameters. Thus, the results (Table 6) will be used as comparisons between species, zones or size classes rather than absolute values.

Inter-species, intra-species and inter-zones differences were found in the estimated proportions of prey clusters (Table 6). According to SIAR models, cod diet was benthic as largest proportions were assigned for benthic or demersal clusters. Whiting seemed to feed on more pelagic prey including primary consumers and the pelagic fish in zone 1 whereas in zone 2, estimated proportions were spread over both benthic and pelagic clusters. In zone 1, hake was widely a pelagic feeder. It had a more important proportion of demersal preys in zone 2. Blue whiting was also a pelagic feeder with a preference for primary consumers (mainly copepods).

Table 6: Estimated proportions of assimilated prey clusters (in %) in the diet of the predators in both zones with: mode (1st column), mean (2nd column) and standard error (3rd column) of each prey proportion distribution. A selection of the most probable clusters was made prior of running SIAR in order to limited the number of sources.

	Predator	Pelagic C1			Benthic C1			Pelagic fish			Demersal and pelagic fish cephalopods			Benthic invertebrates			Benthic fish and predator invertebrates			Demersal predator fish (1)			Demersal predator fish (2)		
		Mode	Mean	SE	Mode	Mean	SE	Mode	Mean	SE	Mode	Mean	SE	Mode	Mean	SE	Mode	Mean	SE	Mode	Mean	SE	Mode	Mean	SE
Zone 1	Cod 1							13	14	7	21	21	9	11	12	6	25	24	8	30	29	6			
	Cod 2							13	15	9	24	21	11	2	12	8	24	21	11	30	31	11			
	Whiting 1	40	40	8	4	9	6	27	27	11	16	16	9	1	7	6									
	Whiting 2							44	45	11	27	23	12	14	15	8	2	8	7	2	8	6			
	Hake 1	55	53	10	1	7	6	26	23	12	2	11	8	1	6	5									
	Hake 2	30	31	7	6	9	6	30	29	11	22	22	10	2	9	6									
Blue whiting	50	50	9	10	12	7	20	21	10	2	10	7	1	7	6										
Zone 2	Cod 1										27	25	10				28	27	8	26	25	10	27	23	8
	Cod 2										9	16	10				16	17	9	30	27	12	41	40	9
	Whiting 1	27	27	10							26	24	12				22	17	11	21	18	10	2	12	8
	Whiting 2	28	28	8							25	23	10				23	21	6	18	18	9	4	9	6
	Hake 2	27	27	10	10	12	6				27	27	11				5	16	10	20	18	9			
	Blue whiting	35	33	11	17	17	6				33	33	10				11	17	10						

The main food source for small whiting in zone 1 was copepods (around 40% of their diet) whereas larger individuals consumed higher trophic levels as pelagic fish (44%) and demersal and pelagic fish/cephalopods (27%). The same pattern was observed for hake in zone 1. In zone 2, large cod fed on both clusters of demersal predator fish whereas small individuals also

fed on lower trophic levels as benthic fish and predator invertebrates (28%) and demersal and pelagic fish (27%).

Generally, it seemed that species in zone 2 fed on more benthic sources than in zone 1. Indeed, both size of whiting consumed benthic and demersal prey in zone 2 whereas pelagic prey were preferred in zone 1. Large hake had around 20% of its diet estimated from strictly benthic sources in zone 2 and not in zone 1. In the same way, large cod fed more on benthic prey in zone 2, preying on demersal predator fish.

Stable isotopes analyses in a nutshell

Cod appeared to be a top predator in the Celtic Sea in terms of trophic level compared to other Gadiformes studied here. It also had the most benthic diet evaluated from mixing models (mixing model was not performed on haddock because of a lack of potential sources). Hake did not seem to be as top predator as described by Moullec et al. (2017) but was an intermediate predator mostly feeding on pelagic prey. Whiting fed on both pelagic and benthic sources and large individuals had food preference for higher trophic level prey resulting in a high trophic level for this predator category. Blue whiting appeared to have a lower trophic level as expected, and to feed on pelagic prey, especially primary consumers.

Ontogenetic shifts seemed to occur for hake, from pelagic sources for small individuals to more benthic sources for larger ones. The same pattern could be observed for whiting in zone 1. Overlaps also tended to demonstrate shifts for haddock and cod in zone 2.

Isotopic carbon ratios were higher in zone 2 which suggested a more benthic diet in zone 2. Moreover, isotopic nitrogen ratios were higher in zone 2 which lead to higher trophic levels and then suggested a preference for prey with a higher position in the food web. Mixing models confirmed that observations.

Finally, at a community scale, global niche breadth is larger in zone 1.

4 DISCUSSION

In this study, we presented results on the feeding ecology of five species considering two size classes in two areas in Celtic Sea. It fits within a context of ecosystem based fisheries management and a need of local data and information on trophic niche of considerable importance commercial species. Within a more ecologist context, studying feeding ecology is a key component of the understanding of marine predatory position and role in the ecosystem.

This study is based on two types of data and their associated analyses. The aim was to combine both approaches. In order to facilitate a better understanding of the results, it is necessary to remind the inherent limits of the data and the methods used. Gut contents show a snapshot of the diet and the identification is dependent on the person who did the laboratory work. By contrast, stable isotopes give a longer temporal integration of the diet as muscle cells' turnover is several weeks. However, these quantitative data cannot be interpreted without qualitative information of the diet. Moreover, results from GCA and their interpretation were dependent on the choices made to construct prey groups. Prey were grouped as this procedure allowed to keep all the data even the rare ones. It was made upon three criteria: taxonomy, trophic guild and position in the water column. We are confident on

the fact that the use of several combined criteria produced coherent trophic groups as done by Giraldo et al. (2017) for example.

4.1 Usefulness of improving our knowledge on the enrichment factor

Results from isotopic mixing models SIAR were highly dependent of the TEFs chosen. We tested to run the models with different TEFs (not presented here) and the outputs could vary significantly using these parameters. Bond and Diamond (2011) found that outputs from mixing models are very sensitive and so significantly affected by TEFs put in entrance of the model. They recommend using good estimation of this factor in order to get a robust estimate of the relative contributions of prey items. To do so, laboratory experiments should be conducted on the species of interest in control conditions. This can allow one to estimate fractionation factor with precision. However, to our knowledge, such experimentations had not been made on the species studied here. However, for the species studied, such experimental procedures seem inappropriate as their tolerance towards captivity conditions is unknown. Additionally, extrapolation of parameter obtained in experimental condition to natural environment is not recommended. Hence, we decided to set TEFs to realistic values (see Methods; Hussey et al., 2014; Zanden and Rasmussen, 2001) and to use models' outputs only to compare species' diet rather than used them as absolute diet descriptors. With more and more studies based on isotopes ratio and mixing models (Phillips et al., 2014), it is necessary to improve our knowledges on fractionation factor. It appeared that TEF is related to processes of assimilation and excretion of nitrogen (Vanderklift and Ponsard, 2003). Taking into consideration species' metabolism could improve our estimation for TEF. The tissue considered also plays an important role. Using information from different tissues could help in enhancing TEF estimators (Dalerum and Angerbjörn, 2005).

4.2 Limits of the baseline correction of isotopic values

The data had been corrected using the great scallop *Pecten maximus* as species for baseline as indicated by several authors (Cabana and Rasmussen, 1996; Jennings and Warr, 2003). The correction had been realised as a function of depth. Results from SIA on spatial differences are closely tied to the baseline correction applied. This correction was essential to compare the results between the two areas.

Another solution would have been to correct data using a geostatistical interpolation technique named kriging (see Kopp et al., 2015; Giraldo et al., 2017 for specific details). However, kriging requires rich data sets in order to be robust. In this study, the spatial sampling was not dense enough to use this technique.

P. maximus is a benthic suspensive feeder and was chosen as the baseline species (Jennings and Warr, 2003). We showed with gut contents analysis that *M. poutassou* is a strict pelagic feeder and *M. merluccius*, *M. merlangus* and *G. morhua* feed on both pelagic and benthic communities. It does not seem satisfactory to correct isotopic values from benthopelagic feeders with a benthic baseline. A solution could be to apply a weighed correction which integrates the proportions of benthic and pelagic prey in the diet. Turschak and Bootsma (2015) used this solution in studying trophic structure in Michigan Lake from Post's equation (2000). We decided not to implement this method here as we had few isotopic values for a potential pelagic baseline (copepods: n = 9), which are known to be highly variable in time

and space. However, with a more important sampling on pelagic baseline species, it would be interesting to combine both baselines in correcting raw data and to study the impact of this new correction on the results.

4.3 Species trophic niche in the Celtic Sea

Trophic niche

Our results support the common finding that gadiformes are globally generalist feeders as the different populations had a relative high number of taxa per individual. Generalist feeders are expected to face changes in their environment and habitat more easily than specialists as they should be able to adapt. This is an argument in favour of some resilience of the species studied to a major perturbation. Diet compositions observed here are globally in accordance with previous studies in the Celtic Sea and in adjacent ecosystems. However, some differences are notable and reflect specificities of the Celtic Sea.

M. merlangus consume crustaceans and fish in the demersal compartment as well as in the pelagic one. Diet composition and mixing model agree on this finding. Fish items were present in average in 30 % of the fish sampled. This proportion seems rather low compared to the 1980's when fish represent 97 % of the diet of the whiting in the Celtic Sea (Du Buit and Merlinat, 1985). However, this number is an estimation of the weight of fish prey consumed by whiting and the fish were sampled throughout the year. Their preferential fish prey were *Micromesistius poutassou*, *Trisopterus minutus* and clupeiformes in the 1980's and are *Micromesistius poutassou*, *Trisopterus esmarkii* and *Trachurus trachurus* in 2014. Pinnegar et al. (2003) also found a positive selection for clupeoids in the Celtic Sea. This slight evolution could be linked to the prey availability as *M. merlangus* seem to be an opportunistic feeder.

M. aeglefinus is a benthic feeder with large food preferences for echinoderms and to a lesser extend molluscs. Echinoderms are known to be a consistent prey of haddock in several populations of the Atlantic Ocean (Tam et al., 2016). The proportion of fish found in haddock's guts was close to zero. However, it has been showed that fish proportion in its diet varies greatly according to the ecosystem considered, as for example in the North Sea, the Barrent Sea or in Rockall bank (Tam et al., 2016). Hence, *M. aeglefinus* presents a pronounced capacity for adaptation depending on biotic environmental conditions. Brawn et al. (1968) found that prey fishes contained more energy than echinoderms (two to three times more). It seems counter intuitive that haddock choses low energy prey. However, we can hypothesis that sea urchins are more easily captured than species with fast movements. Then, this choice illustrates the trade-off between the allocated energy for searching and capturing food and the gained energy from the prey. Additionally, it can be suggested that gravid echinoderms probably have much higher energy or that this counter intuitive choice reflects the trophic segregation from other gadiformes. *M. aeglefinus* showed a particular feeding strategy specialized in echinoderms and molluscs. Thus, its trophic niche is segregated from the other gadiformes studied here. Besides, its stomach can realize very powerfully contractions which allow it to crush and grind hard prey (Mattson, 1992). Finally, we can note that *E. pusillus*, found in many guts in this study was not observed by Du Buit (1982) in the Celtic Sea. This finding could be explained either by good sea urchin recruitment or a change in the benthic community.

G. morhua is a benthic feeder although it preys occasionally on pelagic prey. As mixing model also showed it was a benthic feeder. It consumes an important part of crustaceans including large decapods as brachyurans and anomurans. Fish were secondary prey. Du Buit (1995) studied the feeding behaviour and diet composition of Atlantic cod in the Celtic Sea at all times of the year. She concluded that cod was an opportunist feeder consuming half decapods half fish. Twenty years later, the repartition between decapods and fish seems to have changed (remaining that GCA represents a snapshot of the diet). This change towards a diet composed by crustaceans could reflect a change of feeding strategy. The recent hake recovery (ICES, 2016a) could have led to an increase in the competition for food resources between the two species.

M. aeglefinus and *G. morhua* were the species with the highest number of taxa per fish. They have a large trophic niche viewed through gut contents but their isotopic niches were relatively small in comparison, especially in the deepest area. Moreover, they share benthic prey (crustaceans and molluscs). It is interesting to note that these two species are often studied together such as in the northern Norway using an isotopic approach (Ramsvatn and Pedersen, 2012) or in Canada using stomach contents (Kohler and Fitzgerald, 1969) among several examples. They are presented as opportunistic feeders, feeding on the abundant crustaceans in the fjords by Ramsvatn and Pedersen (2012).

M. merluccius was the most piscivorous species studied here with preferences for pelagic perciforms, gadiforms and clupeiforms. Guichet (1995) also depicted hake as a piscivore with 98 % of the weight of stomach contents being fish. In the Celtic Sea and in northern European waters hake feed mainly on *T. trachurus*, *M. poutassou* and *Trisopterus* spp., with a particular affinity for *M. poutassou* (Du Buit, 1996; Mahe et al., 2007) not observed here. Its feed preference changes in Mediterranean waters with targeting *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. There is evidence that juveniles of European hake move into midwater at night following their prey movements (Bozzano et al., 2005). This study as the one from Mahe et al. (2007) tends to indicate that large hake could have a similar behaviour of pelagic hunter at night. Vacuity rates were around 50% for this species which is another clue for the night hunting behaviour. Moreover, several studies suggest that cannibalism occurs within hake populations as in the Mediterranean Sea (Carpentieri et al., 2005), in the Bay of Biscay (Guichet, 1995) and even in the Bay of Biscay (Mahe et al., 2007). Such feature was not observed here.

M. poutassou has a very different diet composition compared to other species, feeding on small pelagic primary consumers as copepods, pelagic carideans or amphipods. Its trophic niche is small from taxonomic richness estimation but much larger from SEAc estimation in the shallow area. This difference can be explained by the high temporal variability of copepods and small pelagic crustaceans' isotopic signatures. As stable isotopes have a temporal integration of several weeks, this could lead to a large isotopic niche whereas in reality, it is much smaller. Blue whiting and hake shared a pelagic diet with pelagic Caridea prey in common and so their isotopic niches overlap. This result could be surprising as blue whiting is one of the prey of hake. The diet observed here is consistent with blue whiting's diet over other systems as in the Bay of Biscay (Sorbe, 1980), the Barents Sea (Dolgov et al., 2010) or off Portugal (Cabral and Murta, 2002). This last study also found that *Pasiphaea sivado* is one of the main prey of blue whiting. This species seems not to have particular feeding habits in the Celtic Sea.

Trophic levels

We calculated trophic levels from nitrogen isotopic values and according to the most common equation (Post 2002). Cod appears to be a top predator in the Celtic Sea (TL: 4.2-4.7) as well as large whiting and haddock. Even if hake is a piscivorous species it is an intermediate predator in terms of TL. As expected, based on gut content analysis blue whiting's TL was lower compared to others. This finding is consistent with Jennings et al. (2002) as they estimated TLs in the North Sea for cod (TL: 5.2), haddock (4.7), whiting (5.3) and hake (4.4) using the same equation. They considered that base material (bivalves) had a trophic level at 2.5 whereas we considered a TL of 2. This difference explains the higher values of TLs for Jennings et al. (2002). TLs can be calculated from stomach contents as done in the Celtic Sea by Chassot et al. (2008) using data collected between 1981 and 1985 during fishing operations (2008). The TL of an individual is the sum of its prey TL weighted by their relative importance in guts. TLs of prey were assessed from a literature review of stable isotopes in close ecosystems. The predators studied were found to be top predators with high mean TLs: cod (4.4), haddock (4.9) whiting (5.2) and hake (5.0). Results were quite different with higher TLs for haddock, whiting and hake, compared to cod. They also were dependant on the TLs affected to prey.

The position of top predator for cod results here from high $\delta^{15}\text{N}$ values. This could be explained by the important consummation of scavengers as *N. norvegicus* or *Munida* spp. Whiting was also found to be a top predator in the Celtic Sea. Hislop et al. (1991) also presented whiting as one of the most piscivorous species in the North Sea. In this study and Hislop's one, whiting consumed cephalopods which are known to be at the top of the food web. Using isotopic values, hake does not appear as a top predator as observed from gut contents. However, isotopic values imply a lower TL for hake as in the North Sea. Jennings and van der Molen (2015) developed a model to estimate TLs and the associated uncertainty of fish and squids taking account variations of $\delta^{15}\text{N}$ baseline values and different fractionation factor. They used data from Irish and Celtic Sea to test the model and found the same order of magnitude and ordination as in this study.

4.4 Ontogenetic shift in diet and trophic niche

Data were collected during the EVHOE campaigns and so the sampling plan had to be adapted to this practical constraint. The size distributions from previous campaigns were used to define the cut between small and large individuals of this study. Results should be interpreting knowing that for *G. morhua*, *M. merlangus* and *M. aeglefinus* we are comparing immature juveniles with mature adults (Brander, 2005; Gerritsen et al., 2003; Wright et al., 2011) and for *M. merluccius*, small juveniles with large juveniles and adults (Domínguez-Petit et al., 2008).

M. merluccius exhibited a clear shift in isotopic values between small and large individuals in both zones as both approaches showed no marked overlap between the trophic niche of small and large individuals. Small hake was $\delta^{13}\text{C}$ -depleted compared to large ones which means that they feed on more pelagic prey (France, 1995). Guts analysis confirmed that hake <21 cm is a pelagic feeder as they consumed pelagic carideans, amphipods and clupeiformes. Le Loc'h and Hily (2005) also found an increase in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with fish size increase indicating a $\delta^{13}\text{C}$ -enrichment and a higher trophic level for large *M. merluccius*. However,

large hake maintains a part of its diet on the pelagic compartment, consuming pelagic gadiformes and perciformes. Moreover, large hake was clearly more piscivore than small ones with between 66 and 80 % of its diet composed by fish prey. This finding was already described by other authors in the Celtic Sea (Mahe et al., 2007) and in other areas such as Mediterranean Sea (Carpentieri et al., 2005). They demonstrated a gradual change towards an entirely piscivorous diet. This change was gradual from around 16 cm to 40 cm. Thus, the diet change was completed when sexual maturity occurs. Mahe et al. (2007) also found a gradual change using 3 size classes in a stomach contents approach. They suggested that this change was concordant with ontogenetic development of the mouth size and the mobility. Indeed, mouth area and fish length are positively correlated for many fish species (Karpouzi and Stergiou, 2003). Moreover, the visual (Mas-Riera, 1991) and hearing (Lombarte and Popper, 1994) acuities of the European hake are known to increase with growth, allowing it to catch more mobile prey. Using SEAc as a proxy of the niche breadth, we found larger niche for small hake compared to large one in both zones. Guts revealed no significant change in niche breadth with Piélou index being similar and with the same number of different taxa per gut for both size classes studied. Mahe et al. (2007) also found a decrease in the niche breadth with an increase size, suggesting a less generalist feeding strategy for large hake.

M. merlangus showed a shift in isotopic niche in the isoscape in zone 1 with large whiting being $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ -enriched. Based on gut contents, small and large whittings had similar diet in the shallowest area, but exhibited a difference in prey items in the deepest area with large whiting preying on fish and cephalopods whereas small one consume more crustaceans. These findings tend to make us think about an ontogenetic effect on the diet and the trophic niche of whiting. However, it is difficult to conclude for that species, especially in the deep zone knowing that only 3 and 4 individuals were sampled for GCA and SIA respectively.

M. aeglefinus exhibited a strong difference in $\delta^{13}\text{C}$ between small and large individuals in zone 2 and to a lesser extend in zone 1. Small organisms were $\delta^{13}\text{C}$ -depleted compared to large ones with isotopic niches not overlapping. This could indicate a shift from pelagic to benthic diet (France, 1995). However, guts didn't reveal significant changes in diet between the two size classes: small and large haddock had benthic diet mostly composed of echinoderms and molluscs. Ramsvatn and Pedersen (2012) also found a significant difference in $\delta^{13}\text{C}$ and in $\delta^{15}\text{N}$ between small (<20 cm) haddocks and large (>20 cm) ones in northern Norway. Juveniles have a pelagic diet before juveniles' settlement (Bastrikin et al., 2014). The benthic proportion of the diet increases with size until they settle. However, settlement occurs around 10 cm long for Haddock in local nursery grounds in the north-western North Sea (Bastrikin et al., 2014; Demain et al., 2011). Hence, we could not hypothesis that the marked ontogenetic shift showed by SIA could be explained by a recent settlement of small haddocks in zone 2, SIA being more time-integrative than guts analysis representing the last benthic prey ingested by fishes. Indeed, small haddocks ranged from 14 to 21 cm in zone 2 and probably had settled in the summer and so months before the sampling. Weidel et al. (2011) showed that the half-life of $\delta^{13}\text{C}$ freshwater species at the age of 0 was comprised between 8 to 18 days. It is unlikely that stable compositions of small haddock of this study reflect the pelagic diet they had before settlement. Further analysis should be made on young juveniles of *M. aeglefinus* in order to determine the origin of the $\delta^{13}\text{C}$ -depleted signature found here and by Ramsvatn and Pedersen (2012).

G. morhua does not seem to have a clear shift in its diet or trophic niche. Niche overlaps between size classes approximated with Schoener index or isotopic overlaps both showed a common trophic niche and share diet. Gut contents revealed nevertheless that large cod had a

larger proportion of its diet composed by fish and *Nephrops norvegicus* than small one. Mixing models suggested a diet on higher trophic levels for large individuals. Ramsvatn and Pedersen (2012) found a gradual change in cod's isotopic composition from small cods to large ones. A study conducted in 1995 by Du Buit found an increase of the fish items in the diet of cod with size in the Celtic Sea, as well as Hüsey et al. (2016) in the North Sea. The proportion of fish in cod diet >70 cm was estimated around 70 % (Hüsey et al., 2016) whereas in this study, it was estimated around 20 % for cod >60cm. Hence, at the time of sampling Celtic Sea cod seems to keep an important part of its diet of decapods unlike North Sea cod. Furthermore, guts revealed that cod had a more diverse diet with size as a taxonomic richness calculated from rarefaction curves higher for large cod.

Generally speaking, large individuals studied consumed more fish than small ones (except for the haddock). Pinnegar et al. (2003) observed the same pattern in the Celtic Sea analysing the feeding ecology of six species: cod, hake, whiting, megrim *Lepidorhombus whiffiagonis*, and saithe *Pollachius virens*. They also found that body length plays an important role in the diet composition as it determines the size of the prey predator can handle and swallow.

Moreover, TLs were systematically superior for second size classes. This finding stem from the higher $\delta^{15}\text{N}$ values for large individuals. For three out four of the species for which ontogenetic shifts is studied here, the cut between the two size classes almost corresponds to the maturity. Maturity leads to gonad development, reproduction and breeding activities. Hence, the increased energy demands occurring with maturity seem to be a key component in the change of trophic niche and feeding strategy of these species.

Finally, EVHOE campaigns in the Celtic Sea do not sample in the coastal zone as the shallowest station is at 80 m deep. Thus, small individuals are not small juveniles as they were at least 11 cm long (except for *M. merluccius* with individuals until 8 cm long). It was sometimes difficult to find small individuals in the deep area as for example for *M. merlangus* with a few samples collected in the deepest zone (3 guts sampled and 4 muscle's samples for SIA). Indeed, for some species, small juveniles are currently found near the shore in the nurseries and not on the continental shelf (Lenanton and Potter, 1987). Hence, even if the sampling design is still slightly unbalanced due to species distribution along the depth gradient, a major sampling effort was made in order to realise this study. There is a global tendency of greater size with increasing depth for several demersal species (Macpherson and Duarte, 1991). Hence, species migrate (or diffuse) towards deep waters with ontogeny. It would be very interesting to analyse the species distribution from EVHOE campaigns considering different size classes.

4.5 Spatial effect on trophic niche

EVHOE is divided in several sampling strata according to the depth. To ease on-board sampling, the decision was made to study the spatial component of this study using EVHOE strata grouped into zones.

Our results on isotopic data suggest that predators' diet is more benthic in the deep area with individuals being $\delta^{13}\text{C}$ -enriched compared to the shallow area. Mixing models reinforce this finding showing a preference for pelagic sources in the shallow area whereas benthic sources are more important in the deep area. Gut analysis could not conclude on a change in the proportion of benthic and pelagic sources in the diet of the predators as the identified

taxonomic level often could not allow to precisely determining the position in the column water of the prey. Hence, isotopic data only suggest that the coupling between the pelagic and the benthic compartment is weaker in the deep zone than in the shallow one as demersal species studied seemed to preferred benthic sources in the deepest zone. Giraldo et al. (2017) found a weakness of the coupling with increase depth. In order to investigate the effect of depth on diet, they used MixSIAR (Semmens et al., 2015), a Bayesian mixing model which can include environmental (depth for example) as covariable. Hence, the sources' contributions to a consumer's diet can be estimated according to this covariable. However, the study in the Eastern English Channel was realized in a semi-enclosed sea (Giraldo et al., 2017; Kopp et al., 2015), with very different environment conditions compared to the open sea studied here.

Our finding is to take with caution as it depends on baseline correction applied to isotopic data (see 4.2) and guts did allow us to confirm it. Moreover, *M. merlangus* and to a lesser extent *M. merluccius* were placed close to pelagic prey on the nMDS plot.

Globally, guts revealed more different taxa in the shallow area compared to the deep one. We can hypothesis than the benthic community view through five species of gadiformes is richer in the shallow area. Isotopic approach agrees on that point as the isotopic niche of the five species was larger in shallow area. Indeed, δN and δC ranges were higher in zone 1. The global niche breadth was larger in the shallow area. However, at a specific level the two approaches did not always agree: cod and haddock had small isotopic niches in the deep area contrary to their high taxonomic richness. Along with a potential change of benthic community richness, gut contents seemed to reveal a change in the benthic composition. For example, we noted the near absence of polychaetes in the diet of the predators (except for haddock) in zone 2 compared to zone 1. Moreover, haddock mainly feeds on *E. pusillus* in zone 1 and on ophiuroids in zone 2.

One major limit with this spatial comparison is the lack of information on the available prey within the two zones. Gut contents and so trophic niche depend on the local availability of prey. To our knowledge, there is no quantitative a reliable information available on the benthic fauna community on the studied area of the Celtic Sea. Rees et al. (1999) found that sediment type is the main "structuring force" of the distribution of the benthic assemblages around the UK coasts. They also demonstrated that factors such as proximity to the coast, depth or temperature greatly helped to explain the spatial variation in epifaunal community. It would be very interesting to estimate the benthic community in this area.

5 CONCLUSION AND PERSPECTIVES

On the use of two methodological approaches

The use of isotopic compositions and gut contents as trophic markers give us two pictures of the trophic niche. They are both a way to depict the trophic interactions and competition between species, potential ontogenetic shifts and spatial changes. In the last decades, gut contents analyses have been associated and sometimes replaced by isotopic composition analyses. Using nitrogen and carbon ratios, scientists have been studied trophic position in a web, sources of diet, etc. Overall conclusions on feeding ecology studies could vary according to the trophic marker used. For example, isotopes suggest that *M. aeglefinus* clearly shift its niche with ontogeny whereas gut contents analysis indicate no difference in haddock's diet.

Once again, the time-integration of these two methods differs: stable isotopes provide a time-integrated view of assimilated prey whereas gut contents provide a snapshot of the recently swallowed prey. Moreover, the degree of identification of the prey in guts hardly depends on the prey type. However, identified prey provide information about the reality of trophic links existing between species that stable isotopes could not have raised. Finally, there is a cost difference between these approaches. Vinson and Budy (2011) compared the costs of the methods on a salmonids study. They estimated that isotopes analyses averaged about one-third of the cost of stomach content analyses. In conclusion, both methods are complementary and much information can be gained by combining them together. This combination is a real asset for this study as it enables us to have a more interesting, nuanced and diverse vision of the trophic interactions.

Spatial and temporal variations

We studied the feeding ecology of five species from data of a survey conducted in October 2014/2015. However, many studies showed that diet and trophic niche may vary seasonally (prey composition, physiological stage of the fish ...) or annually. Seasonal variations should also be monitored as temperature changes can affect prey distribution and water stratification. In the Celtic Sea, hake, cod and whiting have a spatial and seasonal prey-switching behaviour (Trenkel et al., 2005). Hake in the Bay of Biscay consumed preferentially anchovy the first half of the year and horse mackerel the second half (Guichet, 1995). Blue whiting also present seasonal variations in its diet with an alternation between *Pasiphaea sivado* (in summer and autumn) and *Meganyctiphanes norvegica* (in winter) off Portugal (Cabral and Murta, 2002). Comparing our results with Du Buit studies (1982; 1995) we found some differences in the diets of haddock and cod. These changes could reflect long-term change in the benthic communities or annual variations in recruitment of species consumed. Further analysis should help in completing this study.

Better understanding evolution of feeding ecology throughout the year and between years would help scientist understanding and projecting effect of fishing on ecosystems structure and potentially anticipate responses of community and species to climate change. In order to investigate this kind of variations, new data (isotope and gut) should be sampled during different periods of the year and on a yearly based to provide time series estimates.

On the use of gut samples as proxy of the benthic community

In order to answer to the question: does the potential difference between zones reflect a difference in prey available or a difference in prey selection by predator, it would be very interesting to compare gut contents with benthic species availability, abundance and distribution in the Celtic Sea. Indeed, to our knowledge, this area has not been studied until now in terms of benthic community. There is a real need of characterization of the benthos by a specialist. Such data could inform us on prey availability and distribution and then improve our understanding on trophic web functioning. However, benthos sampling appears to be quite hard, particularly at the scale of large marine ecosystems. Grab can allow sampling both sediment and fauna is not adapted as there is a great dispersion of species especially in deeper places and grab is a small content. The sampling could be performed using a scientific bottom trawl with a small mesh size. Trawl enables covering larger zones. However, trawl surveys can be ambiguous in terms of sampling because they mainly sample epifauna.

Link (2004) studied 13 omnivorous and benthivorous species, including *G. morhua* and *M. aeglefinus*, to evaluate if their stomach contents could be used as samplers of the benthic community at a broad spatial scale. This is an indirect method using the frequency of occurrence of benthic species in the diet as an index of relative abundance. He concluded that this approach could be useful for inferring benthos distribution and abundance.

Some recommendations for future ecosystemic model for the Celtic sea

This work revealed amongst others that the five species studied presented particularities in trophic niche compared to other ecosystems. This fresh local information could be transported to a Ewe diet matrix. Actual diet matrix for the Celtic Sea ecosystem indicates that around 30 % of the haddock diet is composed by fish (Moullec et al., 2017) whereas this study showed that fish is clearly not a preferential prey for *M. aeglefinus* in the Celtic Sea. The fact that commercially important fishes, such as haddock, have a food preference for echinoderms is rarely raised in fisheries management and ecosystem modelling (Tam et al., 2016). However, echinoderms seem to have a significant role in the regulation of energy flow in marine food web (Francour, 1997; McClintock, 1994; Zamarro, 1992).

From our study, we also recommend a separation based on size for hake and to a lesser extend to cod and whiting. For haddock, further investigation need to be done to establish if an ontogenetic shift occurs. This is for trophic consideration but different compartment for size classes could also be introduced to measure the impact of fisheries. Additionally, there are clues that the prey community is different between the two areas considered but it is difficult at the present time to status on the need to spatialize an ecosystemic model in the Celtic Sea.

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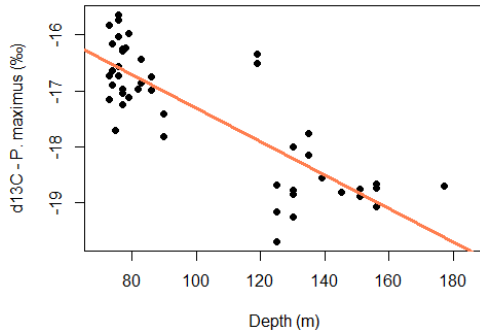
APPENDICES

Appendix I: Sample design for guts and stable isotopes samples.

Zone	Predator	Guts			Stable isotopes
		Number of samples	Number of non-empty samples	Vacuity rate (%)	Number of samples
1	Cod 1	44	41	7	15
1	Cod 2	15	15	0	7
1	Haddock 1	30	30	0	11
1	Haddock 2	37	37	0	14
1	Whiting 1	33	21	36	8
1	Whiting 2	43	26	40	14
1	Hake 1	27	23	15	9
1	Hake 2	45	30	33	14
1	Blue whiting	45	37	18	12
2	Cod 1	28	28	0	7
2	Cod 2	20	20	0	7
2	Haddock 1	25	22	12	7
2	Haddock 2	30	30	0	7
2	Whiting 1	3	3	0	4
2	Whiting 2	33	19	42	9
2	Hake 1	37	23	38	7
2	Hake 2	59	27	54	8
2	Blue whiting	39	34	13	10

Appendix III: Linear regression of isotopic values of *Pecten maximus* in function of depth

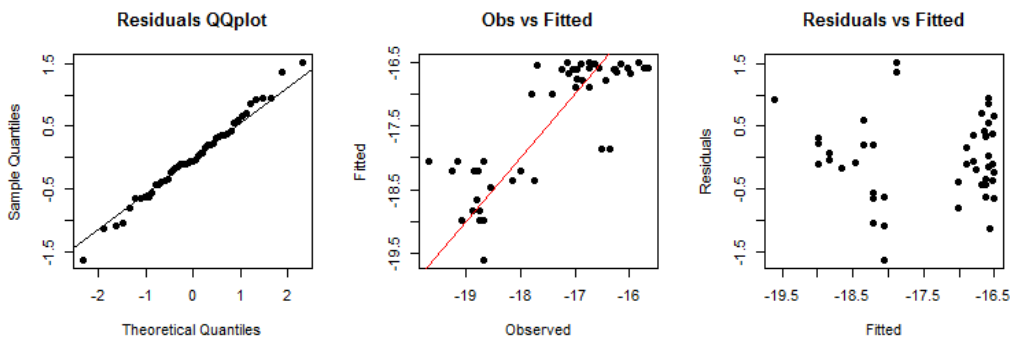
Carbon:



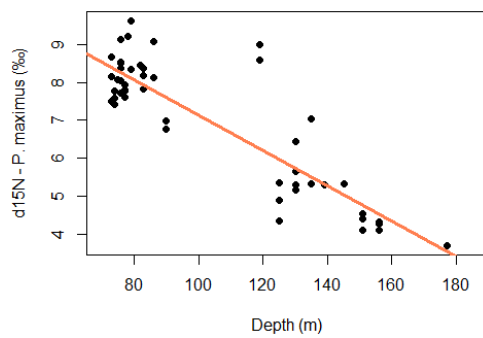
$$\delta^{13}\text{C} (\text{estimated}) = -14.31 - 0.030 * \text{depth}$$

$$\text{Adjusted } R^2 = 0.68$$

Residuals - CARBON



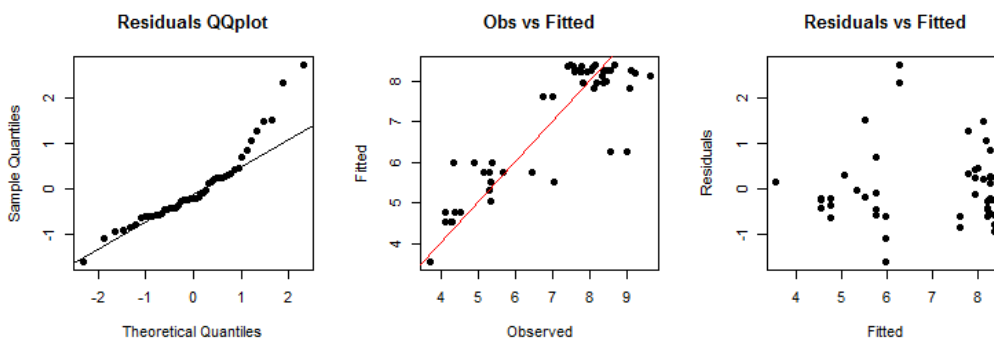
Nitrogen:



$$\delta^{15}\text{N} (\text{estimated}) = 11.82 - 0.047 * \text{depth}$$

$$\text{Adjusted } R^2 = 0.76$$

Residuals - NITROGEN



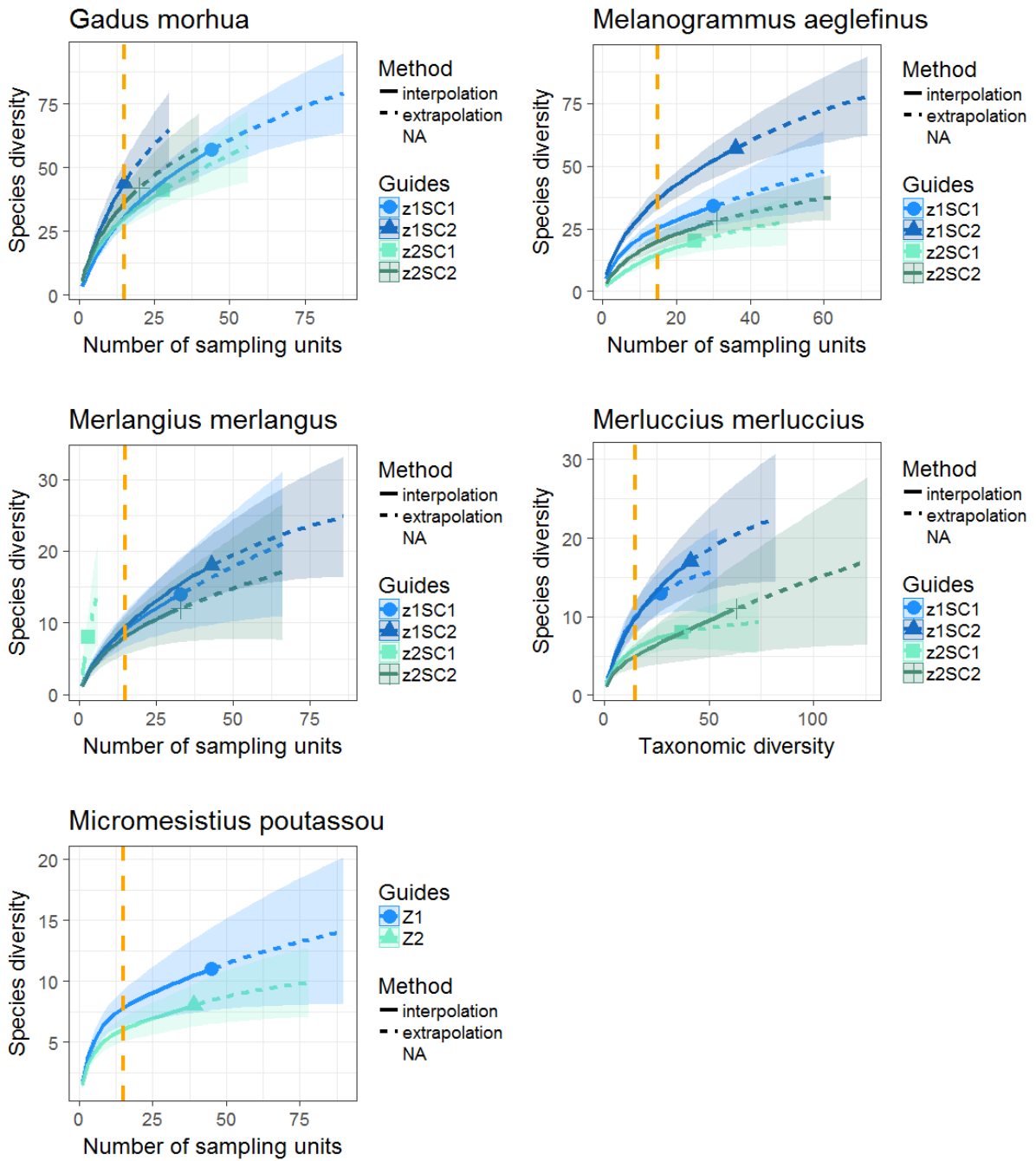
Appendix IV: Occurrence (%) of prey groups for each predator category and for both zones.

	Zone 1									Zone 2								
	Cod 1	Cod 2	Haddock 1	Haddock 2	Whiting 1	Whiting 2	Hake 1	Hake 2	Blue whiting	Cod 1	Cod 2	Haddock 1	Haddock 2	Whiting 1	Whiting 2	Hake 1	Hake 2	Blue whiting
Polychaeta-carn-ben	4.9	13.3	3.3	13.5	0	3.8	0	0	0	0	5.0	0	0	0	0	0	0	0
Polychaeta-dep-ben	7.3	6.7	33.3	8.1	19.0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta-ni-ben	12.2	0	30	40.5	9.5	7.7	0	3.3	0	0	0	22.7	16.7	0	0	0	0	0
Amphipoda-dep-ben	0	0	23.3	13.5	0	0	0	0	0	0	0	0	6.7	0	0	0	0	0
Amphipoda-carn-ben	2.4	0	0	8.1	0	0	0	0	0	3.6	0	4.5	0	0	0	0	0	0
Amphipoda-ni-ni	2.4	0	40	70.3	4.8	7.7	0	0	0	7.1	5.0	22.7	43.3	0	15.8	0	0	2.9
Amphipoda-carn-pel	0	0	0	0	0	3.8	0	0	45.9	0	5.0	0	0	0	10.5	8.7	0	23.5
Cumacea-dep-ben	0	0	10	0	0	0	4.3	0	0	0	0	0	0	0	0	0	0	0
Brachyura-carn-ben	61.0	86.7	3.3	45.9	4.8	3.8	0	0	0	89.3	70	9.1	30	0	0	0	0	0
Caridea-carn-ben	39.0	40	40	40.5	19.0	23.1	26.1	16.7	5.4	42.9	40	18.2	3.3	100	10.5	0	14.8	0
Anomura-carn-ben	24.4	33.3	0	21.6	0	0	0	0	0	67.9	50	4.5	0	0	0	0	0	2.9
Astacidea-carn-ben	4.9	6.7	0	0	0	0	0	0	0	3.6	15.0	0	0	0	0	0	0	0
Caridea-carn-pel	0	0	0	0	0	0	13.0	10	37.8	0	0	0	0	0	0	4.3	0	20.6
Eumalacostraca-ni-ni	48.8	13.3	20	40.5	47.6	38.5	26.1	6.7	29.7	60.7	55.0	13.6	10	66.7	26.3	73.9	0	44.1
Isopoda-ni-ben	0	0	0	21.6	0	0	0	0	0	21.4	0	4.5	26.7	0	5.3	0	0	0
Mysida-carn-ben	0	0	0	0	4.8	7.7	0	0	0	0	0	0	0	0	0	0	0	0
Copepoda-susp-pel	0	0	0	0	0	0	0	0	32.4	0	0	0	0	33.3	5.3	0	0	58.8
Clupeiiformes-carn-pel	0	0	0	0	4.8	0	8.7	3.3	0	0	0	0	0	0	0	0	0	0
Gadiformes-carn-pel	9.8	20	0	0	4.8	15.4	0	13.3	0	3.6	15.0	0	0	0	31.6	0	59.3	0
Gadiformes-carn-ni	0	26.7	0	0	0	0	0	13.3	0	0	0	0	0	0	0	0	0	0
Actinopteri other-carn-dem	2.4	20	0	0	0	0	0	6.7	0	3.6	5.0	0	0	0	0	0	0	0
Perciformes-carn-dem	4.9	6.7	0	0	0	0	8.7	0	2.7	3.6	10	0	0	0	0	17.4	0	0
Perciformes-carn-pel	0	6.7	0	0	0	3.8	13.0	16.7	0	3.6	10	0	0	0	0	4.3	7.4	0
Actinopteri other-carn-pel	0	0	0	0	0	0	0	3.3	0	0	0	0	0	0	0	0	0	0
Actinopteri other-ni-ni	24.4	26.7	0	8.1	19.0	7.7	26.1	33.3	0	10.7	40	0	6.7	33.3	15.8	13.0	29.6	0
Actinaria-carn-ben	0	0	0	0	0	0	0	0	0	0	0	0	6.7	0	0	0	0	0
Echinodermata other-ni-ben	0	0	10	5.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinoidea-omn-ben	4.9	13.3	90	94.6	0	0	0	0	0	0	0	9.1	43.3	0	0	0	0	0
Ophiuridea-carn-ben	2.4	0	53.3	48.6	0	0	0	0	0	0	10	63.6	66.7	0	0	0	0	0
Bivalvia-susp-ben	12.2	13.3	10	45.9	0	0	0	3.3	0	0	5.0	0	13.3	0	0	0	0	0
Bivalvia-dep-ben	2.4	6.7	76.7	40.5	0	0	0	0	0	3.6	0	13.6	13.3	0	0	0	0	0
Bivalvia-ni-ben	9.8	13.3	3.3	2.7	0	0	0	0	0	0	15.0	4.5	10	0	0	0	0	0
Cephalopoda-carn-dem	4.9	33.3	0	0	0	7.7	0	0	5.4	14.3	20	0	3.3	0	10.5	0	3.7	0
Gastropoda-carn-ben	7.3	26.7	23.3	13.5	0	3.8	0	0	2.7	0	0	4.5	0	0	0	0	0	2.9
Gastropoda-susp-ben	0	0	0	0	0	0	0	0	0	0	5.0	0	0	0	0	0	0	0
Gastropoda-ni-ben	7.3	0	0	0	0	0	0	0	0	0	5.0	0	0	0	0	0	0	0
Mollusca other-ni-ben	2.4	0	0	2.7	0	0	0	0	0	35.7	0	4.5	0	0	0	0	0	0

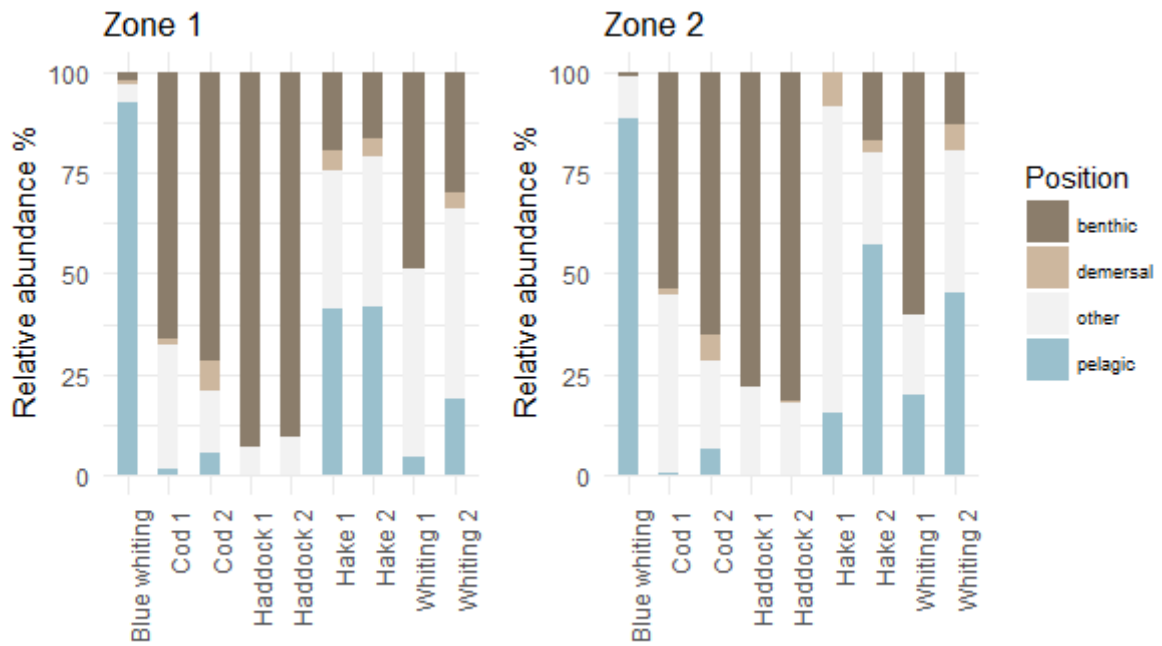
Appendix V: Relative abundance (%) of prey groups for each predator category and for both zones.

	Zone 1									Zone 2								
	Cod 1	Cod 2	Haddock 1	Haddock 2	Whiting 1	Whiting 2	Hake 1	Hake 2	Blue whiting	Cod 1	Cod 2	Haddock 1	Haddock 2	Whiting 1	Whiting 2	Hake 1	Hake 2	Blue whiting
Polychaeta-carn-ben	0.6	1.3	0.2	0.5	0	2.1	0	0	0	0	0.3	0	0	0	0	0	0	0
Polychaeta-dep-ben	0.9	0.7	2.3	0.3	9.3	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta-ni-ben	1.9	0	1.7	1.6	4.7	4.3	0	2.1	0	0	0	8.5	3.2	0	0	0	0	0
Amphipoda-dep-ben	0	0	4.4	0.9	0	0	0	0	0	0	0	0	2.6	0	0	0	0	0
Amphipoda-carn-ben	0.3	0	0	1.6	0	0	0	0	0	0.5	0	3.4	0	0	0	0	0	0
Amphipoda-ni-ni	0.3	0	5.9	6.6	2.3	4.3	0	0	0	0.5	0.3	16.9	14.8	0	9.7	0	0	0.4
Amphipoda-carn-pel	0	0	0	0	0	8.5	0	0	48.1	0	0.3	0	0	0	16.1	12.1	0	18.5
Cumacea-dep-ben	0	0	0.6	0	0	0	2.4	0	0	0	0	0	0	0	0	0	0	0
Brachyura-carn-ben	25.8	42.3	0.2	1.9	2.3	2.1	0	0	0	19.0	19.8	3.4	7.1	0	0	0	0	0
Caridea-carn-ben	22.0	12.8	2.5	3.8	20.9	14.9	17.1	12.5	0.6	12.2	18.8	6.8	0.6	60	9.7	0	17.1	0
Anomura-carn-ben	5.3	5.4	0	1.1	0	0	0	0	0	15.9	19.5	1.7	0	0	0	0	0	0.4
Astacidea-carn-ben	1.6	2.0	0	0	0	0	0	0	0	0.2	3.4	0	0	0	0	0	0	0
Caridea-carn-pel	0	0	0	0	0	0	29.3	8.3	37.2	0	0	0	0	0	0	1.7	0	4.4
Eumalacostraca-ni-ni	27.4	4.0	1.3	2.6	34.9	36.2	19.5	8.3	4.2	43.1	17.8	5.1	1.9	13.3	16.1	70.7	0	9.7
Isopoda-ni-ben	0	0	0	1.6	0	0	0	0	0	1.4	0	1.7	9.7	0	3.2	0	0	0
Mysida-carn-ben	0	0	0	0	11.6	4.3	0	0	0	0	0	0	0	0	0	0	0	0
Copepoda-susp-pel	0	0	0	0	0	0	0	0	7.4	0	0	0	0	20	3.2	0	0	65.6
Clupeiformes-carn-pel	0	0	0	0	2.3	0	4.9	2.1	0	0	0	0	0	0	0	0	0	0
Gadiformes-carn-pel	1.6	4.7	0	0	2.3	8.5	0	8.3	0	0.2	3.7	0	0	0	25.8	0	51.4	0
Gadiformes-carn-ni	0	4.0	0	0	0	0	0	8.3	0	0	0	0	0	0	0	0	0	0
Actinopteri other-carn-dem	0.3	2.0	0	0	0	0	0	4.2	0	0.2	0.3	0	0	0	0	0	0	0
Perciformes-carn-dem	0.6	2.0	0	0	0	0	4.9	0	0.3	0.6	3.7	0	0	0	0	8.6	0	0
Perciformes-carn-pel	0	0.7	0	0	0	2.1	7.3	18.8	0	0.5	2.3	0	0	0	0	1.7	5.7	0
Actinopteri other-carn-pel	0	0	0	0	0	0	0	4.2	0	0	0	0	0	0	0	0	0	0
Actinopteri other-ni-ni	3.1	7.4	0	0.3	9.3	6.4	14.6	20.8	0	0.8	4.0	0	1.3	6.7	9.7	5.2	22.9	0
Actinaria-carn-ben	0	0	0	0	0	0	0	0	0	0	0	1.3	0	0	0	0	0	0
Echinodermata other-ni-ben	0	0	0.6	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinoidea-omn-ben	0.9	1.3	40.1	66.3	0	0	0	0	0	0	0	3.4	21.3	0	0	0	0	0
Ophiuridea-carn-ben	0.3	0	3.2	2.4	0	0	0	0	0	0	0.7	30.5	24.5	0	0	0	0	0
Bivalvia-susp-ben	1.9	1.3	0.6	3.5	0	0	0	2.1	0	0	1.0	0	3.9	0	0	0	0	0
Bivalvia-dep-ben	0.3	0.7	34.7	3.9	0	0	0	0	0	0.2	0	13.6	4.5	0	0	0	0	0
Bivalvia-ni-ben	1.3	1.3	0.2	0.1	0	0	0	0	0	0	1.0	1.7	2.6	0	0	0	0	0
Cephalopoda-carn-dem	0.6	3.4	0	0	0	4.3	0	0	0.6	0.6	2.3	0	0.6	0	6.5	0	2.9	0
Gastropoda-carn-ben	1.3	2.7	1.5	0.8	0	2.1	0	0	1.6	0	0	1.7	0	0	0	0	0	0.9
Gastropoda-susp-ben	0	0	0	0	0	0	0	0	0	0	0.3	0	0	0	0	0	0	0
Gastropoda-ni-ben	0.9	0	0	0	0	0	0	0	0	0	0.3	0	0	0	0	0	0	0
Mollusca other-ni-ben	0.6	0	0	0.1	0	0	0	0	0	4.5	0	1.7	0	0	0	0	0	0

Appendix VI: Rarefaction curves for the five Gadiformes for each size class and each zone (the orange line represents $n = 15$ sampling units, the lowest common denominator).

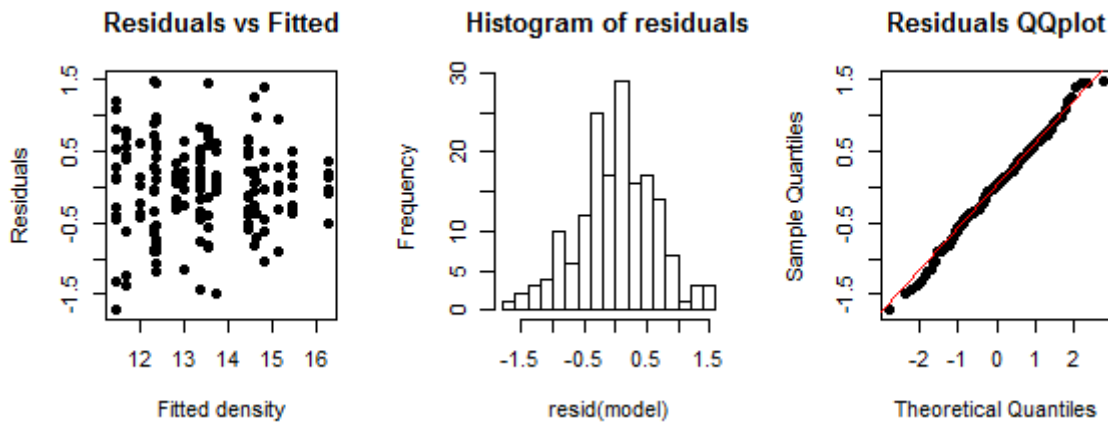


Appendix VII: Relative abundance (%N) of prey position in the water column (benthic, demersal, pelagic or non-identified) in the digestive content of each predator categories for both zones.

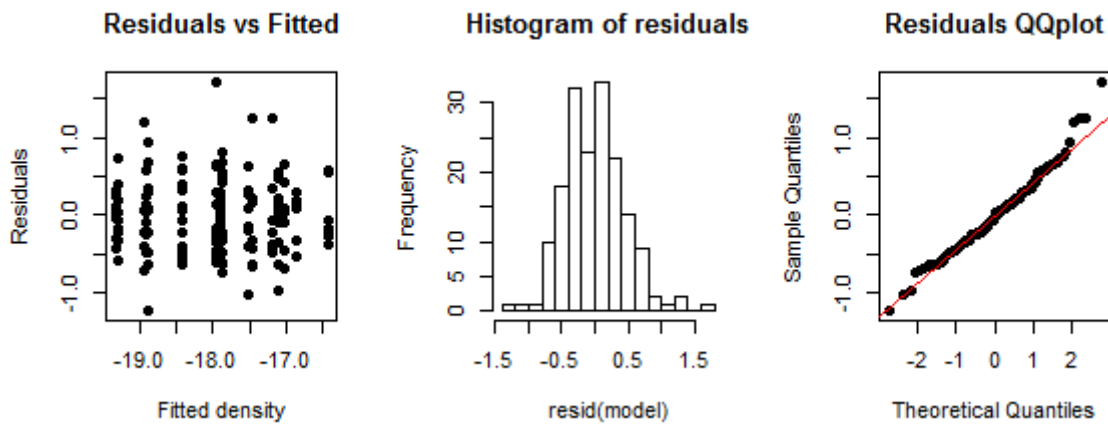


Appendix VIII: Residuals' analyses for Gaussian linear model on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

$$\delta^{15}\text{N} \sim \text{zone} + \text{predator category} + \text{zone} * \text{predator category}$$



$$\delta^{13}\text{C} \sim \text{zone} + \text{predator category} + \text{zone} * \text{predator category}$$



Appendix IX: Summary of the M_N and M_C (where the null hypothesis corresponds to the nullity of the difference between the first coefficient for a given factor and the other coefficients)

	$\delta^{15}\text{N}$					$\delta^{13}\text{C}$				
	Estimate	Std. Error	t value	Pr(> t)		Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	11.42	0.19	61.09	7.14E-109	***	-18.89	0.14	-137.74	1.71E-161	***
Cod 1	3.04	0.25	12.14	3.87E-24	***	1.78	0.18	9.66	1.62E-17	***
Cod 2	3.39	0.31	11.02	4.05E-21	***	1.70	0.23	7.52	4.51E-12	***
Haddock 1	0.90	0.27	3.32	0.001	**	0.95	0.20	4.77	4.33E-06	***
Haddock 2	1.94	0.25	7.62	2.48E-12	***	1.36	0.19	7.29	1.55E-11	***
Hake 1	0.24	0.29	0.83	0.406		-0.40	0.21	-1.89	0.060	
Hake 2	0.92	0.25	3.62	0.000	***	0.47	0.19	2.50	0.014	*
Whiting 1	0.58	0.30	1.97	0.051		-0.03	0.22	-0.12	0.902	
Whiting 2	2.13	0.25	8.35	3.92E-14	***	1.01	0.19	5.39	2.63E-07	***
zone2	1.95	0.28	7.03	6.62E-11	***	0.98	0.20	4.82	3.52E-06	***
Cod 1:zone2	-0.94	0.41	-2.31	0.022		-0.74	0.30	-2.48	0.014	*
Cod 2:zone2	-0.47	0.44	-1.06	0.291		-0.22	0.33	-0.69	0.493	
Haddock 1:zone2	-1.47	0.42	-3.52	0.001	***	-2.36	0.31	-7.70	1.64E-12	***
Haddock 2:zone2	-0.16	0.41	-0.38	0.701		-0.48	0.30	-1.61	0.109	
Hake 1:zone2	-0.61	0.43	-1.42	0.158		-0.62	0.31	-1.97	0.051	
Hake 2:zone2	-0.57	0.40	-1.44	0.152		-0.45	0.29	-1.53	0.128	
Whiting 1:zone2	0.67	0.48	1.39	0.167		-0.02	0.35	-0.06	0.951	
Whiting 2:zone2	-0.90	0.39	-2.29	0.024	*	-0.55	0.29	-1.90	0.059	

Appendix X-A: Overlaps between ellipses of the 9 predator categories in the zone 1.

A value represents the proportion of the estimated standard ellipse area (SEAc) of a species (in line) overlapped by the ellipse of another species (in column). For example, 58% of the Cod 1 ellipse is overlapped by Cod 2 and 31% of the Cod 2 ellipse is overlapped by Cod 1.

Zone 1	Cod 1	Haddock 1	Whiting 1	Hake 1	Blue whiting	Cod 2	Haddock 2	Whiting 2	Hake 2
Cod 1		0.00	0.00	0.00	0.00	0.58	0.00	0.08	0.00
Haddock 1	0.00		0.01	0.00	0.08	0.00	0.04	0.06	0.09
Whiting 1	0.00	0.04		0.48	0.99	0.00	0.00	0.00	0.08
Hake 1	0.00	0.00	0.24		0.60	0.00	0.00	0.00	0.00
Blue whiting	0.00	0.08	0.20	0.24		0.00	0.00	0.00	0.05
Cod 2	0.31	0.00	0.00	0.00	0.00		0.00	0.11	0.00
Haddock 2	0.00	0.11	0.00	0.00	0.00	0.00		0.21	0.00
Whiting 2	0.07	0.14	0.00	0.00	0.00	0.17	0.16		0.04
Hake 2	0.00	0.69	0.13	0.00	0.44	0.00	0.01	0.15	

Appendix X-B: Overlaps between ellipses of the 9 predator categories in the zone 2.

Zone 2	Cod 1	Haddock 1	Whiting 1	Hake 1	Blue whiting	Cod 2	Haddock 2	Whiting 2	Hake 2
Cod 1		0.00	0.00	0.00	0.00	0.00	0.80	0.02	0.00
Haddock 1	0.00		0.00	0.90	0.00	0.00	0.00	0.00	0.00
Whiting 1	0.00	0.00		0.00	0.03	0.00	0.07	0.17	0.07
Hake 1	0.00	0.08	0.00		0.00	0.00	0.00	0.00	0.00
Blue whiting	0.00	0.00	0.10	0.00		0.00	0.00	0.00	0.39
Cod 2	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00
Haddock 2	0.38	0.00	0.17	0.00	0.00	0.00		0.31	0.00
Whiting 2	0.02	0.00	0.67	0.00	0.00	0.00	0.49		0.11
Hake 2	0.00	0.00	0.47	0.00	0.66	0.00	0.00	0.18	



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Titre français : Etude compare de l'écologie trophique de cinq espèces de Gadiformes en mer Celtique à partir de deux approches : les isotopes stables et les contenus digestifs

Titre anglais : Investigating the trophic ecology of five species of Gadiformes in the Celtic Sea combining stable isotopes and gut contents.

Résumé (1600 caractères maximum) :

L'approche écosystémique des pêches se traduit techniquement par le développement de modèles explicitant la structure des réseaux trophiques et les interactions entre espèces. Un travail en amont de ces modèles est essentiel afin de déterminer les interactions trophiques entre espèces, ainsi que les éventuels besoins de considération des classes de taille différentes ou de spatialisation. En utilisant des contenus digestifs et des compositions isotopiques, l'écologie trophique des cinq espèces de gadiformes a été étudiée en s'attachant à répondre également aux questions de shifts ontogénétiques et de différence spatiale. Les espèces étudiées sont la morue, l'églefin, le merlan, le merlu et le merlan bleu et possèdent donc des traits biologiques communs. Elles sont également capturées par des pêcheries mixtes en mer Celtique. Ainsi, cette étude montre une certaine ségrégation des niches trophiques de ces cinq espèces avec des spécificités locales. Des changements de régimes alimentaires apparaissent essentiellement pour le merlu et dans une moindre mesure pour le merlan et l'églefin. Enfin, une ségrégation spatiale n'apparaît pas nettement mais différents indices tendent à nous faire imaginer des disparités en termes de ressources disponibles et structure trophique. La combinaison de ces deux d'approches permet d'avoir une vision plus fournie, nuancée et diversifiée, et parfois contradictoire.

Abstract (1600 caractères maximum) :

Ecosystem-based fisheries management is technically possible through the development of models relying on food web structure and species interactions. In order to determine the trophic interactions between species, potential consideration of size classes and potential spatial consideration of such models, it is necessary to study feeding ecology. Using gut contents and stable isotopes, we studied the trophic ecology of five gadiformes species. We also analyzed ontogenetic shifts in trophic niche and the effect of the depth through two zones. Species are cod, haddock, whiting, hake and blue whiting and share biological traits. They are captured by mixed-fisheries in the Celtic Sea. Hence, this study showed segregation in the trophic niche of these species and local feeding strategies. Moreover, changes in diet occurred for hake and to a lesser extend whiting and haddock. Finally, it was difficult to conclude on a spatial difference but several clues tended to exhibit differences in available and consumed resources and food web structure. Combining both approaches was a real asset for this study as it enables us to have a more interesting, nuanced and diverse vision of the trophic interactions.

Mots-clés : Gadiformes, contenus digestifs, compétition trophique, changements ontogénétiques, considération spatiale, double approche méthodologique

Key Words: Gadiformes, gut contents, isotopes, trophic competition, ontogenetic shifts, spatial consideration, dual methodologic approach