Deep–Sea Research I 182 (2022) 103708

Contents lists available at ScienceDirect

Deep-Sea Research Part I

journal homepage: www.elsevier.com/locate/dsri

Diet consistency but large-scale isotopic variations in a deep-sea shark: The case of the velvet belly lantern shark, *Etmopterus spinax*, in the northeastern Atlantic region and Mediterranean Sea

Lucien Besnard[a,*], Laurent Duchatelet[b], Christopher S. Bird[c,d], Gaël Le Croizier[e], Loïc Michel[f], Nicolas Pinte[b], Gilles Lepoint[g], Gauthier Schaal[a], Rui P. Vieira[c,h], Jorge M.S. Gonçalves[i], Ulrich Martin[b], Jérôme Mallefet[b]

[a] Univ Brest, CNRS, IRD, Ifremer, LEMAR, F-29280, Plouzane, France
[b] University of Louvain - UCLouvain, Earth and Life Institute, Marine Biology Laboratory, Croix du Sud 3, 1348, Louvain-la-Neuve, Belgium
[c] Centre for Environment, Fisheries, & Aquaculture Sciences (CEFAS), Pakefield Road, Lowestoft, UK
[d] Ocean and Earth Science, University of Southampton, National Oceanography Centre, Southampton, UK
[e] UMR Géosciences Environnement Toulouse (GET), Observatoire Midi Pyrénées (OMP), 14 Avenue Edouard Belin, 31400, Toulouse, France
[f] Univ Brest, Ifremer, CNRS, Unité Biologie et Ecologie des Ecosystèmes marins Profonds (BEEP), F-29280, Plouzane, France
[g] University of Liège (ULg), Laboratoire d'Ecologie trophique et isotopique (LETIS), B6 Sart Tilman, 4000, Liège, Belgium
[h] School of Environmental Sciences, University of East Anglia, Norwich, UK
[i] CCMAR - Centro de Ciências do Mar, Universidade do Algarve, 8005-139, Faro, Portugal

ARTICLE INFO

Keywords:
Trophic ecology
Stable isotopes
Stomach content
Mesopredator
Food webs
Benthopelagic predator

ABSTRACT

Deep-sea elasmobranchs are commonly reported as bycatch of deep-sea fisheries and their subsequent loss has been highlighted as a long-running concern to the ecosystem ecological functioning. To understand the possible consequences of their removal, information on basic ecological traits, such as diet and foraging strategies, is needed. Such aspects have been widely studied through stomach content analysis but the lack of long-term dietary information requires other tools to be used such as stable isotopes. This study examines nitrogen and carbon isotope compositions of the velvet belly lantern shark, *Etmopterus spinax*, one of the most impacted shark species in northeastern Atlantic fisheries as a result of accidental catches. *E. spinax* was sampled at four different locations, characterized by contrasting oceanographic and ecological conditions: the western Mediterranean Sea (near the Balearic Islands), the southern Iberian upwelling system, Rockall Trough and southwestern Norwegian fjords. Stomach content analysis revealed similar prey species among sites, with a diet dominated by Euphausiacea (mostly *Meganyctiphanes norvegica*) and an ontogenetic shift towards small teleost fishes, cephalopods or other crustaceans. Despite these similarities, muscle stable isotope compositions differed across sampled locations. Rather than clear dietary differences, the contrasted isotopic values are likely to reflect differences in environmental settings and biogeochemical processes affecting nutrient dynamics at the base of the food webs.

1. Introduction

Under the footprint of anthropogenic activities and climate change, many coastal and epipelagic fisheries have significantly declined (Chavez et al., 2003; Pinsky et al., 2011; Tu et al., 2018), diverting fishing efforts toward deep-sea stocks (Bailey et al., 2009; Devine et al., 2006; Priede et al., 2011; Vieira et al., 2019). As a consequence, significant population decreases have been observed in these deep water ecosystems with unknown and potentially disruptive impacts on ecological processes and functions (Benn et al., 2010; Vieira et al., 2020). However, despite their ecological importance, fragility and current state of exploitation, deep-sea ecosystems are still relatively understudied compared to their shallower counterparts (Benn et al., 2010; Thurber et al., 2014). In order to predict how deep-sea ecosystems will respond to natural or human-induced changes, information on the functioning of deep-sea communities is urgently needed (Howell et al., 2021).

Previous descriptions of deep-sea habitats have established that food webs are complexly structured and include a range of trophic levels

---

* Corresponding author.Laboratoire des Sciences de l'Environnement Marin (LEMAR), UMR 6539 CNRS/UBO/IRD/IFREMER, BP 70, 29280, Plouzané, France.
E-mail address: lbesnard.research@gmail.com (L. Besnard).

https://doi.org/10.1016/j.dsr.2022.103708
Received 8 July 2021; Received in revised form 18 January 2022; Accepted 28 January 2022

fuelled by a mixture of primary production, secondary production and benthic recycling (Newman et al., 2011; Shipley et al., 2017b; Trueman et al., 2014). Due to the absence of light for autochthonous primary production, deep-sea fauna relies on the downward vertical transport of nutrients (Polunin et al., 2001; Preciado et al., 2017), either actively by species diel vertical migrations or passively due to particulate organic matter sinking and re-suspension (Trueman et al., 2014). Within these food webs, deep-sea elasmobranch species are meso-to top predators (Churchill et al., 2015; Simpfendorfer and Kyne, 2009) which are of critical importance through their potential top-down or more complex regulation of communities (Heithaus et al., 2008; Shipley et al., 2017a). By connecting different depth layers, they also influence energy flux and carbon cycling, further enhancing their key ecological role (Trueman et al., 2014). Unfortunately, information on deep-sea sharks is still lacking due to the logistical challenges of accessing and studying them (Hussey et al., 2018; Moura et al., 2018; Simpfendorfer and Kyne, 2009).

In deep-sea sharks, most trophic studies have relied upon stomach content analysis (Barría et al., 2018; Cortés, 1999). Even if this approach allows a complete qualitative description of the diet, it requires a large number of samples, represents only a snapshot of the last meal(s) and differences in digestion rates may also bias the importance of prey items (Albo-Puigserver et al., 2015). In contrast, biochemical tracers such as stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) can help to describe the trophic structure, niche width and energy fluxes on a long-term basis with potential quantitative approaches (Layman et al., 2012; Shipley et al., 2017a). Carbon isotope signatures are considered as a good proxy to characterize the primary producers at the base of food webs (Fry and Sherr, 1984; Layman et al., 2012). Nitrogen isotope composition is mainly used as a proxy of trophic position due to a global increase in $\delta^{15}N$ signal from prey to predator (Cabana and Rasmussen, 1994; Post, 2002) and has been linked to foraging depth in benthopelagic communities (Trueman et al., 2014). By extension, the combination of carbon and nitrogen isotopes constitutes a proxy of the trophic niche crucial for assessing the ecological role of a given species or population (Newsome et al., 2007).

Deep-sea shark isotopic values depend on their diet but also on the isotopic compositions at the base of food webs, which exhibit spatial and temporal variations (Magozzi et al., 2017; Somes et al., 2010). Environmental conditions and local biogeochemical processes are known to affect baseline isotopic profiles due to changes in nutrient dynamics. For example, latitudinal differences in baseline isotopic values can be influenced by temperature (Magozzi et al., 2017; Rau et al., 1997), river discharges (Chouvelon et al., 2012) and upwelling events (Lopez-Lopez et al., 2017; Puccinelli et al., 2019). The extent to which large-scale spatial variations in isotopic baselines are reflected in deep-sea ichtyofauna remains unclear. Moreover, deep-sea sharks are mobile species that can shift their feeding ground while migrating. Isotopically, this shift will follow baseline changes and these variations need to be considered when analysing the trophic niche of a species over time or space (Bird et al., 2018; Lorrain et al., 2015).

Along the northeastern Atlantic and Mediterranean continental shelfs and slopes, the trophic ecology of a small deep-sea shark, the velvet belly lantern shark, *Etmopterus spinax* (Linnaeus, 1758), has been extensively studied using stomach content analysis (Klimpel et al., 2003; Neiva et al., 2006; Valls et al., 2017). Beyond those habitats, luminous velvet belly lantern sharks inhabit deep layers of fjords in Norway (Claes et al., 2010; Duchatelet et al., 2021). The first objective of this study is to present a description of the species diet inside these semi-enclosed habitats. More generally, throughout its distribution area, only a few studies took into account stable isotopes to specifically investigate *E. spinax* trophic habitat (Albo-Puigserver et al., 2015; Valls et al., 2017). Consequently, the second objective of this study is to investigate muscle carbon and nitrogen isotopic compositions of *E. spinax* at four different locations in the Mediterranean Sea and in the northeastern Atlantic to gain long-term dietary data. Information on the trophic ecology of *E. spinax* gathered by stomach content analysis were ultimately compared to stable isotope values and discussed in terms of local habitat ecological characteristics and physical processes affecting nutrient dynamics.

2. Materials and methods

2.1. Stomach content

In Norway, stomach content analysis of *Etmopterus spinax* came from eleven scientific expeditions from 2008 to 2012 inside the Raunefjord (Fig. 1). Based on morphological analysis of less-digested or undigested component, preys were identified at the lowest taxonomic level possible. For Euphausiacea, eyes were digested at a lower rate than the rest of the body parts. Therefore, each pair of eyes was identified as one Euphausiacea individual unless morphological characteristics allowed identification to the species level. Cephalopods were identified through their remaining beaks. For large fishes, species identification was possible when the whole body was present or based on dental bone dimension. To assess and compare prey composition, four indices were calculated: the numeric percentage %N (a prey item abundance as a percent of the total prey abundance), the gravimetric percentage %W (a prey item remaining mass as a percent of the total prey mass), the occurrence percentage %O (number of stomachs containing a prey item in percent compare to all stomachs) and finally the index of relative importance IRI: $IRI = (\%N + \%W) \times \%O$ (Cortés, 1997). Empty stomachs were not considered in indices calculation.

2.2. Stable isotope analysis

From 2014 to 2017, *Etmopterus spinax* specimens were sampled in four different areas of the northeast Atlantic and the Mediterranean Sea (Fig. 1). Individuals from Rockall Trough and Portugal were sampled during annual-fisheries surveys run by Marine Science Scotland (MSS) and Instituto Português do Mar e da Atmosfera (IPMA) respectively. Additional samples were collected in Portugal from bycatches of the commercial black scabbardfish (*Aphanopus carbo*) longline and of the crustacean bottom trawl fisheries. In the Mediterranean Sea, *E. spinax* samples from the Balearic Islands were obtained from research cruises conducted by the Mediterranean International Trawl Survey (MEDITS). In the Raunefjord (Norway), sharks were caught using deep-water longlines during scientific surveys. Each collected specimen was sexed and measured for total length (TL). Following dissection, white muscle was quickly frozen before analysis.

Samples were dried (48 h at 60 °C) and ground using pestle and mortar prior analysis. To avoid possible biases linked to polar compound contents (i.e. lipids, urea and trimethylamine *N*-oxide), all samples were washed in distilled water and their $\delta^{13}C$ mathematically corrected (Kiljunen et al., 2006; Li et al., 2016). Only samples from Norway obtained in 2017 underwent lipid chemical extraction using a modified Folch method based on repetitive wash in a 2:1 dichloromethane: methanol mix (Folch et al., 1957). Carbon and nitrogen isotope compositions were subsequently compared between individuals sampled in Norway in 2014 (i.e. corrected $\delta^{13}C$ values) and in 2017 (i.e. $\delta^{13}C$ values measured after extraction) at the same locations. They were all kept in the dataset because no significant difference in mean isotopic values was observed. As pure protein samples exhibit a C:N ratio around 3.0 for shark muscle, a good lipid, urea and trimethylamine *N*-oxide extraction for all samples were considered as those with a C:N ratio lower than 4.0 (Hussey et al., 2012) leading to no discard or additional chemical extractions.

Isotopic ratios (δ) were expressed in per mille (‰) following: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$ where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. $\delta^{13}C$ values are expressed with reference to the Vienna Pee Dee Belemnite and $\delta^{15}N$ values are expressed relative to Atmospheric air. Depending on sites and sampling year, samples were analysed in different facilities. Samples from Norway obtained in 2017

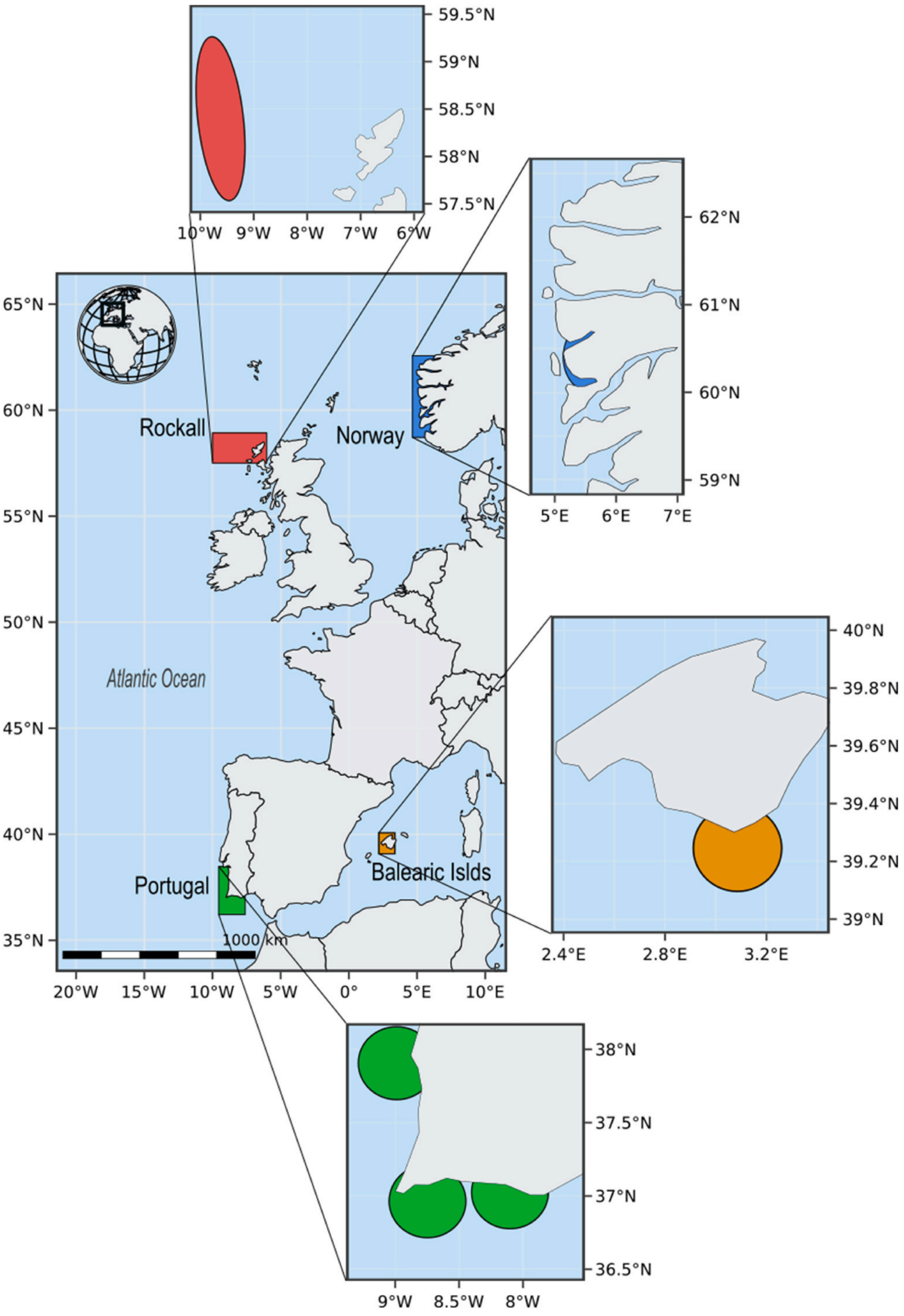

Fig. 1. Sampling locations of velvet belly lantern sharks, *Etmopterus spinax*. Sampling area in Norway both corresponds to specimens analysed for stomach content and stable isotopes analysis.

were processed in Liege (Oceanology, ULiege, Belgium) using a continuous flow isotope ratio mass spectrometer (Isoprime 100, Isoprime, United Kingdom) coupled to a C–N–S elemental analyser (MicroVario, Elementar, Germany). The certified substances, provided by the International Atomic Energy Agency IAEA (Vienna) were IAEA–CH–6 (sucrose) for δ^{13}C and IAEA-N-1 (ammonium sulfate) for δ^{15}N. Cod (*Gadus morhua*) muscle was used as a natural replicate showing precision of ±0.05‰ for δ^{13}C and ±0.23‰ for δ^{15}N (based on the standard deviation of the replicate measurements). Stable isotope ratios of samples obtained along the southern Iberian coast of Portugal in 2015 were measured using a Thermo Scientific Delta V Advantage IRMS via Conflo IV interface at Marinnova – Marine and Environmental Innovation, Technology and Services (Portugal). Samples from Rockall were analysed in two separate laboratories at the Scottish University Environmental Research Council (SUERC) and at the OEA Labs (Exeter, United Kingdom). The remaining samples from 2014 (i.e. Norway, Portugal and Balearic Islands) were processed in Elemtex (Gunnislake, United Kingdom). SUERC samples were run on a continuous flow Elementar vario PYRO cube elemental analyser coupled with a Thermo Scientific Delta V plus isotope ratio mass spectrometer (SUERC, NERC

LSMSF, East Kilbride facility). OEA Labs and Elemtex samples were run on a Thermo EA 110 elemental analyser linked to a Europa Scientific 2020 isotope ratio mass spectrometer running in continuous flow mode.

2.3. Data analysis

To assess isotopic baseline effects (i.e. change of primary producer isotopic composition) in each sampling site, isotope values were extracted from predictive models established for $\delta^{13}C$ (Magozzi et al., 2017) and $\delta^{15}N$ (Somes et al., 2010). Baseline values were extracted from the shark specific sampling locations (details of the specific latitudes and longitudes can be found in supplementary information). To overcome the baseline effect when comparing sharks between locations, the modelled baseline (i.e. phytoplankton) value was subtracted from shark stable isotope composition for each individual geographic coordinate: $\Delta X = \delta X_{shark} - \delta X_{phyto}$ where X is ^{13}C or ^{15}N. Modelled $\delta^{15}N$ baseline values inside the fjord were not available and values from the adjacent North Sea were subsequently used.

All statistical analyses were performed on the open source software R (R Core Team, 2020). For each site, the SIBER package (Jackson et al., 2011) was used to estimate the size of the isotopic niches (i.e. using $\Delta^{13}C$ and $\Delta^{15}N$) and their associated Layman metrics (Layman et al., 2007). Layman metrics were first used to characterize trophic niche space using four metrics. Isotopic ranges ($\Delta^{13}C$ rg and $\Delta^{15}N$ rg) described the distance between the most ^{13}C- and ^{15}N-enriched and most depleted individuals respectively, the total area (TA), the size of the isotopic niche based on convex hull area and the mean distance to the centroid (CD), the mean distance of each individual to the $\Delta^{13}C/\Delta^{15}N$ centroid. The other two metrics reflected trophic redundancy (i.e. the relative position of individuals from one another inside their isotopic niche). Mean nearest neighbor distance (NND and its standard deviation SDNND) measured the overall density of individuals clustering in a way that smaller NND and SDNND would describe small differences between individual isotopic values (Layman et al., 2007). The SIBER package was finally used to calculate the standard ellipse area (SEA) encompassing 40% of the bulk $\delta^{13}C/\delta^{15}N$ data at each site and the isotopic overlaps between them as a proportion of the non-overlapping area of two given ellipses.

For between-site comparisons, data was first checked for normality by Shapiro-Wilk tests and homoscedasticity by Bartlett's tests. As both conditions were not met, Kruskal-Wallis tests followed by Conover-Iman (C–I) post-hoc tests were applied. Comparisons between sexes were carried out using Student's t-tests or its non-parametric analogue, the Wilcoxon test. Pearson correlation tests were used to assess linear correlations between $\Delta^{13}C$, $\Delta^{15}N$ and TL. Finally, an analysis of covariance (ANCOVA) was performed to test for slope differences between linear regressions. For all statistical analyses, the significance threshold was set at $p < 0.05$.

3. Results

3.1. Stomach content analysis

In the Raunefjord, a set of 255 stomachs was analysed (on different specimens than for stable isotope analysis), among which 80 contained remains of prey items. Individuals that had food remains in their stomach ranged from 14.3 to 52.0 cm (TL) and included 51 females and 29 males. Euphausiacea was the major prey items of *E. spinax* with occurrence of *Meganyctiphanes norvegica*. Other prey included other crustaceans (mostly decapods), teleost fishes and cephalopods (Table 1). Until they reached 36.0 cm, Euphausiacea was the only prey item identified in the guts of *E. spinax*. Beyond this size, a diet shift was observed with occurrence of teleost fishes (such as *Scomber scombrus* and *Maurolicus muelleri*) and, to a lesser extent, decapods and cephalopods, therefore decreasing the importance of Euphausiacea overall.

Table 1
Number (N), numeric index (%N), gravimetric index (%W), occurrence index (%O) and index of relative importance (%IRI) for each prey item found in stomachs of *E. spinax* sampled from 2008 to 2012 in the Raunefjord (Norway).

Prey items	N	%N	%W	%O	%IRI
Euphausiacea	**39**	**41.94**	**7.04**	**55.10**	**45.55**
Meganyctiphanes norvegica	*12*	12.90	3.29	18.37	7.63
Euphausiacea unidentified	27	29.03	3.75	44.90	37.75
Decapoda	**7**	**7.53**	**17.17**	**14.29**	**5.95**
Pasiphaea sivado	*2*	2.15	1.71	4.08	0.40
Pasiphaea multidentata	*1*	1.08	1.28	2.04	0.12
Pandalus montagui	*1*	1.08	11.78	2.04	0.67
Decapoda unidentified	3	3.23	2.40	6.12	0.88
Crustacea unidentified	**10**	**10.75**	**5.92**	**20.41**	**5.74**
Teleostei	**7**	**7.53**	**52.76**	**14.29**	**14.54**
Scomber scombrus	*1*	1.08	50.00	2.04	2.67
Maurolicus muelleri	*2*	2.15	2.32	4.08	0.47
Teleostei unidentified	4	4.30	0.45	8.16	0.99
Cephalopoda	**10**	**10.75**	**4.53**	**18.37**	**4.74**
Rossia macrosoma	*5*	5.38	1.18	10.20	1.72
Cephalopoda unidentified	5	5.38	3.35	10.20	2.28
Unidentified prey	**20**	**21.51**	**12.57**	**40.82**	**23.48**

3.2. Stable isotopes

Muscle tissues from 147 *E. spinax* individuals were recovered from the four different stations (Table 2). As fishing methodologies differed between stations, capture depth significantly varied among sampling sites ($\chi^2_{146,3} = 98.2$, $p < 0.001$). Samples from Norway were caught on average at a depth of 243 m, which was significantly shallower than the other sites where catch depth was around 600 m. *E. spinax* TL varied from 11.0 to 57.4 cm and was significantly different between sampling sites ($\chi^2_{146,3} = 74.2$, $p < 0.001$). Individuals from Norway and Rockall were significantly larger than in Portugal and in the Balearic Islands (C–I test, $p < 0.001$ for all pairs of comparison). Females were larger than males considering the entire dataset ($W = 1860$, $p < 0.01$), as observed in Portugal ($W = 148$, $p < 0.05$) and in Norway ($t = -6.91$, $p < 0.001$). No significant difference in TL was found between sexes in the Balearic Islands and Rockall Trough.

Modelled phytoplanktonic baselines significantly differed among sites ($\chi^2_{146,3} = 101.4$, $p < 0.001$ for $\delta^{13}C_{phyto}$; $\chi^2_{146,3} = 142.5$, $p < 0.001$ for $\delta^{15}N_{phyto}$). $\delta^{13}C_{phyto}$ was significantly lower in the Balearic Islands than in Rockall and Portugal, while Norway displayed higher values than all other sites (C–I test, $p < 0.001$). Concerning $\delta^{15}N_{phyto}$, all locations significantly differed (C–I test, $p < 0.001$, for all pairs of comparison) with Portugal being the most ^{15}N-enriched, followed by the Balearic Islands, Rockall Trough and southwestern Norway.

Shark bulk isotopic values (i.e. $\delta^{13}C$ and $\delta^{15}N$) differed among sampling sites (Fig. 2) with the only overlapping SEAs (Standard Ellipse Areas) reported between *E. spinax* sampled in the Portugal Iberian system and Rockall Trough (39.89%). $\Delta^{15}N$ values differed between locations ($\chi^2_{146,3} = 118.3$, $p < 0.001$; Fig. 3a). Norway individuals exhibited the highest $\Delta^{15}N$ and individuals sampled in Portugal the lowest (C–I test, $p < 0.001$ for all pairs of comparison). Rockall $\Delta^{15}N$ value was also significantly higher than in Portugal (C–I test, $p < 0.01$). $\Delta^{13}C$ also varied significantly among sampling locations ($\chi^2_{146,3} = 89.4$, $p < 0.001$; Fig. 3b) with individuals from the Balearic Islands having the highest $\Delta^{13}C$ and individuals from Norway the lowest (C–I test, $p < 0.001$ for all pairs of comparison). *E. spinax* sampled in Rockall Trough and Portugal had similar $\Delta^{13}C$ (C–I test, $p > 0.05$). At each location, there was no depth-related or sex differences in $\Delta^{13}C$ and $\Delta^{15}N$ except in the Norwegian fjord where both values were significantly higher in males.

Individuals from Portugal had a singular profile encompassing the highest $\Delta^{13}C$ rg, TA and CD suggesting higher isotopic diversity (Table 3). In Norway and in the Balearic Islands, *E. spinax* presented the smallest TA, CD and the lowest $\Delta^{13}C$ and $\Delta^{15}N$ rg. While displaying intermediate TA and CD, *E. spinax* sampled in Rockall exhibited the

Table 2

Summary of stable isotope data from white muscle tissue of *E. spinax*, from different locations, showing sampling depth (in meters), number of samples analysed (including male:female sex ratio) and individual total length (TL). Sampled depth and TL are expressed in mean (minimum-maximum values). Carbon and nitrogen ratios are given as mean (standard deviation). All isotopic values are expressed in ‰ with $\delta^{13}C/\delta^{15}N$ representing *E. spinax* muscle isotopic composition, $\delta^{13}C_{phyto}$ and $\delta^{15}N_{phyto}$ the phytoplankton values extracted from predictive models and $\Delta^{13}C$ and $\Delta^{15}N$ the difference between shark muscle isotope values and phytoplankton modelled isotopic baselines.

Location	Depth (m)	N (M:F)	TL (cm)	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C_{phyto}$	$\delta^{15}N_{phyto}$	$\Delta^{13}C$	$\Delta^{15}N$
Balearic Islands	589 (230–754)	33 (17:16)	26.2 (11.0–57.4)	−17.8 (0.5)	10.0 (0.4)	−27.7	4.0	9.9 (0.5)	6.0 (0.4)
Norway	243 (230–250)	51 (18:33)	43.4 (33.0–53.0)	−18.6 (0.3)	12.5 (0.7)	−25.0	0.2	6.4 (0.3)	12.3 (0.7)
Portugal	569 (490–670)	44 (19:25)	28.3 (18.6–49.0)	−18.4 (0.5)	11.1 (0.6)	−25.1 (0.6)	5.9 (0.4)	6.7 (0.7)	5.3 (0.8)
Rockall	634 (500–850)	19 (11:8)	41.6 (19.5–55.0)	−18.3 (0.5)	11.6 (0.8)	−25.2 (0.1)	0.4	7.0 (0.5)	11.2 (0.8)

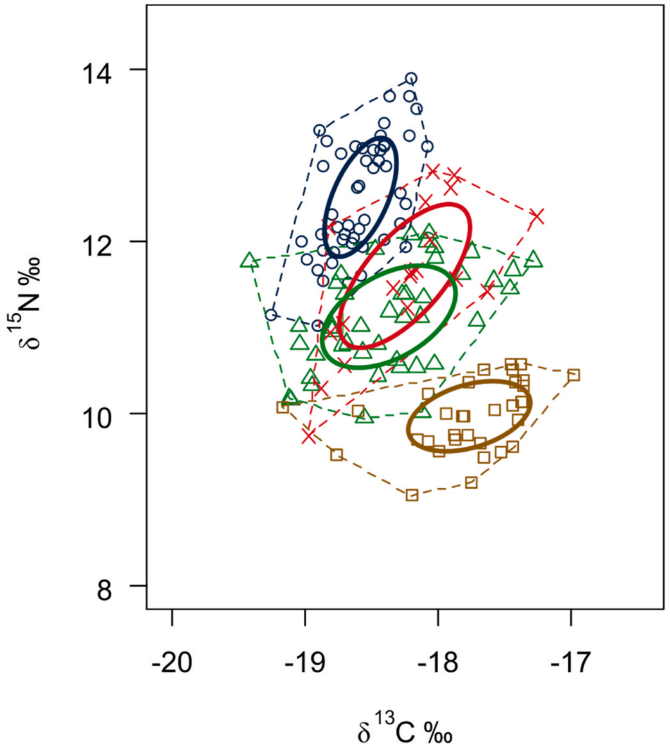

Fig. 2. Muscle $\delta^{13}C$ and $\delta^{15}N$ values of *E. spinax*. Brown square points correspond to the Balearic Islands, blue circle points to Norway, green triangle points to Portugal and red cross points to Rockall samples. Solid lines delimit the standard ellipse areas (SEA) and dashed lines the convex hull areas for each sampling location. The only overlapping regions between SEA occurs between Portugal and Rockall individuals (39.89%). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

highest $\Delta^{15}N$ rg.

For all sampling sites, significant linear relations were established between $\Delta^{15}N$ and TL (Fig. 4a). $\Delta^{15}N$ increased with TL in three sites: Portugal, Rockall and the Balearic Islands. *E. spinax* sampled in Portugal and Rockall had equivalent slopes while specimens from the Balearic Islands showed a flatter one (ANCOVA, $F = 5.83$ $p < 0.05$ for Rockall and $F = 21.32$ $p < 0.001$ for Portugal). Specimens in Norway were the only ones with a significant decrease in $\Delta^{15}N$ values with TL. $\Delta^{13}C$ increased with TL in the Balearic Islands and Rockall with no differences in slopes (Fig. 4b). At each location, linear regressions did not significantly change between sexes or with depth.

4. Discussion

4.1. Trophic ecology of E. spinax

4.1.1. Prey composition (Stomach content analysis)

In Norway, *E. spinax* stomach content composition inside the Raunefjord matched previous reports in the surrounding North and Norwegian Sea (Bergstad et al., 2003; Klimpel et al., 2003). The diet was dominated by *M. norvegica*, the most abundant prey in the ecosystem (Bergstad et al., 2003; Klimpel et al., 2003), with an ontogenetic diet switch toward the consumption of teleost fishes. The only difference was a later switch observed in the fjord, probably due to a sampling difference with the two previous studies as sampled individuals inside the fjord were larger.

At all locations sampled for stable isotope analysis, previously published studies have highlighted an ontogenetic shift in the diet of *E. spinax*, except for two studies on Portugal and the Balearic Islands (Table 4). Before the ontogenetic diet shift, Euphausiacea was generally the major prey item, mostly represented by the northern krill, *Meganyctiphanes norvegica*. Ontogenetic diet shift occurred at different lengths depending on the site, from 19.4 cm in Norway to 39.0 cm in Rockall Trough. Beyond these sizes, Euphausiacea decreased in importance due to the increasing occurrence of teleost fishes, cephalopods, or other crustaceans. This result was in line with previous analyses of *E. spinax* diet in the Atlantic Ocean and Mediterranean Sea (Bengil et al., 2019; Isbert et al., 2015; Preciado et al., 2009, 2017). In Rockall, the later shift toward the consumption of the decapod crustacean, *Pasiphaea tarda*, has been explained by larger individuals foraging closer to the sea bottom where prey availability is different (Mauchline and Gordon, 1983). Ontogenetic diet shifts are commonly observed in mesopredator fishes due to increasing body length, mouth gap and stomach size, hunting capacities and energetic demands, or to avoid intra-specific competition (Klimpel et al., 2003; Neiva et al., 2006).

Stomach contents analysed in the Balearic Islands showed contrasting results between studies. *E. spinax* either foraged following the previously described ontogenetic shift from small Euphausiacea to teleost fishes (Fanelli et al., 2009; Macpherson, 1980) or fed on cephalopods throughout their entire size range in more recent studies (Valls et al., 2011, 2017). A higher proportion of cephalopod consumption by *E. spinax* was previously observed in the adjacent Catalan Sea and has been linked to the high exploitation rate of the area, depleting fish stocks in favour of cephalopods (Barría et al., 2018; Doubleday et al., 2016). In deep-sea sharks, smaller adult size and earlier maturity due to oligotrophic conditions in the Mediterranean Sea could also explain cephalopod consumption by small specimens (Catarino et al., 2015; Massutí et al., 2004). However, this trend was not yet observed in *E. spinax* (Coelho et al., 2010).

4.1.2. Nitrogen and carbon isotope compositions ($\Delta^{15}N$ and $\Delta^{13}C$)

Stable isotope values were measured in multiple laboratories which may result in potential biases (Mill et al., 2008). The analysis of a reference sample (USGS 40 glutamic acid) to ensure comparability was performed on two of the four instruments used in this study (i.e. for

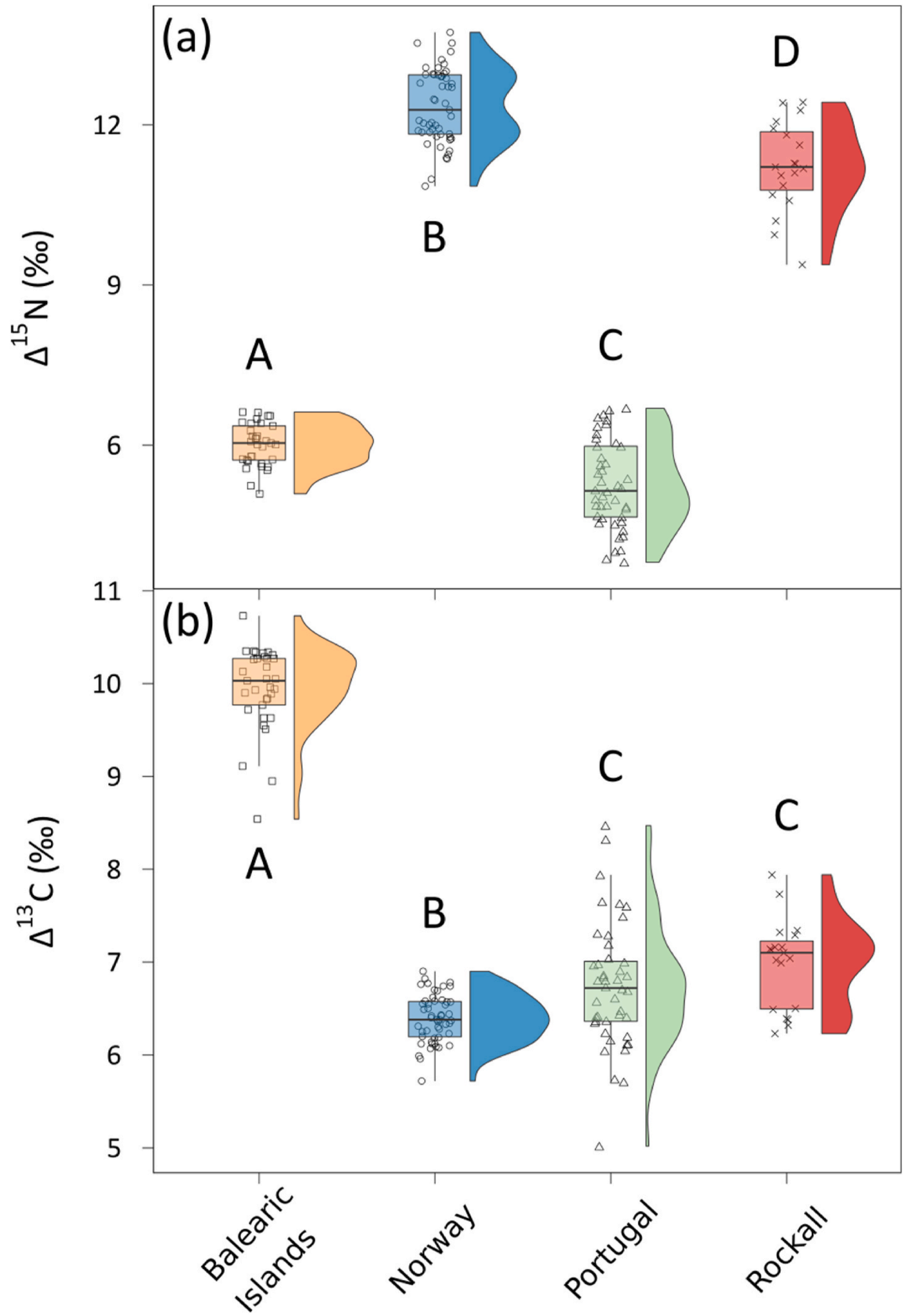

Fig. 3. Boxplots of Δ^{15}N (a) and Δ^{13}C (b) values of *E. spinax* at each location. Significant differences are indicated by letters ($p < 0.05$).

Table 3

Summary of Layman metrics calculated on *E. spinax* isotopic niches (Δ^{13}C/Δ^{15}N values) and based on convex hull areas. Δ^{13}C rg and Δ^{15}N rg represent both isotopic ranges, TA the total area, CD the mean distance to centroid, NND (as mean ± standard deviation) the nearest neighbor distance (details of Layman metrics calculation can be found in Materials and Methods). All values are presented in ‰ except for TA (in ‰^{2}).

Location	Δ^{13}C rg	Δ^{15}N rg	TA	CD	NND
Balearic Islands	2.19	1.53	1.85	0.51	0.16 ± 0.16
Norway	1.18	2.88	1.95	0.66	0.12 ± 0.07
Portugal	3.45	2.88	5.88	0.95	0.21 ± 0.14
Rockall	1.71	3.04	2.84	0.79	0.28 ± 0.21

Elemtex and OEA laboratories). δ^{13}C values were on average 0.23 ± 0.40‰ higher from Elemtex than those obtained from OEA Labs. This difference, although significant, is quite small in regard of isotope patterns interpreted in this study, and comparable to error estimates considered acceptable in many ecological studies using stable isotope tracers. Nevertheless, this difference was subtracted from all shark δ^{13}C values measured by Elemtex. There were no observed differences in δ^{15}N values. Specimens sampled in Norway in 2017 and in Portugal in 2015 were analysed in facilities where glutamic acid samples could not be measured. However, all facilities follow recommended procedures for stable isotope analyses, and use certified materials that are all calibrated against the same international references (Vienna Pee Dee Belemnite for δ^{13}C, Atmospheric air for δ^{15}N). Therefore, we argue that analytical biases are unlikely to have a major impact on stable isotope trends

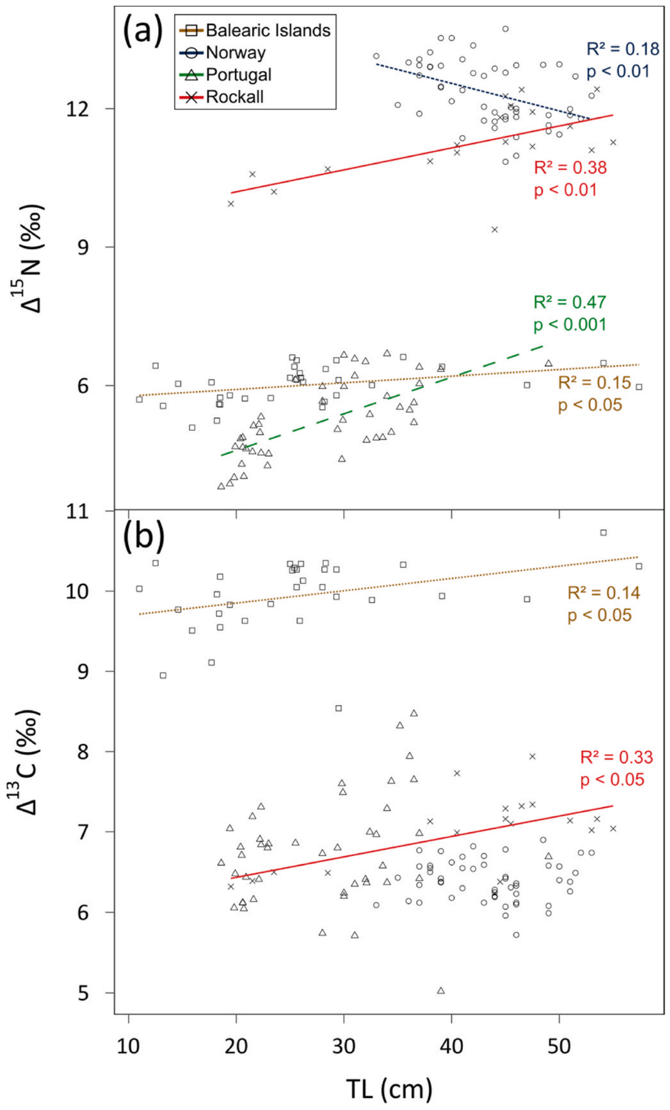

Fig. 4. Relationships between individual Δ^{15}N (a)/Δ^{13}C (b) values and total length (TL) of *E. spinax*. Pearson linear regressions were applied for each location with their corresponding R^2 and p-value reported in the figure.

depicted here.

Ecological differences in *E. spinax* isotopic niches between sites were analysed by standardising values (i.e. Δ^{15}N and Δ^{13}C) to mitigate baseline effects (Bird et al., 2018). The absence of significant differences in isotopic ratios between females and males suggests a uniform diet across sexes, as globally observed in stomach content analyses of the species.

Nitrogen isotope composition is commonly used as a proxy of trophic position in marine food web (Cabana and Rasmussen, 1994). *M. norvegica*, the main prey of *E. spinax*, is a low trophic level omnivorous species feeding on both phytoplankton and copepods (Gomes et al., 2001; Kaartvedt et al., 2002). It is therefore unlikely that divergences in food web length might have contributed to the marked Δ^{15}N differences. Moreover, the suspected Δ^{15}N switch with TL was not observed at all sites. The relevance of Δ^{15}N as a good proxy of the trophic level could be conditioned by the occurrence of a clear ontogenetic change as observed in Portugal and Rockall sharks. Along the Iberian slope, the rapid sedimentation of phytoplankton (Lopez-Lopez et al., 2017) results in a direct linear energy flow, with phytoplankton mainly consumed by Euphausiacea, themselves consumed by secondary predators such as juvenile *E. spinax* (Gomes et al., 2001). Older *E. spinax* fed on higher trophic level species such as *Pasiphaea sivado* or *Micromesistius poutassou* (Neiva et al., 2006; Santos and Borges, 2001) explaining the ^{15}N-enrichment (Fig. 4a). In Rockall the same phenomenon is suspected to occur, with *M. norvegica* being replaced by possibly ^{15}N-enriched prey like the decapod crustacean *P. tarda* or the teleost *M. muelleri* (Mauchline and Gordon, 1983). However, more recent information on *E. spinax* diet are needed to confirm this effect as the only stomach content description available came from samples obtained between 1973 and 1981 (Mauchline and Gordon, 1983) and major environmental and anthropogenic changes could have modified the shark diet over time.

In benthopelagic communities, the higher degradation of sinking particles is leading to higher δ^{15}N values in deeper species (Trueman et al., 2014). Bathymetric segregation at the inter- and intra-specific levels is commonly observed among deep-sea sharks (Clarke et al., 2005; Neat et al., 2015) and has been reported for *E. spinax* (Coelho and Erzini, 2010). At each site, changes in capture depth were not associated with an increase in δ^{15}N or Δ^{15}N values. However, differences in *E. spinax* vertical segregation of maturity stages or bathymetric constraint among sites could explain Δ^{15}N differences and would need to be specifically addressed in the future.

Except for the Balearic Islands, *E. spinax* likely shared a pelagic habitat owing to their lower Δ^{13}C values (Fig. 3b). This is in accordance with the high rate of phytoplanktonic production fuelling the deeper layers of Portugal and Rockall continental slope systems (Gomes et al., 2001; Mauchline and Gordon, 1983). In the Raunefjord, *E. spinax* Δ^{13}C values agree with a diet dominated by pelagic preys (Bergstad et al., 2003; Klimpel et al., 2003).

E. spinax sampled in the Balearic Islands exhibited higher Δ^{13}C values (Fig. 3b), suggesting reliance on different forms of primary production, such as ^{13}C-enriched benthic prey (Madurell et al., 2008). It could correspond to the higher occurrence of cephalopods in *E. spinax* diet at that site (i.e. mainly Teuthoidea and Sepioidea). These cephalopods exhibit an ontogenetic diet shift from benthic to pelagic prey (Valls et al., 2011, 2017). As scavenging was not reported in the area and because mature cephalopods exceed *E. spinax* length, sharks are expected to forage on juvenile early benthic life stages possibly explaining their Δ^{13}C values.

4.2. *Habitat characteristics influence on isotope compositions*

E. spinax in the Iberian slope ecosystems and Rockall Trough, even if mainly relying on pelagic production, presented similarly high indices of isotopic diversity (Table 3). Both sites are large continuous continental slopes (Mauchline and Gordon, 1991; Ribeiro et al., 2005) and topographic similarities might drive these similitudes. Indeed, ichthyofauna inhabiting continental slope ecosystems are known to integrate nutrient from a mixture of pelagic and benthic origins (Mauchline and Gordon, 1991; Trueman et al., 2014). This trophic diversity is possibly further enhanced by the access to different topographic features (e.g. canyons, banks or steep slopes) (Romero-Romero et al., 2016; Rowden et al., 2010).

In Portugal, from spring to late summer, changes in wind-driven mesoscale currents induce an upwelling of nutrient-rich cold water (Loureiro et al., 2005) that influences shelf and slope ecosystems over great distances (Pérez et al., 2010; Ribeiro et al., 2005) and resulting in shifting isotopic signals. Due to upwelling seasonality and geographical influence, temporal and spatial variations in δ^{13}C values are observed in species at the base of the food web (Lopez-Lopez et al., 2017). The small-scale variability in the activity of the upwelling associated with the spatial scale at which individuals were fished might contribute to the overall isotopic variability, a dynamic also observed in Rockall where the pelagic production is seasonally stimulated over the shelf area (White et al., 2005).

The Balearic Islands deep ecosystem is characterized by a smaller continental slope, deep escarpments and canyons (Acosta et al., 2003). While topographic conditions might be similar to large continental slope

Table 4

Summary of *E. spinax* feeding habits. For each study, total length of sampled individuals (TL), length at which ontogenetic diet shift occurred (TL OS) and major prey before and after *E. spinax* ontogenetic diet shift (except for two studies describing constant diet) are reported. Prey groups accounting for more than 50% IRI (Index of Relative Importance) are given in bold character.

Location	TL (cm)	TL OS (cm)	Major prey before OS	Major prey after OS	Publication
Balearic Islands	10.0–49.0	~20.0	**Euphausiacea (*M. norvegica*)**, Cephalopoda	Osteichthyes, Cephalopoda	Macpherson, 1980
	15.0–45.0	~25.0 (*)	Natantian decapods, Euphausiacea, Cephalopoda	**Osteichthyes** (Stomiidae, Myctophidae), Cephalopoda	Fanelli et al., 2009
	11.0–47.0	–	**Cephalopoda**, Telesotei, Natantids		Valls et al., 2011
	10.2–48.3	~22.0 (**)	Cephalopoda, Telesotei, Decapods, Euphausiacea	Cephalopoda, Telesotei, Decapods	Valls et al., 2017
Norway	31.0–52.0	~36.0	**Euphausiacea (*M. norvegica*)**	**Euphausiacea (*M. norvegica*)**, Teleostei, Cephalopoda	This study
Portugal	11.0–33.0	–	**Euphausiacea (*M. norvegica*)**, Teleostei, Cephalopoda		Santos & Borges, 2001
	9.1–40.1	~28.0 (***)	**Euphausiacea (*M. norvegica*)**, Natantids, Teleostei	Natantids, Teleostei (Gadoids mainly), Euphausiacea, Cephalopoda	Neiva et al., 2006
Rockall	12.6–53.0	~39.0	Euphausiacea (*M. norvegica*), Teleostei (*M. muelleri*), Cephalopoda, Decapoda	Decapoda (*Pasiphaea tarda*), Cephalopoda, Other Teleostei	Mauchline & Gordon, 1983

(*) Specimens $<$ 15.0 cm presented a diet focused on Euphausiacea, fishes and to a less extend Decapoda, specimens between 15.0 and 25.0 cm had a diet mainly focused on Cephalopoda and to a less extend Decapoda and specimens $>$ 25.0 cm focused mainly on fish. (**) OS corresponded to the absence of Euphausiacea in the diet after 22.0 cm (***) Two OS with the first one observed around 17.0 cm when E. spinax individuals evolved from a diet focusing at 95.11% (IRI) on Euphausiacea to a diet with 50.31% (IRI) of Euphausiacea completed with Natantids (39.98% IRI) and teleost fishes (9.03% IRI). The second OS is described in the Table.

systems, the main difference resides in the oligotrophic nature of the Mediterranean Sea (Bosc et al., 2004; Estrada, 1996). Such conditions might result in the observed small isotopic niche due to limited Δ^{15}N variations and high redundancy index (Table 3). Still, their broad Δ^{13}C rg, with some ^{13}C-depleted specimens, might reveal the existence of resource partitioning within the population, which could be fuelled by a diversity of prey of both benthic and pelagic origin (Albo-Puigserver et al., 2015; Madurell et al., 2008; Newman et al., 2011). Such coupling between reservoirs and reliance on other habitat is probably a response to oligotrophic conditions reducing pelagic production and prey availability (Valls et al., 2014). Sharks could also forage inside canyons where higher benthic prey densities are present (Massutí et al., 2004). Other ^{13}C-enriched sources have been identified in the Balearic Islands such as food falls (Cartes et al., 2016) or seagrass exportation at deeper layers (Boudouresque et al., 2016) but this remains speculative and will need further studies to investigate. Water temperature, higher in the Mediterranean Sea compared to the other locations, could also have led to differences in isotopic values compared to the other locations. Indeed, temperature can affect isotopic turnover rates and discrimination factors (Bloomfield et al., 2011), beyond latitudinal baseline δ^{13}C and δ^{15}N variations (Magozzi et al., 2017).

Fjords are narrow, deep ecosystems delimited by steep flanking slopes (Harris, 2012). Therefore, possible bathymetric constraints (Coelho and Erzini, 2010) might reduce *E. spinax* foraging habitat diversity and explain isotopic niche limited space and high redundancy. Δ^{15}N values (Fig. 3a) may result from the important particle residency time (Saino and Hattori, 1980) in deep basins. Indeed, even if fjords are dynamic systems with quick surface water turnover (Asplin et al., 1999), they are stratified with sometimes limited exchanges between reservoirs (Aure et al., 1996). As sinking particles are trapped in deep layers, especially in fjords, they would exhibit higher baseline δ^{15}N values than suggested by surface model values (Saino and Hattori, 1980; Trueman et al., 2014). Even if experiencing an ontogenetic shift toward higher trophic position preys, *E. spinax* Δ^{15}N decreased with TL (Fig. 4a). Sharks sampled in the Raunefjord were only mature individuals probably post-ontogenetic diet shift. This decrease could result from a shift in feeding habitat with early maturing sharks foraging strictly in fjords while larger sharks could forage outside in offshore areas. This hypothesis would ultimately lead to the observed decreasing Δ^{15}N values with length, as modelled δ^{15}N baseline was extracted from outside of the fjord. Another possibility is that large sharks change their foraging behaviour towards active predation of smaller organisms with lower trophic positions, although this is not supported by the stomach content analysis.

Finally, relatively small deep-sea sharks can exhibit important horizontal migrations (Catarino et al., 2015; Rodríguez-Cabello and Sánchez, 2014). *E. spinax* population structure suggested it might connect distant areas across the northeastern Atlantic with a potential isolation of Mediterranean individuals (Gubili et al., 2016; McMillan et al., 2017). Migrating *E. spinax* are likely to feed on different isotopic baselines and would integrate them throughout the course of their migration (Carlisle et al., 2012). In this study, a significant overlap in bulk isotope niches occurred between Portugal and Rockall samples (Fig. 2), reinforcing the idea of potential large-scale migration of *E. spinax* in the Atlantic Ocean. Conversely, the non-overlapping and reduced isotopic niche spaces observed in the Balearic Islands and in the fjord suggest a certain level of residency, even more when diet is found homogeneous among distant sites. This strengthens the hypothesis of a separated population in the Mediterranean Sea, probably due to the bathymetric limitation at the Strait of Gibraltar (Catarino et al., 2015; Gubili et al., 2016). In Norway, while changes in Δ^{15}N values have been hypothetically linked to migrations outside the fjords, trophic redundancy and isotopic discrimination suggest *E. spinax* could be sedentary in the region. This hypothesis matches the separate stocks of *E. spinax* in Norwegian waters previously identified by vertebral chemistry variations (McMillan et al., 2017).

5. Conclusion

At each location, including inside the fjords, *Etmopterus spinax* appears as a benthopelagic mesopredator, mainly feeding on aggregations of *Meganyctiphanes norvegica* at a juvenile stage with increasing consumption of larger prey, such as teleost fishes, with increasing length. Nonetheless, isotopic niche spaces varied significantly among sampling sites. Observed differences in carbon and nitrogen isotope compositions are likely to be explained by differences in habitat features (e.g. productive continental slopes *vs* oligotrophic conditions in the Mediterranean Sea) and other oceanographic characteristics (e.g. upwelling regime). Resulting variations in pelagic primary production rates and sequestration across the water column are likely to affect the strength of mesopelagic linkage toward deep reservoirs and subsequently *E. spinax* trophodynamic and isotopic values. Our results suggest that considering the influence of nutrient cycle on isotopic baselines allows a better understanding of the trophic ecology of predators in deep-sea habitats.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

The authors would like to thank Christopher J. Somes, Sarah Magozzi and Katie St John Glew for providing the phytoplankton-modelled values; the various teams that helped C.S.B. with data collection (Clive Trueman, Frances Neat, MEDITS); James Bell for his suggestions to early stages of the manuscript; as well as Tomas Sørlie, from the Espeland marine station, for the technical support during the shark sampling in Norway. This work was partially supported by FRIA grant (F.R.S-FNRS Belgium) to L.D. and N.P.. G.L and J.M are appointed by F.R.S-FNRS Belgium. The authors thank the Université de Bretagne Occidentale (UBO) and the École Doctorale des Sciences de la Mer et du Littoral (EDSML) for L.B. doctoral grant. This project is supported by ISblue project, interdisciplinary graduate school for the blue planet (ANR-17-EURE-0015) and co-funded by a grant from the French government under the program "Investissements d'Avenir". This study is the contribution BRC #374 of the Biodiversity Research Center (UCLouvain) from the Earth and Life Institute Biodiversity (ELIV) and the "Center Interuniversitaire de Biologie Marine" (CIBIM). Thanks are also due to the Portuguese Science Foundation for the financial support to R.P.V. (SFRH/BD/84030/2012) and CCMAR (UIDB/04326/2020) through national funds.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2022.103708.

References

Acosta, J., Canals, M., Lopez-Martinez, J., Muñoz, A., Herranz, P., Urgeles, R., Palomo, C., Casamor, J.L., 2003. The Balearic Promontory geomorphology (western Mediterranean): morphostructure and active processes. Geomorphology 49, 177–204. https://doi.org/10.1016/S0169-555X(02)00168-X.

Albo-Puigserver, M., Navarro, J., Coll, M., Aguzzi, J., Cardona, L., Sáez-Liante, R., 2015. Feeding ecology and trophic position of three sympatric demersal chondrichthyans in the northwestern Mediterranean. Mar. Ecol. Prog. Ser. 524, 255–268. https://doi.org/10.3354/meps11188.

Asplin, L., Salvanes, A.G.V., Kristoffersen, J.B., 1999. Nonlocal wind-driven fjord–coast advection and its potential effect on plankton and fish recruitment. Fish. Oceanogr. 8, 255–263. https://doi.org/10.1046/j.1365-2419.1999.00109.x.

Aure, J., Molvær, J., Stigebrandt, A., 1996. Observations of inshore water exchange forced by a fluctuating offshore density field. Mar. Pollut. Bull. 33, 112–119. https://doi.org/10.1016/S0025-326X(97)00005-2.

Bailey, D.m., Collins, M.a., Gordon, J.d. m., Zuur, A.f., Priede, I.g., 2009. Long-term changes in deep-water fish populations in the northeast Atlantic: a deeper reaching effect of fisheries? Proc. R. Soc. B Biol. Sci. 276, 1965. https://doi.org/10.1098/rspb.2009.0098, 1969.

Barría, C., Navarro, J., Coll, M., 2018. Feeding habits of four sympatric sharks in two deep-water fishery areas of the western Mediterranean Sea. Deep-Sea Res. Part A Oceanogr. Res. Pap. 142, 34–43. https://doi.org/10.1016/j.dsr.2018.09.010.

Bengil, F., Bengil, E.G.T., Mavruk, S., Heral, O., Karaman, O.D., Ozaydin, O., 2019. Feeding ecology of four demersal shark species (Etmopterus spinax, Galeus melastomus, Scyliorhinus canicula and Squalus blainville) from the Eastern Aegean sea. Turk. J. Fish. Aquat. Sci. 19, 475–484.

Benn, A.R., Weaver, P.P., Billet, D.S.M., van den Hove, S., Murdock, A.P., Doneghan, G. B., Bas, T.L., 2010. Human activities on the deep seafloor in the north east Atlantic: an Assessment of spatial extent. PLoS One 5, e12730. https://doi.org/10.1371/journal.pone.0012730.

Bergstad, O., Wik, D., Hildre, O., 2003. Predator-prey relationships and food sources of the Skagerrak deep-water fish assemblage. J. Northwest Atl. Fish. Sci. 31, 165–180. https://doi.org/10.2960/J.V31.A12.

Bird, C.S., Veríssimo, A., Magozzi, S., Abrantes, K.G., Aguilar, A., Al-Reasi, H., Barnett, A., Bethea, D.M., Biais, G., Borrell, A., Bouchoucha, M., Boyle, M., Brooks, E. J., Brunnschweiler, J., Bustamante, P., Carlisle, A., Catarino, D., Caut, S., Cherel, Y., Chouvelon, T., Churchill, D., Ciancio, J., Claes, J., Colaço, A., Courtney, D.L., Cresson, P., Daly, R., de Necker, L., Endo, T., Figueiredo, I., Frisch, A.J., Hansen, J. H., Heithaus, M., Hussey, N.E., Iitembu, J., Juanes, F., Kinney, M.J., Kiszka, J.J., Klarian, S.A., Kopp, D., Leaf, R., Li, Y., Lorrain, A., Madigan, D.J., Maljković, A., Malpica-Cruz, L., Matich, P., Meekan, M.G., Ménard, F., Menezes, G.M., Munroe, S.E. M., Newman, M.C., Papastamatiou, Y.P., Pethybridge, H., Plumlee, J.D., Polo-Silva, C., Quaeck-Davies, K., Raoult, V., Reum, J., Torres-Rojas, Y.E., Shiffman, D.S., Shipley, O.N., Speed, C.W., Staudinger, M.D., Teffer, A.K., Tilley, A., Valls, M., Vaudo, J.J., Wai, T.-C., Wells, R.J.D., Wyatt, A.S.J., Yool, A., Trueman, C.N., 2018. A global perspective on the trophic geography of sharks. Nat. Ecol. Evol. 2, 299–305. https://doi.org/10.1038/s41559-017-0432-z.

Bloomfield, A.L., Elsdon, T.S., Walther, B.D., Gier, E.J., Gillanders, B.M., 2011. Temperature and diet affect carbon and nitrogen isotopes of fish muscle: can amino acid nitrogen isotopes explain effects? J. Exp. Mar. Biol. Ecol. 399, 48–59. https://doi.org/10.1016/j.jembe.2011.01.015.

Bosc, E., Bricaud, A., Antoine, D., 2004. Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. Global Biogeochem. Cycles 18. https://doi.org/10.1029/2003GB002034.

Boudouresque, C.F., Pergent, G., Pergent-Martini, C., Ruitton, S., Thibaut, T., Verlaque, M., 2016. The necromass of the Posidonia oceanica seagrass meadow: fate, role, ecosystem services and vulnerability. Hydrobiologia 781, 25–42. https://doi.org/10.1007/s10750-015-2333-y.

Cabana, G., Rasmussen, J.B., 1994. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. Nature 372, 255–257. https://doi.org/10.1038/372255a0.

Carlisle, A.B., Kim, S.L., Semmens, B.X., Madigan, D.J., Jorgensen, S.J., Perle, C.R., Anderson, S.D., Chapple, T.K., Kanive, P.E., Block, B.A., 2012. Using stable isotope analysis to understand the migration and trophic ecology of northeastern Pacific white sharks (Carcharodon carcharias). PLoS One 7, e30492. https://doi.org/10.1371/journal.pone.0030492.

Cartes, J.E., Soler-Membrives, A., Stefanescu, C., Lombarte, A., Carrassón, M., 2016. Contributions of allochthonous inputs of food to the diets of benthopelagic fish over the northwest Mediterranean slope (to 2300m). Deep-Sea Res. Part A Oceanogr. Res. Pap. 109, 123–136. https://doi.org/10.1016/j.dsr.2015.11.001.

Catarino, D., Knutsen, H., Veríssimo, A., Olsen, E.M., Jorde, P.E., Menezes, G., Sannæs, H., Stanković, D., Company, J.B., Neat, F., Danovaro, R., Dell'Anno, A., Rochowski, B., Stefanni, S., 2015. The Pillars of Hercules as a bathymetric barrier to gene flow promoting isolation in a global deep-sea shark (Centroscymnus coelolepis). Mol. Ecol. 24, 6061–6079. https://doi.org/10.1111/mec.13453.

Chavez, F.P., Ryan, J., Lluch-Cota, S.E., C, M.Ñ., 2003. From Anchovies to Sardines and back: multidecadal change in the Pacific ocean. Science 299, 217–221. https://doi.org/10.1126/science.1075880.

Chouvelon, T., Spitz, J., Caurant, F., Mèndez-Fernandez, P., Chappuis, A., Laugier, F., Le Goff, E., Bustamante, P., 2012. Revisiting the use of δ15N in meso-scale studies of marine food webs by considering spatio-temporal variations in stable isotopic signatures – the case of an open ecosystem: the Bay of Biscay (North-East Atlantic). Prog. Oceanogr. 101, 92–105. https://doi.org/10.1016/j.pocean.2012.01.004.

Churchill, D.A., Heithaus, M.R., Vaudo, J.J., Grubbs, R.D., Gastrich, K., Castro, J.I., 2015. Trophic interactions of common elasmobranchs in deep-sea communities of the Gulf of Mexico revealed through stable isotope and stomach content analysis. Deep Sea Res. Part II Top. Stud. Oceanogr., Biology of Deep-Water Chondrichthyans 115, 92–102. https://doi.org/10.1016/j.dsr2.2014.10.011.

Claes, J.M., Aksnes, D.L., Mallefet, J., 2010. Phantom hunter of the fjords: Camouflage by counterillumination in a shark (Etmopterus spinax). J. Exp. Mar. Biol. Ecol. 388, 28–32. https://doi.org/10.1016/j.jembe.2010.03.009.

Clarke, M.W., Borges, L., Officer, R.A., 2005. Comparisons of trawl and longline catches of deepwater elasmobranchs west and north of Ireland. J. Northwest Atl. Fish. Sci. 35, 429–442.

Coelho, R., Erzini, K., 2010. Depth distribution of the velvet belly, Etmopterus spinax, in relation to growth and reproductive cycle: the case study of a deep-water lantern shark with a wide-ranging critical habitat. Mar. Biol. Res. 6, 381–389. https://doi.org/10.1080/17451000802644706.

Coelho, R., Rey, J., Sola, L.G. de, Carvalho, J.F. de, Erzini, K., 2010. Comparing Atlantic and Mediterranean populations of the velvet belly lanternshark, Etmopterus spinax, with comments on the efficiency of density-dependent compensatory mechanisms. Mar. Biol. Res. 6, 373–380. https://doi.org/10.1080/17451000903300885.

Cortés, E., 1999. Standardized diet compositions and trophic levels of sharks. ICES J. Mar. Sci. 56, 707–717. https://doi.org/10.1006/jmsc.1999.0489.

Cortés, E., 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can. J. Fish. Aquat. Sci. 54, 726–738. https://doi.org/10.1139/f96-316.

Devine, J.A., Baker, K.D., Haedrich, R.L., 2006. Deep-sea fishes qualify as endangered. Nature 439. https://doi.org/10.1038/439029a, 29–29.

Doubleday, Z.A., Prowse, T.A.A., Arkhipkin, A., Pierce, G.J., Semmens, J., Steer, M., Leporati, S.C., Lourenço, S., Quetglas, A., Sauer, W., Gillanders, B.M., 2016. Global proliferation of cephalopods. Curr. Biol. 26, R406–R407. https://doi.org/10.1016/j.cub.2016.04.002.

Duchatelet, L., Claes, J.M., Delroisse, J., Flammang, P., Mallefet, J., 2021. Glow on sharks: state of the Art on Bioluminescence research. Oceans 2, 822–842. https://doi.org/10.3390/oceans2040047.

Estrada, M., 1996. Primary production in the northwestern Mediterranean. Sci. Mar. 60.

Fanelli, E., Rey, J., Torres, P., Sola, L.G. de, 2009. Feeding habits of blackmouth catshark Galeus melastomus Rafinesque, 1810 and velvet belly lantern shark Etmopterus spinax (Linnaeus, 1758) in the western Mediterranean. J. Appl. Ichthyol. 25, 83–93. https://doi.org/10.1111/j.1439-0426.2008.01112.x.

Folch, J., Lees, M., Sloane Stanley, G.H., 1957. A simple method for the isolation and purification of total lipides from animal tissues. J. Biol. Chem. 226, 497–509.

Fry, B., Sherr, E.B., 1984. δ13C measurements as indicators of carbon flow in marine and freshwater ecosystems. In: Rundel, P.W., Ehleringer, J.R., Nagy, K.A. (Eds.), Stable

Isotopes in Ecological Research, Ecological Studies. Springer, New York, NY, pp. 196–229. https://doi.org/10.1007/978-1-4612-3498-2_12.

Gomes, M.C., Serrão, E., de Fátima Borges, M., 2001. Spatial patterns of groundfish assemblages on the continental shelf of Portugal. ICES J. Mar. Sci. 58, 633–647. https://doi.org/10.1006/jmsc.2001.1052.

Gubili, C., Macleod, K., Perry, W., Hanel, P., Batzakas, I., Farrell, E.D., Lynghammar, A., Mancusi, C., Mariani, S., Menezes, G.M., Neat, F., Scarcella, G., Griffiths, A.M., 2016. Connectivity in the deep: Phylogeography of the velvet belly lanternshark. Deep-Sea Res. Part A Oceanogr. Res. Pap. 115, 233–239. https://doi.org/10.1016/j.dsr.2016.07.002.

Harris, P.T., 2012. Seafloor geomorphology—coast, shelf, and Abyss. In: Harris, P.T., Baker, E.K. (Eds.), Seafloor Geomorphology as Benthic Habitat. Elsevier, London, pp. 109–155. https://doi.org/10.1016/B978-0-12-385140-6.00006-2.

Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B., 2008. Predicting ecological consequences of marine top predator declines. Trends Ecol. Evol. 23, 202–210. https://doi.org/10.1016/j.tree.2008.01.003.

Howell, K.L., Hilário, A., Allcock, A.L., Bailey, D., Baker, M., Clark, M.R., Colaço, A., Copley, J., Cordes, E.E., Danovaro, R., Dissanayake, A., Escobar, E., Esquete, P., Gallagher, A.J., Gates, A.R., Gaudron, S.M., German, C.R., Gjerde, K.M., Higgs, N.D., Le Bris, N., Levin, L.A., Manea, E., McClain, C., Menot, L., Mestre, N.C., Metaxas, A., Milligan, R., Muthumbi, A.W.N., Narayanaswamy, B.E., Ramalho, S.P., Ramirez-Llodra, E., Robson, L.M., Rogers, A.D., Sellanes, J., Sigwart, J.D., Sink, K., Snelgrove, P.V.R., Stefanoudis, P.V., Sumida, P.Y., Taylor, M.L., Thurber, A.R., Vieira, R., Watanabe, H.K., Woodall, L.C., Xavier, J.R., 2021. A decade to study deep-sea life. Nat. Ecol. Evol. 5, 265–267. https://doi.org/10.1038/s41559-020-01352-5.

Hussey, N.E., MacNeil, M.A., Olin, J.A., McMeans, B.C., Kinney, M.J., Chapman, D.D., Fisk, A.T., 2012. Stable isotopes and elasmobranchs: tissue types, methods, applications and assumptions. J. Fish. Biol. 80, 1449–1484. https://doi.org/10.1111/j.1095-8649.2012.03251.x.

Hussey, N.E., Orr, J., Fisk, A.T., Hedges, K.J., Ferguson, S.H., Barkley, A.N., 2018. Mark report satellite tags (mrPATs) to detail large-scale horizontal movements of deep water species: first results for the Greenland shark (Somniosus microcephalus). Deep-Sea Res. Part A Oceanogr. Res. Pap. 134, 32–40. https://doi.org/10.1016/j.dsr.2018.03.002.

Isbert, W., Rodríguez-Cabello, C., Frutos, I., Preciado, I., Montero, F.E., Pérez-del-Olmo, A., 2015. Metazoan parasite communities and diet of the velvet belly lantern shark Etmopterus spinax (Squaliformes: Etmopteridae): a comparison of two deep-sea ecosystems. J. Fish. Biol. 86, 687–706. https://doi.org/10.1111/jfb.12591.

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER – stable Isotope Bayesian Ellipses in R. J. Anim. Ecol. 80, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x.

Kaartvedt, S., Larsen, T., Hjelmseth, K., Onsrud, M.S.R., 2002. Is the omnivorous krill Meganyctiphanes norvegica primarily a selectively feeding carnivore? Mar. Ecol. Prog. Ser. 228, 193–204. https://doi.org/10.3354/meps228193.

Kiljunen, M., Grey, J., Sinisalo, T., Harrod, C., Immonen, H., Jones, R.I., 2006. A revised model for lipid-normalizing δ13C values from aquatic organisms, with implications for isotope mixing models. J. Appl. Ecol. 43, 1213–1222. https://doi.org/10.1111/j.1365-2664.2006.01224.x.

Klimpel, S., Palm, H.W., Seehagen, A., 2003. Metazoan parasites and food composition of juvenile Etmopterus spinax (L., 1758) (Dalatiidae, Squaliformes) from the Norwegian Deep. Parasitol. Res. 89, 245–251. https://doi.org/10.1007/s00436-002-0741-1.

Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z. R., Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M., Bearhop, S., 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biol. Rev. 87, 545–562. https://doi.org/10.1111/j.1469-185X.2011.00208.x.

Layman, C.A., Arrington, D.A., Montaña, C.G., Post, D.M., 2007. Can stable isotope ratios Provide for community-wide measures of trophic structure? Ecology 88, 42–48. https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2.

Li, Y., Zhang, Y., Hussey, N.E., Dai, X., 2016. Urea and lipid extraction treatment effects on δ15N and δ13C values in pelagic sharks. Rapid Commun. Mass Spectrom. 30, 1–8. https://doi.org/10.1002/rcm.7396.

Lopez-Lopez, L., Preciado, I., Muñoz, I., Decima, M., Molinero, J.C., Tel, E., 2017. Does upwelling intensity influence feeding habits and trophic position of planktivorous fish? Deep-Sea Res. Part A Oceanogr. Res. Pap. 122, 29–40. https://doi.org/10.1016/j.dsr.2017.01.017.

Lorrain, A., Graham, B.S., Popp, B.N., Allain, V., Olson, R.J., Hunt, B.P.V., Potier, M., Fry, B., Galván-Magaña, F., Menkes, C.E.R., Kaehler, S., Ménard, F., 2015. Nitrogen isotopic baselines and implications for estimating foraging habitat and trophic position of yellowfin tuna in the Indian and Pacific Oceans. Deep Sea Res. Part II Top. Stud. Oceanogr., Impacts of climate on marine top predators 113, 188–198. https://doi.org/10.1016/j.dsr2.2014.02.003.

Loureiro, S., Newton, A., Icely, J., 2005. Microplankton composition, production and upwelling dynamics in Sagres (SW Portugal) during summer of 2001. Sientia Mar 69, 323–341.

Macpherson, E., 1980. Régime alimentaire de Galeus melastomus (Rafinesque, 1810), Etmopterus 8 spinax (L., 1758) et Scymnorhinus licha (Bonaterre, 1788), en Méditerranée Occidentale. Vie Milieu 30, 139–148.

Madurell, T., Fanelli, E., Cartes, J.E., 2008. Isotopic composition of carbon and nitrogen of suprabenthic fauna in the NW Balearic Islands (western Mediterranean). J. Mar. Syst., The Wrapping Up of the IDEA Project 71, 336–345. https://doi.org/10.1016/j.jmarsys.2007.03.006.

Magozzi, S., Yool, A., Zanden, H.B.V., Wunder, M.B., Trueman, C.N., 2017. Using ocean models to predict spatial and temporal variation in marine carbon isotopes. Ecosphere 8, e01763. https://doi.org/10.1002/ecs2.1763.

Massutí, E., Gordon, J., Moranta, J., Swan, S., Stefanescu, C., Merrett, N.R., 2004. Mediterranean and Atlantic deep-sea fish assemblages: differences in biomass composition and size-related structure. Sci. Mar. 68, 101–115.

Mauchline, J., Gordon, J., 1991. Oceanic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. Mar. Ecol.-Prog. Ser. - MAR ECOL-PROGR SER 74, 109–115. https://doi.org/10.3354/meps074109.

Mauchline, J., Gordon, J.D.M., 1983. Diets of the sharks and chimaeroids of the Rockall Trough, northeastern Atlantic Ocean. Mar. Biol. 75, 269–278. https://doi.org/10.1007/BF00406012.

McMillan, M.N., Izzo, C., Junge, C., Albert, O.T., Jung, A., Gillanders, B.M., 2017. Analysis of vertebral chemistry to assess stock structure in a deep-sea shark, Etmopterus spinax. ICES J. Mar. Sci. 74, 793–803. https://doi.org/10.1093/icesjms/fsw176.

Mill, A.C., Sweeting, C.J., Barnes, C., Al-Habsi, S.H., MacNeil, M.A., 2008. Mass-spectrometer bias in stable isotope ecology. Limnol Oceanogr. Methods 6, 34–39. https://doi.org/10.4319/lom.2008.6.34.

Moura, T., Fernandes, A., Figueiredo, I., Alpoim, R., Azevedo, M., 2018. Management of deep-water sharks' by-catch in the Portuguese anglerfish fishery: from EU regulations to practice. Mar. Pol. 90, 55–67. https://doi.org/10.1016/j.marpol.2018.01.006.

Neat, F.C., Burns, F., Jones, E., Blasdale, T., 2015. The diversity, distribution and status of deep-water elasmobranchs in the Rockall Trough, north-east Atlantic Ocean. J. Fish. Biol. 87, 1469–1488. https://doi.org/10.1111/jfb.12822.

Neiva, J., Coelho, R., Erzini, K., 2006. Feeding habits of the velvet belly lanternshark Etmopterus spinax (Chondrichthyes: Etmopteridae) off the Algarve, southern Portugal. J. Mar. Biol. Assoc. U. K. 86, 835–841. https://doi.org/10.1017/S0025315406013762.

Newman, M.C., Xu, X., Cotton, C.F., Tom, K.R., 2011. High mercury Concentrations reflect trophic ecology of three deep-water chondrichthyans. Arch. Environ. Contam. Toxicol. 60, 618–625. https://doi.org/10.1007/s00244-010-9584-4.

Newsome, S.D., Rio, C.M. del, Bearhop, S., Phillips, D.L., 2007. A niche for isotopic ecology. Front. Ecol. Environ. 5, 429–436.

Pérez, F.F., Padín, X.A., Pazos, Y., Gilcoto, M., Cabanas, M., Pardo, P.C., Doval, M.D., Farina-Busto, L., 2010. Plankton response to weakening of the Iberian coastal upwelling. Global Change Biol. 16, 1258–1267. https://doi.org/10.1111/j.1365-2486.2009.02125.x.

Pinsky, M.L., Jensen, O.P., Ricard, D., Palumbi, S.R., 2011. Unexpected patterns of fisheries collapse in the world's oceans. Proc. Natl. Acad. Sci. Unit. States Am. 108, 8317–8322. https://doi.org/10.1073/pnas.1015313108.

Polunin, N., Morales-Nin, B., Pawsey, W.E., Cartes, J., Pinnegar, J., Moranta, J., 2001. Feeding relationships in Mediterranean bathyal assemblages elucidated by nitrogen and carbon isotope data. Mar. Ecol. Prog. Ser. 220, 13–23. https://doi.org/10.3354/meps220013.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2.

Preciado, I., Cartes, J.E., Punzón, A., Frutos, I., López-López, L., Serrano, A., 2017. Food web functioning of the benthopelagic community in a deep-sea seamount based on diet and stable isotope analyses. Deep Sea Res. Part II Top. Stud. Oceanogr., Advances in deep-sea biology: biodiversity, ecosystem functioning and conservation 137, 56–68. https://doi.org/10.1016/j.dsr2.2016.07.013.

Preciado, I., Cartes, J.E., Serrano, A., Velasco, F., Olaso, I., Sánchez, F., Frutos, I., 2009. Resource utilization by Deep-sea sharks at the Le danois bank, Cantabrian sea, north-east Atlantic ocean. J. Fish. Biol. 75, 1331–1355. https://doi.org/10.1111/j.1095-8649.2009.02367.x.

Priede, I., Godbold, J., Niedzielski, T., Collins, M., Bailey, D., Gordon, J., Zuur, A., 2011. A review of the spatial extent of fishery effects and species vulnerability of the deep-sea demersal fish assemblage of the Porcupine Seabight, Northeast Atlantic Ocean (ICES Subarea VII). ICES J. Mar. Sci. 68, 281–289. https://doi.org/10.1093/icesjms/fsq045.

Puccinelli, E., McQuaid, C.D., Dobretsov, S., Christofoletti, R.A., 2019. Coastal upwelling affects filter-feeder stable isotope composition across three continents. Mar. Environ. Res. 147, 13–23. https://doi.org/10.1016/j.marenvres.2019.03.015.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rau, G.H., Riebesell, U., Wolf-Gladrow, D., 1997. CO2aq-dependent photosynthetic 13C fractionation in the ocean: a model versus measurements. Global Biogeochem. Cycles 11, 267–278. https://doi.org/10.1029/97GB00328.

Ribeiro, A.C., Peliz, Á., Santos, A.M.P., 2005. A study of the response of chlorophyll-a biomass to a winter upwelling event off Western Iberia using SeaWiFS and in situ data. J. Mar. Syst. 53, 87–107. https://doi.org/10.1016/j.jmarsys.2004.05.031.

Rodríguez-Cabello, C., Sánchez, F., 2014. Is Centrophorus squamosus a highly migratory deep-water shark? Deep-Sea Res. Part A Oceanogr. Res. Pap. 92, 1–10. https://doi.org/10.1016/j.dsr.2014.06.005.

Romero-Romero, S., Molina-Ramírez, A., Höfer, J., Duineveld, G., Rumín-Caparrós, A., Sanchez-Vidal, A., Canals, M., Acuña, J.L., 2016. Seasonal pathways of organic matter within the Avilés submarine canyon: food web implications. Deep-Sea Res. Part A Oceanogr. Res. Pap. 117, 1–10. https://doi.org/10.1016/j.dsr.2016.09.003.

Rowden, A.A., Schlacher, T.A., Williams, A., Clark, M.R., Stewart, R., Althaus, F., Bowden, D.A., Consalvey, M., Robinson, W., Dowdney, J., 2010. A test of the seamount oasis hypothesis: seamounts support higher epibenthic megafaunal biomass than adjacent slopes. Mar. Ecol. 31, 95–106. https://doi.org/10.1111/j.1439-0485.2010.00369.x.

Saino, T., Hattori, A., 1980. 15 N natural abundance in oceanic suspended particulate matter. Nature 283, 752–754. https://doi.org/10.1038/283752a0.

Santos, J., Borges, T., 2001. Trophic relationships in deep-water fish communities off Algarve, Portugal. In: Fish. Res., Deep-Water Fish And Fisheries:A Selection Of Papers Presented At The Ices Annual Science Conference In Lisbon, PORTUGAL, 51, pp. 337–341. https://doi.org/10.1016/S0165-7836(01)00257-0, 16-18 SEPTEMBER 1998.

Shipley, OliverN., Brooks, E.J., Madigan, D.J., Sweeting, C.J., Dean Grubbs, R., 2017. Stable isotope analysis in deep-sea chondrichthyans: recent challenges, ecological insights, and future directions. Rev. Fish Biol. Fish. 27, 481–497. https://doi.org/10.1007/s11160-017-9466-1.

Shipley, O.N., Polunin, N.V.C., Newman, S.P., Sweeting, C.J., Barker, S., Witt, M.J., Brooks, E.J., 2017. Stable isotopes reveal food web dynamics of a data-poor deep-sea island slope community. Food Webs 10, 22–25. https://doi.org/10.1016/j.fooweb.2017.02.004.

Simpfendorfer, C.A., Kyne, P.M., 2009. Limited potential to recover from overfishing raises concerns for deep-sea sharks, rays and chimaeras. Environ. Conserv. 36, 97–103. https://doi.org/10.1017/S0376892909990191.

Somes, C.J., Schmittner, A., Galbraith, E.D., Lehmann, M.F., Altabet, M.A., Montoya, J. P., Letelier, R.M., Mix, A.C., Bourbonnais, A., Eby, M., 2010. Simulating the global distribution of nitrogen isotopes in the ocean. Global Biogeochem. Cycles 24. https://doi.org/10.1029/2009GB003767.

Thurber, A.R., Sweetman, A.K., Narayanaswamy, B.E., Jones, D.O.B., Ingels, J., Hansman, R.L., 2014. Ecosystem function and services provided by the deep sea. Biogeosciences 11, 3941–3963. https://doi.org/10.5194/bg-11-3941-2014.

Trueman, C.N., Johnston, G., O'Hea, B., MacKenzie, K.M., 2014. Trophic interactions of fish communities at midwater depths enhance long-term carbon storage and benthic production on continental slopes. Proc. R. Soc. B Biol. Sci. 281, 20140669 https://doi.org/10.1098/rspb.2014.0669.

Tu, C.-Y., Chen, K.-T., Hsieh, C., 2018. Fishing and temperature effects on the size structure of exploited fish stocks. Sci. Rep. 8, 1–10. https://doi.org/10.1038/s41598-018-25403-x.

Valls, M., Quetglas, A., Moranta, J., Ordines, F., 2011. Feeding ecology of demersal elasmobranchs from the shelf and slope off the Balearic Sea (western Mediterranean). Sci. Mar. 75, 633–639. https://doi.org/10.3989/scimar.2011.75n4633.

Valls, M., Rueda, L., Quetglas, A., 2017. Feeding strategies and resource partitioning among elasmobranchs and cephalopods in Mediterranean deep-sea ecosystems. Deep-Sea Res. Part A Oceanogr. Res. Pap. 128, 28–41. https://doi.org/10.1016/j.dsr.2017.09.002.

Valls, M., Sweeting, C.J., Olivar, M.P., Fernández de Puelles, M.L., Pasqual, C., Polunin, N.V.C., Quetglas, A., 2014. Structure and dynamics of food webs in the water column on shelf and slope grounds of the western Mediterranean. J. Mar. Syst., The wrapping up of the IDEADOS project: International Workshop on Environment, Ecosystems and Demersal Resources, and Fisheries 138, 171–181. https://doi.org/10.1016/j.jmarsys.2014.04.002.

Vieira, R.P., Bett, B.J., Jones, D.O.B., Durden, J.M., Morris, K.J., Cunha, M.R., Trueman, C.N., Ruhl, H.A., 2020. Deep-sea sponge aggregations (Pheronema carpenteri) in the Porcupine Seabight (NE Atlantic) potentially degraded by demersal fishing. Prog. Oceanogr. 183, 102189 https://doi.org/10.1016/j.pocean.2019.102189.

Vieira, R.P., Trueman, C.N., Readdy, L., Kenny, A., Pinnegar, J.K., 2019. Deep-water fisheries along the British Isles continental slopes: status, ecosystem effects and future perspectives. J. Fish. Biol. 94, 981–992. https://doi.org/10.1111/jfb.13927.

White, M., Mohn, C., de Stigter, H., Mottram, G., 2005. Deep-water coral development as a function of hydrodynamics and surface productivity around the submarine banks of the Rockall Trough, NE Atlantic. In: Freiwald, A., Roberts, J.M. (Eds.), Cold-Water Corals and Ecosystems, Erlangen Earth Conference Series. Springer, Berlin, Heidelberg, pp. 503–514. https://doi.org/10.1007/3-540-27673-4_25.