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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.

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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.

Keywords: Trophic ecology; Stable Isotopes; Stomach content; Mesopredator; Food webs; Benthopelagic predator.

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 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 (δ^{13}C) and nitrogen (δ^{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 δ^{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 information on this species. 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 (Figure 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) × %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 (Figure 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 hours 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 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 $\delta^{13}C$ and IAEA-N-1 (ammonium sulfate) for $\delta^{15}N$. Cod (*Gadus morhua*) muscle was used as a natural replicate showing precision of ± 0.05 ‰ for $\delta^{13}C$ and ± 0.23 ‰ for $\delta^{15}N$ (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.

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 meters, which was significantly shallower than the other sites where catch depth was around 600 meters. *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 (Figure 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 ($\chi^2_{146,3} = 118.3$, $p<0.001$; Figure 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 ($\chi^2_{146,3} = 89.4$, $p<0.001$; Figure 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 highest $\Delta^{15}N$ rg.

For all sampling sites, significant linear relations were established between $\Delta^{15}N$ and TL (Figure 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 (Figure 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., 2017, 2009). 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., 2017, 2011). 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 obtained in this study were measured in multiple laboratories which may result in a potential bias (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 Elemtex and OEA laboratories). $\delta^{13}C$ 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 $\delta^{13}C$ values measured by Elemtex. There were no observed differences in $\delta^{15}N$ 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 $\delta^{13}C$, Atmospheric air for $\delta^{15}N$). Therefore, we argue that analytical biases are unlikely to have a major impact on stable isotope trends depicted here.

Ecological differences in *E. spinax* isotopic niches between sites were analysed by standardising values (i.e. $\Delta^{15}N$ and $\Delta^{13}C$) 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 $\Delta^{15}N$ differences. Moreover, the suspected $\Delta^{15}N$ switch with TL was not observed at all sites. The relevance of $\Delta^{15}N$ 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 (Figure 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 $\delta^{15}N$ 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 $\delta^{15}N$ or $\Delta^{15}N$ values. However, differences in *E. spinax* vertical segregation of maturity stages or bathymetric constraint among sites could explain $\Delta^{15}N$ 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 $\Delta^{13}C$ values (Figure 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* $\Delta^{13}C$ 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 $\Delta^{13}C$ values (Figure 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., 2017, 2011). 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 $\Delta^{13}C$ 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 $\delta^{13}C$ 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 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 $\Delta^{15}N$ variations and high redundancy index (Table 3). Still, their broad $\Delta^{13}C$ 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 $\delta^{13}C$ and $\delta^{15}N$ 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. $\Delta^{15}N$ values (Figure 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 $\delta^{15}N$ 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* $\Delta^{15}N$ decreased with TL (Figure 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 $\Delta^{15}N$ values with length, as modelled $\delta^{15}N$ 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 (Figure 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.

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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 *Etmopterus 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**

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)

<u>Table 3:</u> Summary of Layman metrics calculated on *E. spinax* isotopic niches ($\Delta^{13}C/\Delta^{15}N$ values) and based on convex hull areas. $\Delta^{13}C$ rg and $\Delta^{15}N$ 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	**$\Delta^{13}C$ rg**	**$\Delta^{15}N$ 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

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.

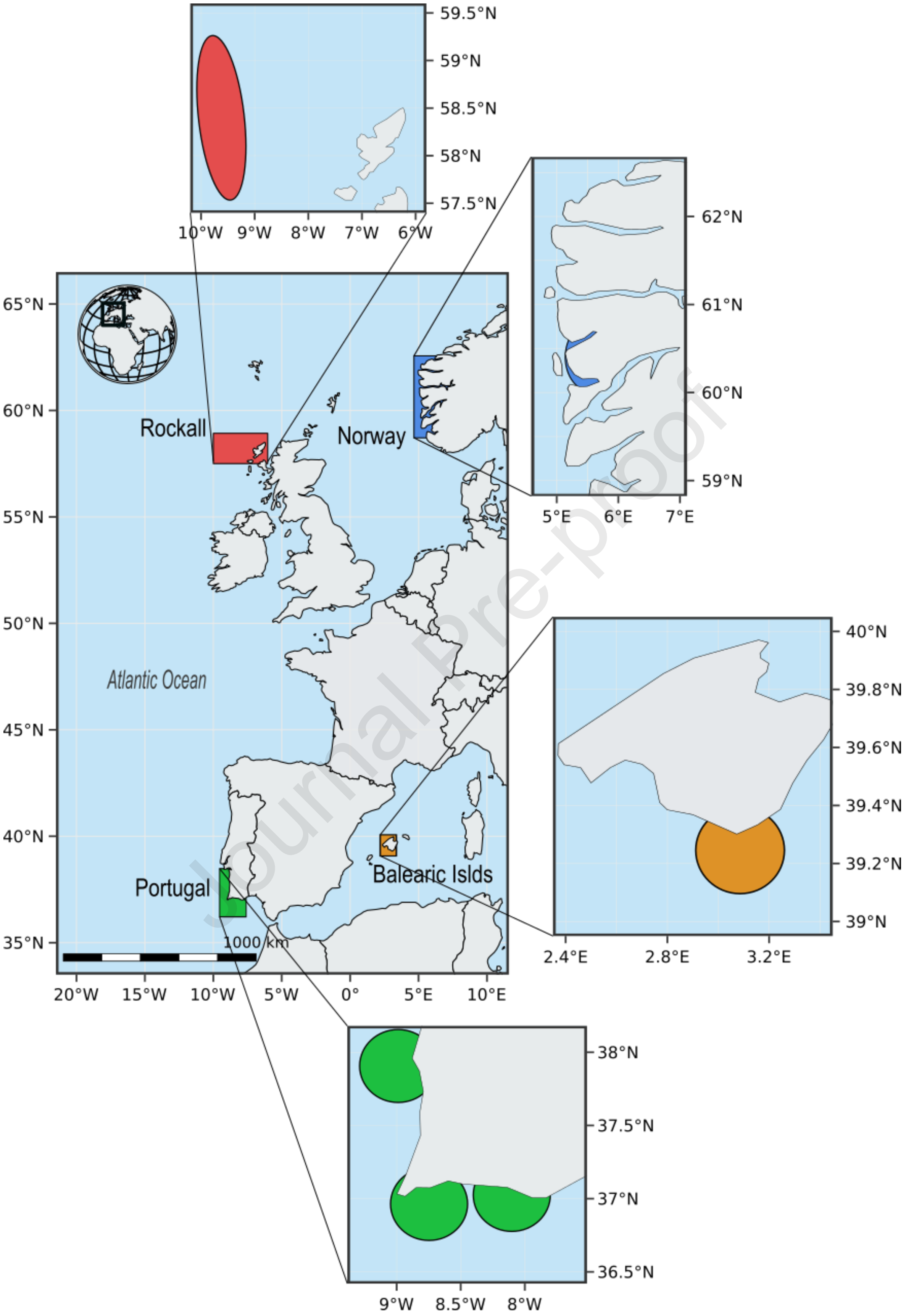

Figure 1: Sampling locations of velvet belly lantern sharks, *Etmopterus spinax*. Sampling area in Norway both corresponds to specimens analysed for stomach content and stable isotopes analysis.

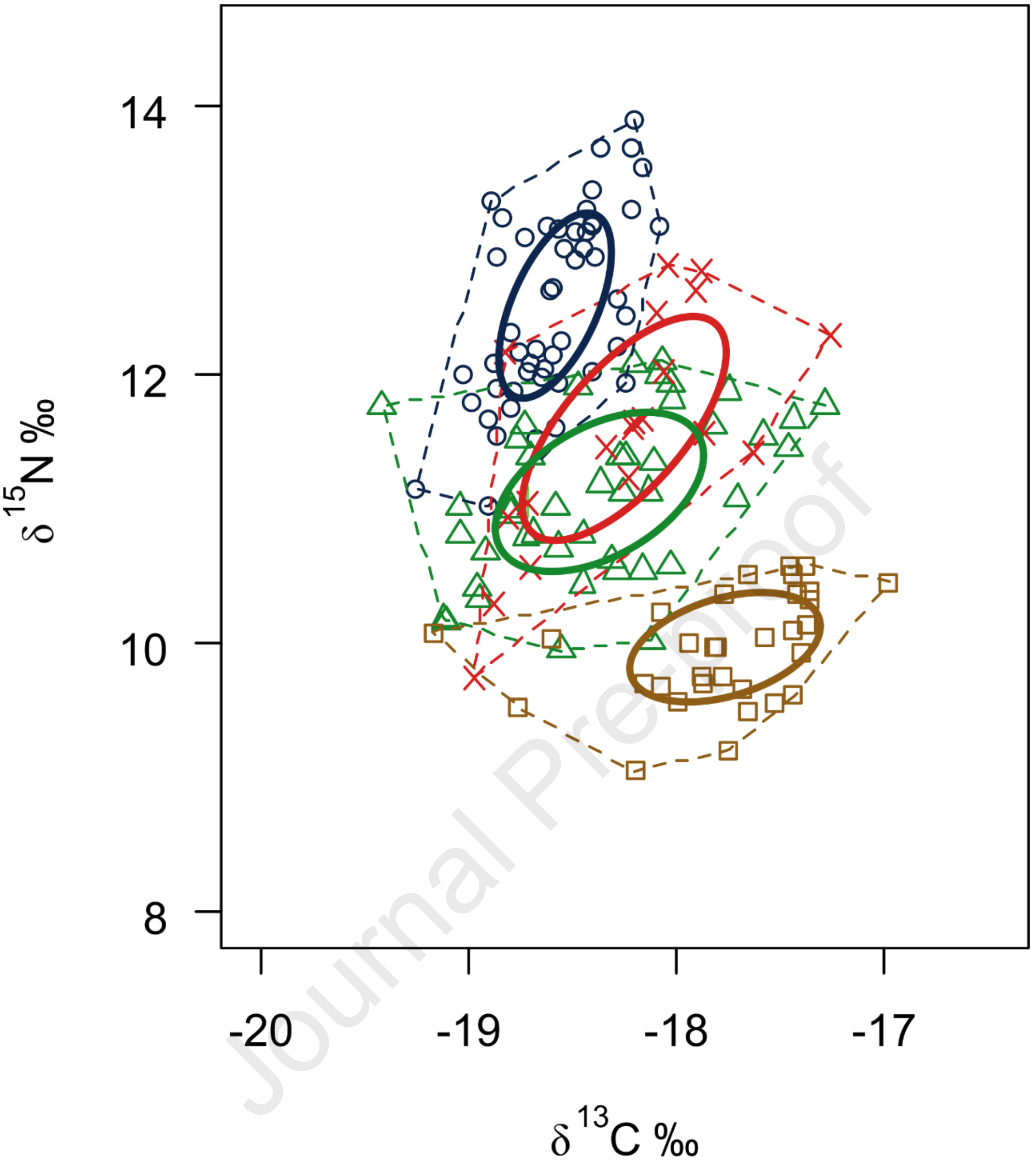

Figure 2: Muscle δ^{13}C and δ^{15}N values of *E. spinax*. Brown square points correspond to the Balearic Islands, blue circle points to Norway, green triangle points to Portugal and red cross points to Rockall samples. Solid lines delimit the standard ellipse areas (SEA) and dashed lines the convex hull areas for each sampling location. The only overlapping regions between SEA occurs between Portugal and Rockall individuals (39.89%).

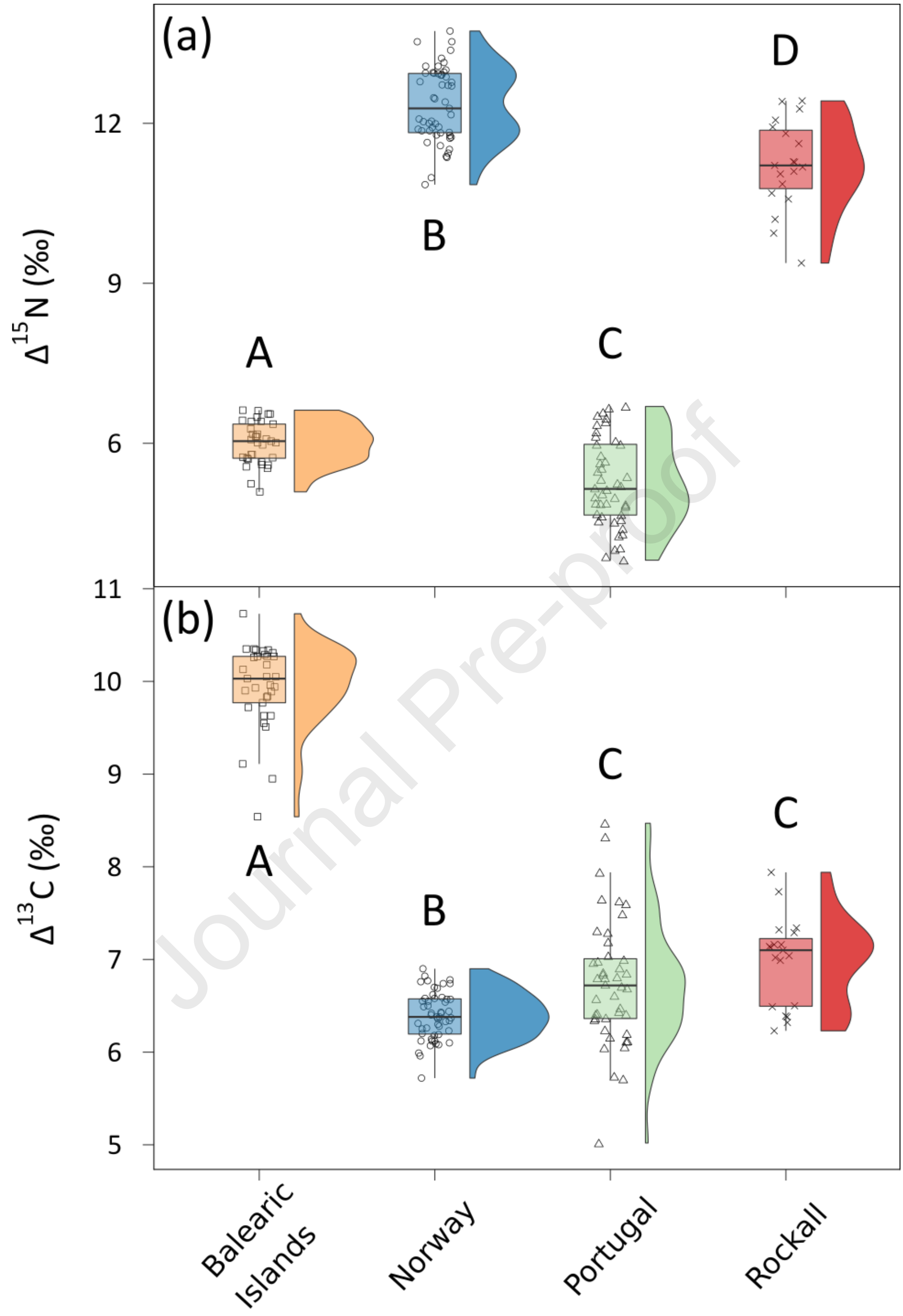

Figure 3: Boxplots of $\Delta^{15}N$ (a) and $\Delta^{13}C$ (b) values of *E. spinax* at each location. Significant differences are indicated by letters ($p < 0.05$).

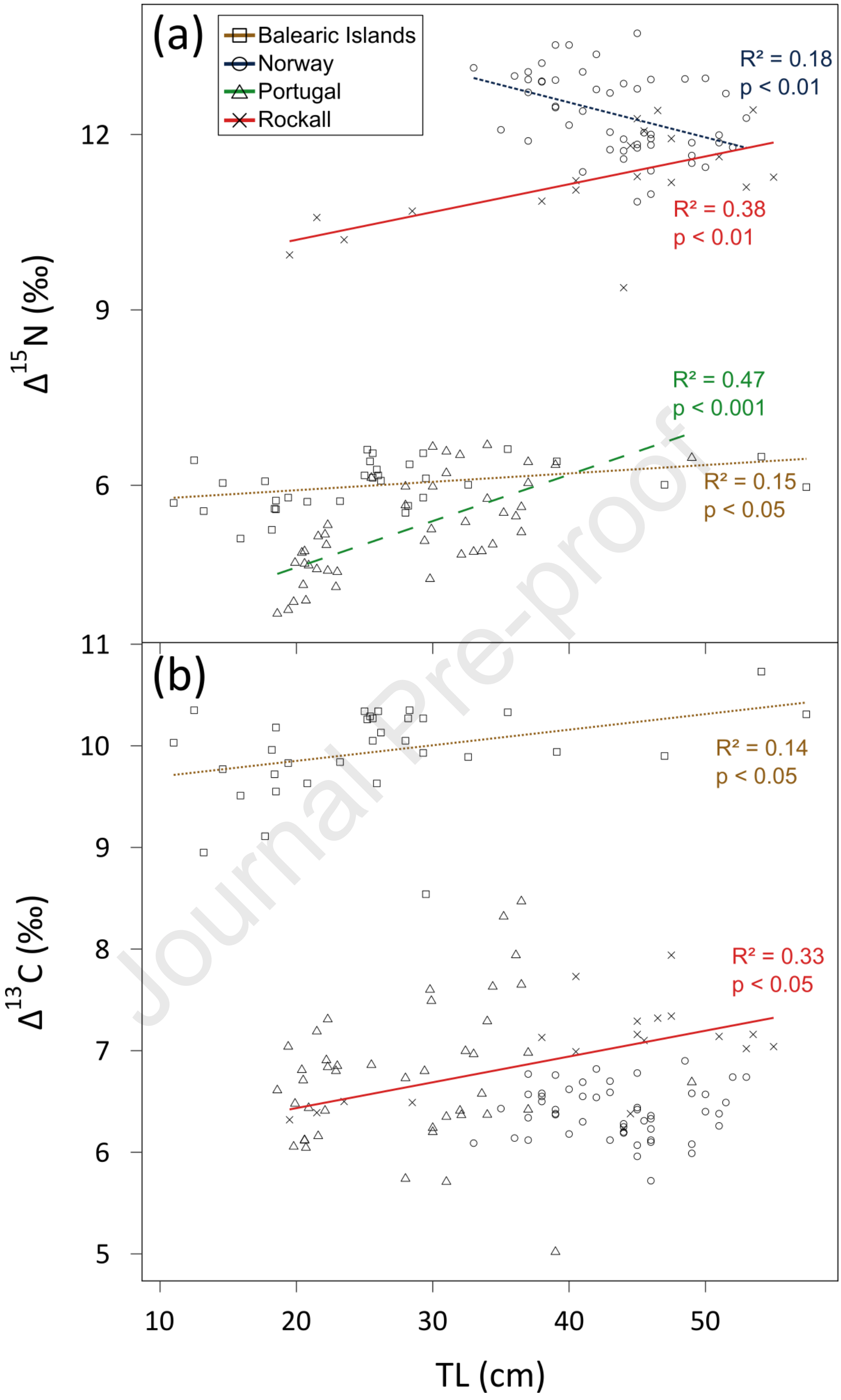

Figure 4: Relationships between individual $\Delta^{15}N$ (a)/$\Delta^{13}C$ (b) values and total length (TL) of *E. spinax*. Pearson linear regressions were applied for each location with their corresponding R² and p-value reported in the figure.

HIGHLIGHTS

- *E. spinax* were sampled across the northeastern Atlantic and Mediterranean Sea.
- Stomach contents suggested a similar diet.
- *E. spinax* fed mainly on Euphausiacea with an ontogenetic diet shift.
- Muscle carbon and nitrogen isotope compositions differed between locations.
- Isotopic differences probably resulted from mechanisms affecting the baselines.

Declaration of interests

☒ 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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: