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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.

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.

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

1. Introduction

23 Under the footprint of anthropogenic activities and climate change, many coastal and
24 epipelagic fisheries have significantly declined (Chavez et al., 2003; Pinsky et al., 2011; Tu et
25 al., 2018), diverting fishing efforts toward deep-sea stocks (Bailey et al., 2009; Devine et al.,
26 2006; Priede et al., 2011; Vieira et al., 2019). As a consequence, significant population
27 decreases have been observed in these deep water ecosystems with unknown and potentially
28 disruptive impacts on ecological processes and functions (Benn et al., 2010; Vieira et al., 2020).
29 However, despite their ecological importance, fragility and current state of exploitation, deep-
30 sea ecosystems are still relatively understudied compared to their shallower counterparts
31 (Benn et al., 2010; Thurber et al., 2014). In order to predict how deep-sea ecosystems will
32 respond to natural or human-induced changes, information on the functioning of deep-sea
33 communities is urgently needed (Howell et al., 2021).

34 Previous descriptions of deep-sea habitats have established that food webs are complexly
35 structured and include a range of trophic levels fuelled by a mixture of primary production,
36 secondary production and benthic recycling (Newman et al., 2011; Shipley et al., 2017b;
37 Trueman et al., 2014). Due to the absence of light for autochthonous primary production,
38 deep-sea fauna relies on the downward vertical transport of nutrients (Polunin et al., 2001;
39 Preciado et al., 2017), either actively by species diel vertical migrations or passively due to
40 particulate organic matter sinking and re-suspension (Trueman et al., 2014). Within these food
41 webs, deep-sea elasmobranch species are meso- to top predators (Churchill et al., 2015;
42 Simpfendorfer and Kyne, 2009) which are of critical importance through their potential top-
43 down or more complex regulation of communities (Heithaus et al., 2008; Shipley et al., 2017a).
44 By connecting different depth layers, they also influence energy flux and carbon cycling,
45 further enhancing their key ecological role (Trueman et al., 2014). Unfortunately, information

46 on deep-sea sharks is still lacking due to the logistical challenges of accessing and studying
47 them (Hussey et al., 2018; Moura et al., 2018; Simpfendorfer and Kyne, 2009).

48 In deep-sea sharks, most trophic studies have relied upon stomach content analysis (Barría et
49 al., 2018; Cortés, 1999). Even if this approach allows a complete qualitative description of the
50 diet, it requires a large number of samples, represents only a snapshot of the last meal(s) and
51 differences in digestion rates may also bias the importance of prey items (Albo-Puigserver et
52 al., 2015). In contrast, biochemical tracers such as stable isotope ratios of carbon ($\delta^{13}\text{C}$) and
53 nitrogen ($\delta^{15}\text{N}$) can help to describe the trophic structure, niche width and energy fluxes on a
54 long-term basis with potential quantitative approaches (Layman et al., 2012; Shipley et al.,
55 2017a). Carbon isotope signatures are considered as a good proxy to characterize the primary
56 producers at the base of food webs (Fry and Sherr, 1984; Layman et al., 2012). Nitrogen
57 isotope composition is mainly used as a proxy of trophic position due to a global increase in
58 $\delta^{15}\text{N}$ signal from prey to predator (Cabana and Rasmussen, 1994; Post, 2002) and has been
59 linked to foraging depth in benthopelagic communities (Trueman et al., 2014). By extension,
60 the combination of carbon and nitrogen isotopes constitutes a proxy of the trophic niche
61 crucial for assessing the ecological role of a given species or population (Newsome et al.,
62 2007).

63 Deep-sea shark isotopic values depend on their diet but also on the isotopic compositions at
64 the base of food webs, which exhibit spatial and temporal variations (Magozzi et al., 2017;
65 Somes et al., 2010). Environmental conditions and local biogeochemical processes are known
66 to affect baseline isotopic profiles due to changes in nutrient dynamics. For example,
67 latitudinal differences in baseline isotopic values can be influenced by temperature (Magozzi
68 et al., 2017; Rau et al., 1997), river discharges (Chouvelon et al., 2012) and upwelling events

69 (Lopez-Lopez et al., 2017; Puccinelli et al., 2019). The extent to which large-scale spatial
70 variations in isotopic baselines are reflected in deep-sea ichthyofauna remains unclear.
71 Moreover, deep-sea sharks are mobile species that can shift their feeding ground while
72 migrating. Isotopically, this shift will follow baseline changes and these variations need to be
73 considered when analysing the trophic niche of a species over time or space (Bird et al., 2018;
74 Lorrain et al., 2015).

75 Along the northeastern Atlantic and Mediterranean continental shelves and slopes, the trophic
76 ecology of a small deep-sea shark, the velvet belly lantern shark, *Etmopterus spinax* (Linnaeus,
77 1758), has been extensively studied using stomach content analysis (Klimpel et al., 2003; Neiva
78 et al., 2006; Valls et al., 2017). Beyond those habitats, luminous velvet belly lantern sharks
79 inhabit deep layers of fjords in Norway (Claes et al., 2010; Duchatelet et al., 2021). The first
80 objective of this study is to present a description of the species diet inside these semi-enclosed
81 habitats. More generally, throughout its distribution area, only a few studies took into account
82 stable isotopes to specifically investigate *E. spinax* trophic habitat (Albo-Puigserver et al.,
83 2015; Valls et al., 2017). Consequently, the second objective of this study is to investigate
84 muscle carbon and nitrogen isotopic compositions of *E. spinax* at four different locations in
85 the Mediterranean Sea and in the northeastern Atlantic to gain long-term dietary information
86 on this species. Information on the trophic ecology of *E. spinax* gathered by stomach content
87 analysis were ultimately compared to stable isotope values and discussed in terms of local
88 habitat ecological characteristics and physical processes affecting nutrient dynamics.

89 **2. MATERIALS AND METHODS**

90 **2.1. Stomach content**

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

105 2.2. Stable isotope analysis

106 From 2014 to 2017, *Etmopterus spinax* specimens were sampled in four different areas
107 of the northeast Atlantic and the Mediterranean Sea (Figure 1). Individuals from Rockall
108 Trough and Portugal were sampled during annual-fisheries surveys run by Marine Science
109 Scotland (MSS) and Instituto Português do Mar e da Atmosfera (IPMA) respectively. Additional
110 samples were collected in Portugal from bycatches of the commercial black scabbardfish
111 (*Aphanopus carbo*) longline and of the crustacean bottom trawl fisheries. In the
112 Mediterranean Sea, *E. spinax* samples from the Balearic Islands were obtained from research
113 cruises conducted by the Mediterranean International Trawl Survey (MEDITS). In the

114 Raunefjord (Norway), sharks were caught using deep-water longlines during scientific surveys.
115 Each collected specimen was sexed and measured for total length (TL). Following dissection,
116 white muscle was quickly frozen before analysis.

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

130 Isotopic ratios (δ) were expressed in per mille (‰) following: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$
131 where X is ^{13}C or ^{15}N and R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. $\delta^{13}\text{C}$ values are expressed with
132 reference to the Vienna Pee Dee Belemnite and $\delta^{15}\text{N}$ values are expressed relative to
133 Atmospheric air. Depending on sites and sampling year, samples were analysed in different
134 facilities. Samples from Norway obtained in 2017 were processed in Liege (Oceanology,
135 ULiege, Belgium) using a continuous flow isotope ratio mass spectrometer (Isoprime 100,
136 Isoprime, United Kingdom) coupled to a C-N-S elemental analyser (MicroVario, Elementar,

137 Germany). The certified substances, provided by the International Atomic Energy Agency IAEA
138 (Vienna) were IAEA-CH-6 (sucrose) for $\delta^{13}\text{C}$ and IAEA-N-1 (ammonium sulfate) for $\delta^{15}\text{N}$. Cod
139 (*Gadus morhua*) muscle was used as a natural replicate showing precision of $\pm 0.05\text{‰}$ for $\delta^{13}\text{C}$
140 and $\pm 0.23\text{‰}$ for $\delta^{15}\text{N}$ (based on the standard deviation of the replicate measurements).
141 Stable isotope ratios of samples obtained along the southern Iberian coast of Portugal in 2015
142 were measured using a Thermo Scientific Delta V Advantage IRMS via ConFlo IV interface at
143 Marinnova – Marine and Environmental Innovation, Technology and Services (Portugal).
144 Samples from Rockall were analysed in two separate laboratories at the Scottish University
145 Environmental Research Council (SUERC) and at the OEA Labs (Exeter, United Kingdom). The
146 remaining samples from 2014 (i.e. Norway, Portugal and Balearic Islands) were processed in
147 Elementex (Gunnislake, United Kingdom). SUERC samples were run on a continuous flow
148 Elementar vario PYRO cube elemental analyser coupled with a Thermo Scientific Delta V plus
149 isotope ratio mass spectrometer (SUERC, NERC LSMSF, East Kilbride facility). OEA Labs and
150 Elementex samples were run on a Thermo EA 110 elemental analyser linked to a Europa Scientific
151 2020 isotope ratio mass spectrometer running in continuous flow mode.

152 **2.3. Data analysis**

153 To assess isotopic baseline effects (i.e. change of primary producer isotopic
154 composition) in each sampling site, isotope values were extracted from predictive models
155 established for $\delta^{13}\text{C}$ (Magozzi et al., 2017) and $\delta^{15}\text{N}$ (Somes et al., 2010). Baseline values were
156 extracted from the shark specific sampling locations (details of the specific latitudes and
157 longitudes can be found in supplementary information). To overcome the baseline effect
158 when comparing sharks between locations, the modelled baseline (i.e. phytoplankton) value
159 was subtracted from shark stable isotope composition for each individual geographic

160 coordinate: $\Delta X = \delta X_{\text{shark}} - \delta X_{\text{phyto}}$ where X is ^{13}C or ^{15}N . Modelled $\delta^{15}\text{N}$ baseline values inside
161 the fjord were not available and values from the adjacent North Sea were subsequently used.

162 All statistical analyses were performed on the open source software R (R Core Team, 2020).
163 For each site, the SIBER package (Jackson et al., 2011) was used to estimate the size of the
164 isotopic niches (i.e. using $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$) and their associated Layman metrics (Layman et al.,
165 2007). Layman metrics were first used to characterize trophic niche space using four metrics.
166 Isotopic ranges ($\Delta^{13}\text{C}$ rg and $\Delta^{15}\text{N}$ rg) described the distance between the most ^{13}C - and ^{15}N -
167 enriched and most depleted individuals respectively, the total area (TA), the size of the
168 isotopic niche based on convex hull area and the mean distance to the centroid (CD), the mean
169 distance of each individual to the $\Delta^{13}\text{C}/\Delta^{15}\text{N}$ centroid. The other two metrics reflected trophic
170 redundancy (i.e. the relative position of individuals from one another inside their isotopic
171 niche). Mean nearest neighbor distance (NND and its standard deviation SDNND) measured
172 the overall density of individuals clustering in a way that smaller NND and SDNND would
173 describe small differences between individual isotopic values (Layman et al., 2007). The SIBER
174 package was finally used to calculate the standard ellipse area (SEA) encompassing 40% of the
175 bulk $\delta^{13}\text{C}/\delta^{15}\text{N}$ data at each site and the isotopic overlaps between them as a proportion of
176 the non-overlapping area of two given ellipses.

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

183 between linear regressions. For all statistical analyses, the significance threshold was set at
184 $p < 0.05$.

185 **3. RESULTS**

186 **3.1. Stomach content analysis**

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

197 **3.2. Stable isotopes**

198 Muscle tissues from 147 *E. spinax* individuals were recovered from the four different
199 stations (Table 2). As fishing methodologies differed between stations, capture depth
200 significantly varied among sampling sites ($\chi^2_{146,3} = 98.2$, $p < 0.001$). Samples from Norway were
201 caught on average at a depth of 243 meters, which was significantly shallower than the other
202 sites where catch depth was around 600 meters. *E. spinax* TL varied from 11.0 to 57.4 cm and
203 was significantly different between sampling sites ($\chi^2_{146,3} = 74.2$, $p < 0.001$). Individuals from

204 Norway and Rockall were significantly larger than in Portugal and in the Balearic Islands (C-I
205 test, $p < 0.001$ for all pairs of comparison). Females were larger than males considering the
206 entire dataset ($W = 1860$, $p < 0.01$), as observed in Portugal ($W = 148$, $p < 0.05$) and in Norway
207 ($t = -6.91$, $p < 0.001$). No significant difference in TL was found between sexes in the Balearic
208 Islands and Rockall Trough.

209 Modelled phytoplanktonic baselines significantly differed among sites ($\chi^2_{146,3} = 101.4$, $p < 0.001$
210 for $\delta^{13}\text{C}_{\text{phyto}}$; $\chi^2_{146,3} = 142.5$, $p < 0.001$ for $\delta^{15}\text{N}_{\text{phyto}}$). $\delta^{13}\text{C}_{\text{phyto}}$ was significantly lower in the
211 Balearic Islands than in Rockall and Portugal, while Norway displayed higher values than all
212 other sites (C-I test, $p < 0.001$). Concerning $\delta^{15}\text{N}_{\text{phyto}}$, all locations significantly differed (C-I test,
213 $p < 0.001$, for all pairs of comparison) with Portugal being the most ^{15}N -enriched, followed by
214 the Balearic Islands, Rockall Trough and southwestern Norway.

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

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

231 For all sampling sites, significant linear relations were established between $\Delta^{15}\text{N}$ and TL (Figure
232 4a). $\Delta^{15}\text{N}$ increased with TL in three sites: Portugal, Rockall and the Balearic Islands. *E. spinax*
233 sampled in Portugal and Rockall had equivalent slopes while specimens from the Balearic
234 Islands showed a flatter one (ANCOVA, $F=5.83$ $p<0.05$ for Rockall and $F=21.32$ $p<0.001$ for
235 Portugal). Specimens in Norway were the only ones with a significant decrease in $\Delta^{15}\text{N}$ values
236 with TL. $\Delta^{13}\text{C}$ increased with TL in the Balearic Islands and Rockall with no differences in slopes
237 (Figure 4b). At each location, linear regressions did not significantly change between sexes or
238 with depth.

239 4. DISCUSSION

240 4.1. Trophic ecology of *E. spinax*

241 4.1.1. Prey composition (Stomach content analysis)

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

249 At all locations sampled for stable isotope analysis, previously published studies have
250 highlighted an ontogenetic shift in the diet of *E. spinax*, except for two studies on Portugal and
251 the Balearic Islands (Table 4). Before the ontogenetic diet shift, Euphausiacea was generally
252 the major prey item, mostly represented by the northern krill, *Meganyctiphanes norvegica*.
253 Ontogenetic diet shift occurred at different lengths depending on the site, from 19.4 cm in
254 Norway to 39.0 cm in Rockall Trough. Beyond these sizes, Euphausiacea decreased in
255 importance due to the increasing occurrence of teleost fishes, cephalopods, or other
256 crustaceans. This result was in line with previous analyses of *E. spinax* diet in the Atlantic
257 Ocean and Mediterranean Sea (Bengil et al., 2019; Isbert et al., 2015; Preciado et al., 2017,
258 2009). In Rockall, the later shift toward the consumption of the decapod crustacean,
259 *Pasiphaea tarda*, has been explained by larger individuals foraging closer to the sea bottom
260 where prey availability is different (Mauchline and Gordon, 1983). Ontogenetic diet shifts are
261 commonly observed in mesopredator fishes due to increasing body length, mouth gap and
262 stomach size, hunting capacities and energetic demands, or to avoid intra-specific competition
263 (Klimpel et al., 2003; Neiva et al., 2006).

264 Stomach contents analysed in the Balearic Islands showed contrasting results between
265 studies. *E. spinax* either foraged following the previously described ontogenetic shift from
266 small Euphausiacea to teleost fishes (Fanelli et al., 2009; Macpherson, 1980) or fed on
267 cephalopods throughout their entire size range in more recent studies (Valls et al., 2017,
268 2011). A higher proportion of cephalopod consumption by *E. spinax* was previously observed
269 in the adjacent Catalan Sea and has been linked to the high exploitation rate of the area,
270 depleting fish stocks in favour of cephalopods (Barría et al., 2018; Doubleday et al., 2016). In
271 deep-sea sharks, smaller adult size and earlier maturity due to oligotrophic conditions in the

272 Mediterranean Sea could also explain cephalopod consumption by small specimens (Catarino
273 et al., 2015; Massutí et al., 2004). However, this trend was not yet observed in *E. spinax*
274 (Coelho et al., 2010).

275 **4.1.2. Nitrogen and carbon isotope compositions ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$)**

276 Stable isotope values obtained in this study were measured in multiple laboratories
277 which may result in a potential bias (Mill et al., 2008). The analysis of a reference sample (USGS
278 40 glutamic acid) to ensure comparability was performed on two of the four instruments used
279 in this study (i.e. for Elemtex and OEA laboratories). $\delta^{13}\text{C}$ values were on average 0.23 ± 0.40
280 ‰ higher from Elemtex than those obtained from OEA Labs. This difference, although
281 significant, is quite small in regard of isotope patterns interpreted in this study, and
282 comparable to error estimates considered acceptable in many ecological studies using stable
283 isotope tracers. Nevertheless, this difference was subtracted from all shark $\delta^{13}\text{C}$ values
284 measured by Elemtex. There were no observed differences in $\delta^{15}\text{N}$ values. Specimens sampled
285 in Norway in 2017 and in Portugal in 2015 were analysed in facilities where glutamic acid
286 samples could not be measured. However, all facilities follow recommended procedures for
287 stable isotope analyses, and use certified materials that are all calibrated against the same
288 international references (Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$, Atmospheric air for $\delta^{15}\text{N}$).
289 Therefore, we argue that analytical biases are unlikely to have a major impact on stable
290 isotope trends depicted here.

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

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

314 In benthopelagic communities, the higher degradation of sinking particles is leading to higher
315 $\delta^{15}\text{N}$ values in deeper species (Trueman et al., 2014). Bathymetric segregation at the inter-
316 and intra-specific levels is commonly observed among deep-sea sharks (Clarke et al., 2005;
317 Neat et al., 2015) and has been reported for *E. spinax* (Coelho and Erzini, 2010). At each site,

318 changes in capture depth were not associated with an increase in $\delta^{15}\text{N}$ or $\Delta^{15}\text{N}$ values.
319 However, differences in *E. spinax* vertical segregation of maturity stages or bathymetric
320 constraint among sites could explain $\Delta^{15}\text{N}$ differences and would need to be specifically
321 addressed in the future.

322 Except for the Balearic Islands, *E. spinax* likely shared a pelagic habitat owing to their lower
323 $\Delta^{13}\text{C}$ values (Figure 3b). This is in accordance with the high rate of phytoplanktonic production
324 fuelling the deeper layers of Portugal and Rockall continental slope systems (Gomes et al.,
325 2001; Mauchline and Gordon, 1983). In the Raunefjord, *E. spinax* $\Delta^{13}\text{C}$ values agree with a diet
326 dominated by pelagic preys (Bergstad et al., 2003; Klimpel et al., 2003).

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

334 **4.2. Habitat characteristics influence on isotope compositions**

335 *E. spinax* in the Iberian slope ecosystems and Rockall Trough, even if mainly relying on
336 pelagic production, presented similarly high indices of isotopic diversity (Table 3). Both sites
337 are large continuous continental slopes (Mauchline and Gordon, 1991; Ribeiro et al., 2005)
338 and topographic similarities might drive these similitudes. Indeed, ichthyofauna inhabiting
339 continental slope ecosystems are known to integrate nutrient from a mixture of pelagic and

340 benthic origins (Mauchline and Gordon, 1991; Trueman et al., 2014). This trophic diversity is
341 possibly further enhanced by the access to different topographic features (e.g. canyons, banks
342 or steep slopes) (Romero-Romero et al., 2016; Rowden et al., 2010).

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

352 The Balearic Islands deep ecosystem is characterized by a smaller continental slope, deep
353 escarpments and canyons (Acosta et al., 2003). While topographic conditions might be similar
354 to large continental slope systems, the main difference resides in the oligotrophic nature of
355 the Mediterranean Sea (Bosc et al., 2004; Estrada, 1996). Such conditions might result in the
356 observed small isotopic niche due to limited $\Delta^{15}\text{N}$ variations and high redundancy index (Table
357 3). Still, their broad $\Delta^{13}\text{C}$ rg, with some ^{13}C -depleted specimens, might reveal the existence of
358 resource partitioning within the population, which could be fuelled by a diversity of prey of
359 both benthic and pelagic origin (Albo-Puigserver et al., 2015; Madurell et al., 2008; Newman
360 et al., 2011). Such coupling between reservoirs and reliance on other habitat is probably a
361 response to oligotrophic conditions reducing pelagic production and prey availability (Valls et
362 al., 2014). Sharks could also forage inside canyons where higher benthic prey densities are

363 present (Massutí et al., 2004). Other ^{13}C -enriched sources have been identified in the Balearic
364 Islands such as food falls (Cartes et al., 2016) or seagrass exportation at deeper layers
365 (Boudouresque et al., 2016) but this remains speculative and will need further studies to
366 investigate. Water temperature, higher in the Mediterranean Sea compared to the other
367 locations, could also have led to differences in isotopic values compared to the other locations.
368 Indeed, temperature can affect isotopic turnover rates and discrimination factors (Bloomfield
369 et al., 2011), beyond latitudinal baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variations (Magozzi et al., 2017).

370 Fjords are narrow, deep ecosystems delimited by steep flanking slopes (Harris, 2012).
371 Therefore, possible bathymetric constraints (Coelho and Erzini, 2010) might reduce *E. spinax*
372 foraging habitat diversity and explain isotopic niche limited space and high redundancy. $\Delta^{15}\text{N}$
373 values (Figure 3a) may result from the important particle residency time (Saino and Hattori,
374 1980) in deep basins. Indeed, even if fjords are dynamic systems with quick surface water
375 turnover (Asplin et al., 1999), they are stratified with sometimes limited exchanges between
376 reservoirs (Aure et al., 1996). As sinking particles are trapped in deep layers, especially in
377 fjords, they would exhibit higher baseline $\delta^{15}\text{N}$ values than suggested by surface model values
378 (Saino and Hattori, 1980; Trueman et al., 2014). Even if experiencing an ontogenetic shift
379 toward higher trophic position preys, *E. spinax* $\Delta^{15}\text{N}$ decreased with TL (Figure 4a). Sharks
380 sampled in the Raunefjord were only mature individuals probably post-ontogenetic diet shift.
381 This decrease could result from a shift in feeding habitat with early maturing sharks foraging
382 strictly in fjords while larger sharks could forage outside in offshore areas. This hypothesis
383 would ultimately lead to the observed decreasing $\Delta^{15}\text{N}$ values with length, as modelled $\delta^{15}\text{N}$
384 baseline was extracted from outside of the fjord. Another possibility is that large sharks

385 change their foraging behaviour towards active predation of smaller organisms with lower
386 trophic positions, although this is not supported by the stomach content analysis.

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

404 5. CONCLUSION

405 At each location, including inside the fjords, *Etmopterus spinax* appears as a
406 benthopelagic mesopredator, mainly feeding on aggregations of *Meganyctiphanes norvegica*
407 at a juvenile stage with increasing consumption of larger prey, such as teleost fishes, with

408 increasing length. Nonetheless, isotopic niche spaces varied significantly among sampling
409 sites. Observed differences in carbon and nitrogen isotope compositions are likely to be
410 explained by differences in habitat features (e.g. productive continental slopes vs oligotrophic
411 conditions in the Mediterranean Sea) and other oceanographic characteristics (e.g. upwelling
412 regime). Resulting variations in pelagic primary production rates and sequestration across the
413 water column are likely to affect the strength of mesopelagic linkage toward deep reservoirs
414 and subsequently *E. spinax* trophodynamic and isotopic values. Our results suggest that
415 considering the influence of nutrient cycle on isotopic baselines allows a better understanding
416 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
<i>Meganyctiphanes norvegica</i>	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
<i>Pasiphaea sivado</i>	2	2.15	1.71	4.08	0.40
<i>Pasiphaea multidentata</i>	1	1.08	1.28	2.04	0.12
<i>Pandalus montagui</i>	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
<i>Scomber scombrus</i>	1	1.08	50.00	2.04	2.67
<i>Maurolicus muelleri</i>	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
<i>Rossia macrosoma</i>	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 (\pm standard deviation). All isotopic values are expressed in ‰ with $\delta^{13}\text{C}/\delta^{15}\text{N}$ representing *E. spinax* muscle isotopic composition, $\delta^{13}\text{C}_{\text{phyto}}$ and $\delta^{15}\text{N}_{\text{phyto}}$ the phytoplankton values extracted from predictive models and $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ the difference between shark muscle isotope values and phytoplankton modelled isotopic baselines.

Location	Depth (m)	N (M:F)	TL (cm)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}_{\text{phyto}}$	$\delta^{15}\text{N}_{\text{phyto}}$	$\Delta^{13}\text{C}$	$\Delta^{15}\text{N}$
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)

Table 3: Summary of Layman metrics calculated on *E. spinax* isotopic niches ($\Delta^{13}\text{C}/\Delta^{15}\text{N}$ values) and based on convex hull areas. $\Delta^{13}\text{C}$ rg and $\Delta^{15}\text{N}$ rg represent both isotopic ranges, TA the total area, CD the mean distance to centroid, NND (as mean \pm 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	$\Delta^{13}\text{C}$ rg	$\Delta^{15}\text{N}$ rg	TA	CD	NND
Balearic Islands	2.19	1.53	1.85	0.51	0.16 \pm 0.16
Norway	1.18	2.88	1.95	0.66	0.12 \pm 0.07
Portugal	3.45	2.88	5.88	0.95	0.21 \pm 0.14
Rockall	1.71	3.04	2.84	0.79	0.28 \pm 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 (<i>M. norvegica</i>) , 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 (<i>M. norvegica</i>)	Euphausiacea (<i>M. norvegica</i>) , Teleostei, Cephalopoda	This study
Portugal	11.0-33.0	-	Euphausiacea (<i>M. norvegica</i>) , Cephalopoda	Teleostei, Cephalopoda	Santos & Borges, 2001
	9.1-40.1	~28.0 (***)	Euphausiacea (<i>M. norvegica</i>) , Natantids, Teleostei	Natantids, Teleostei (Gadoids mainly), Euphausiacea, Cephalopoda	Neiva et al., 2006
Rockall	12.6-53.0	~39.0	Euphausiacea (<i>M. norvegica</i>), Teleostei (<i>M. muelleri</i>), Cephalopoda, Decapoda	Decapoda (<i>Pasiphaea tarda</i>), 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.

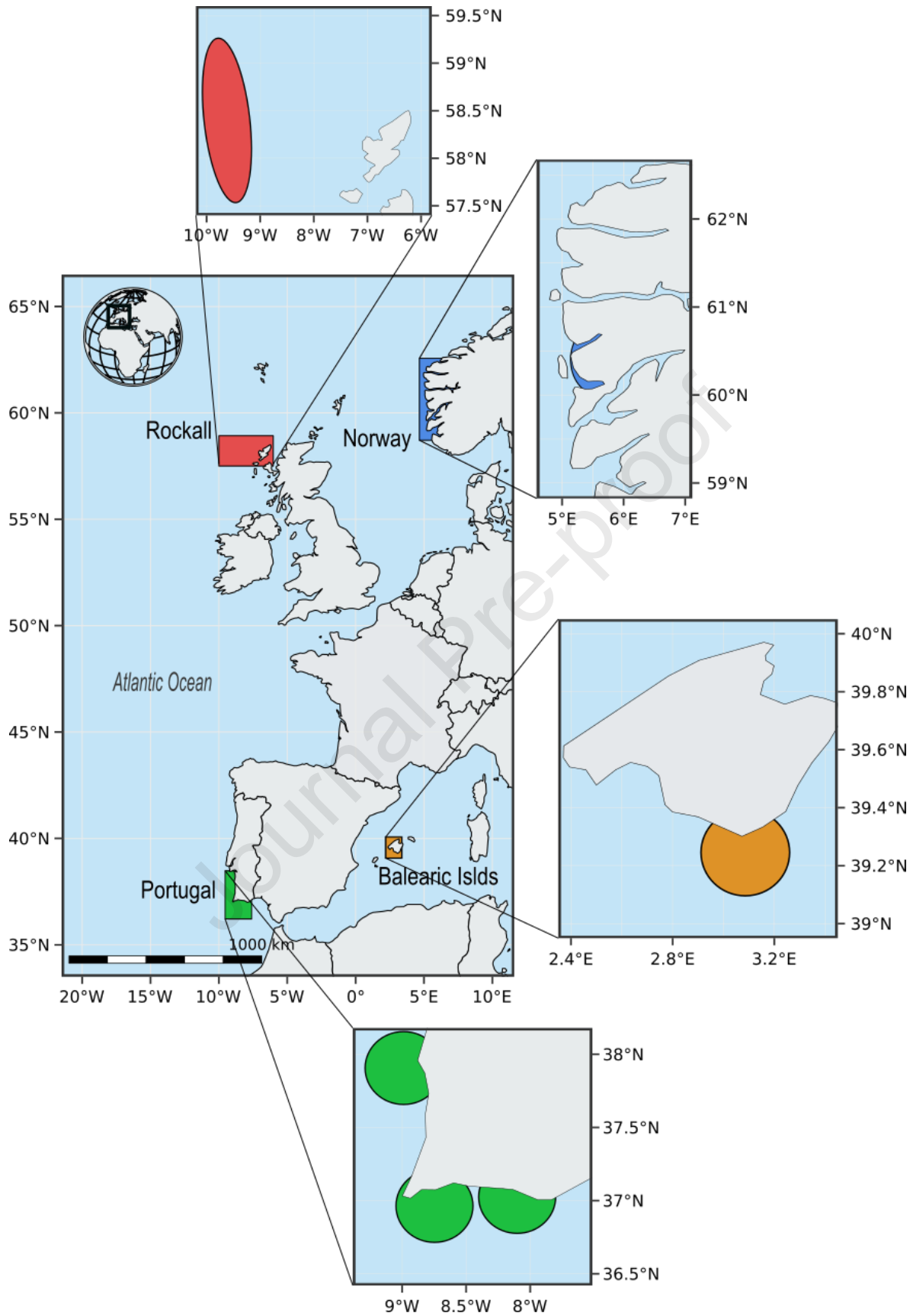


Figure 1: Sampling locations of velvet belly lantern sharks, *Etmopterus spinax*. Sampling area in Norway both corresponds to specimens analysed for stomach content and stable isotopes analysis.

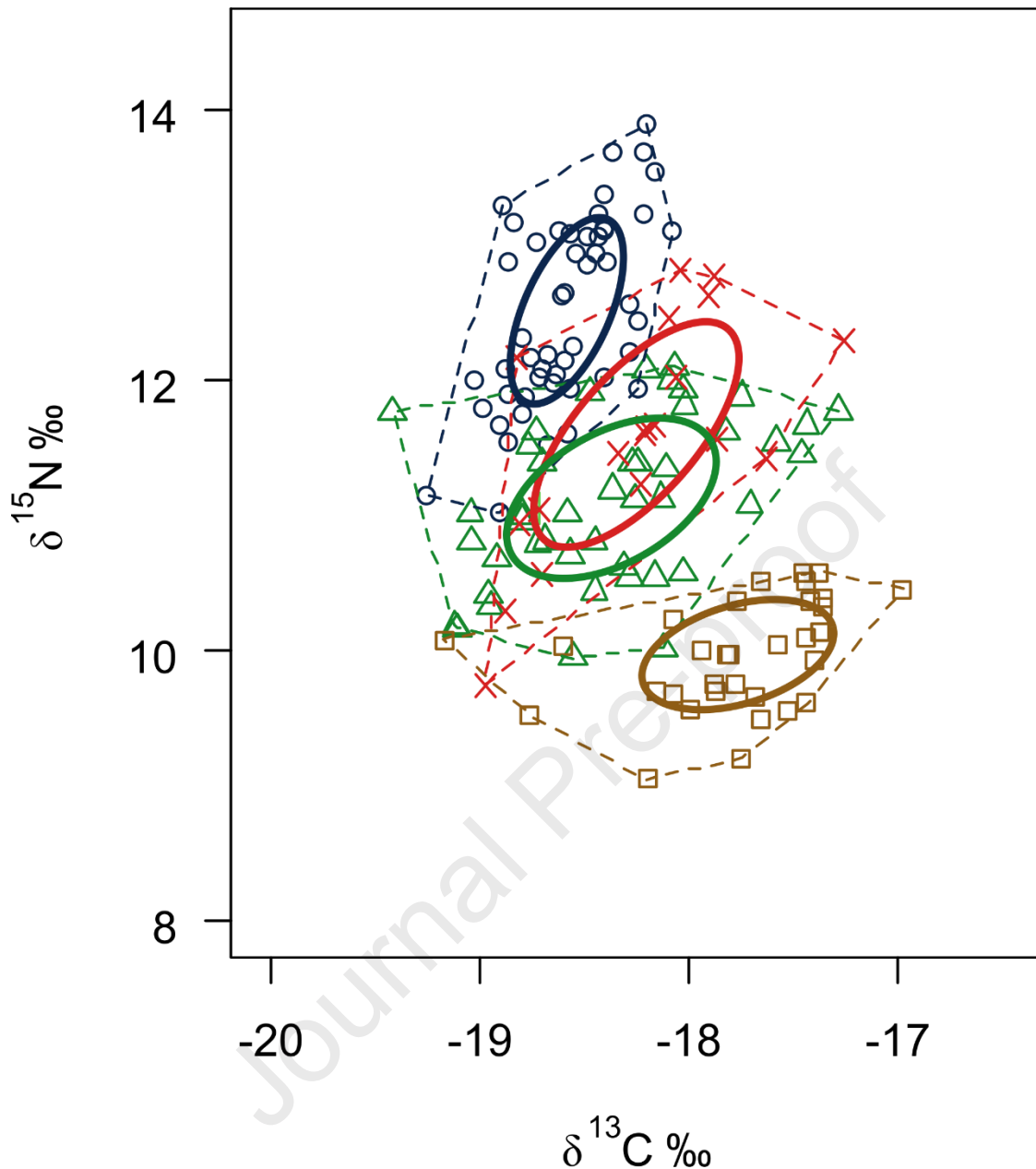


Figure 2: Muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *E. spinax*. Brown square points correspond to the Balearic Islands, blue circle points to Norway, green triangle points to Portugal and red cross points to Rockall samples. Solid lines delimit the standard ellipse areas (SEA) 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%).

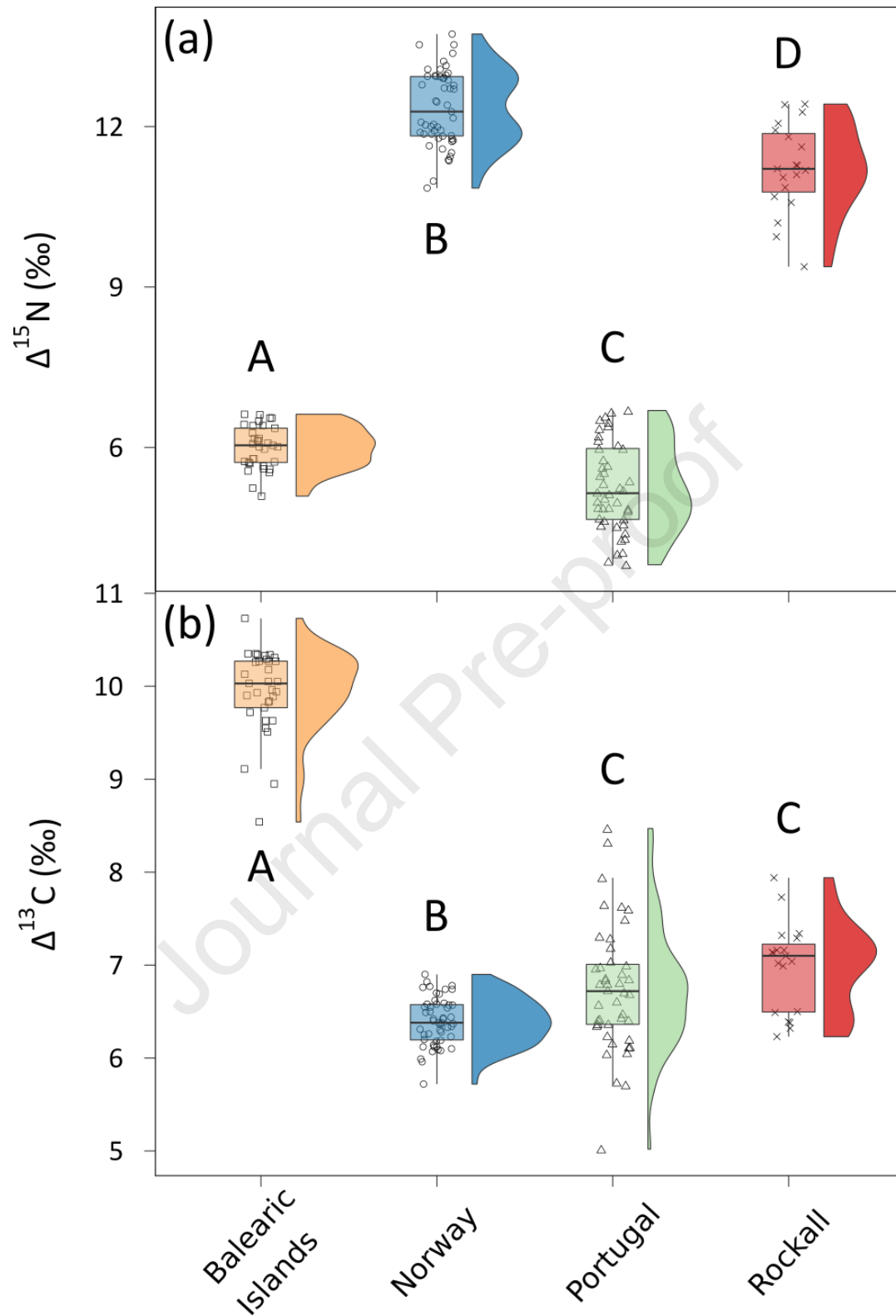


Figure 3: Boxplots of $\Delta^{15}\text{N}$ (a) and $\Delta^{13}\text{C}$ (b) values of *E. spinax* at each location. Significant differences are indicated by letters ($p < 0.05$).

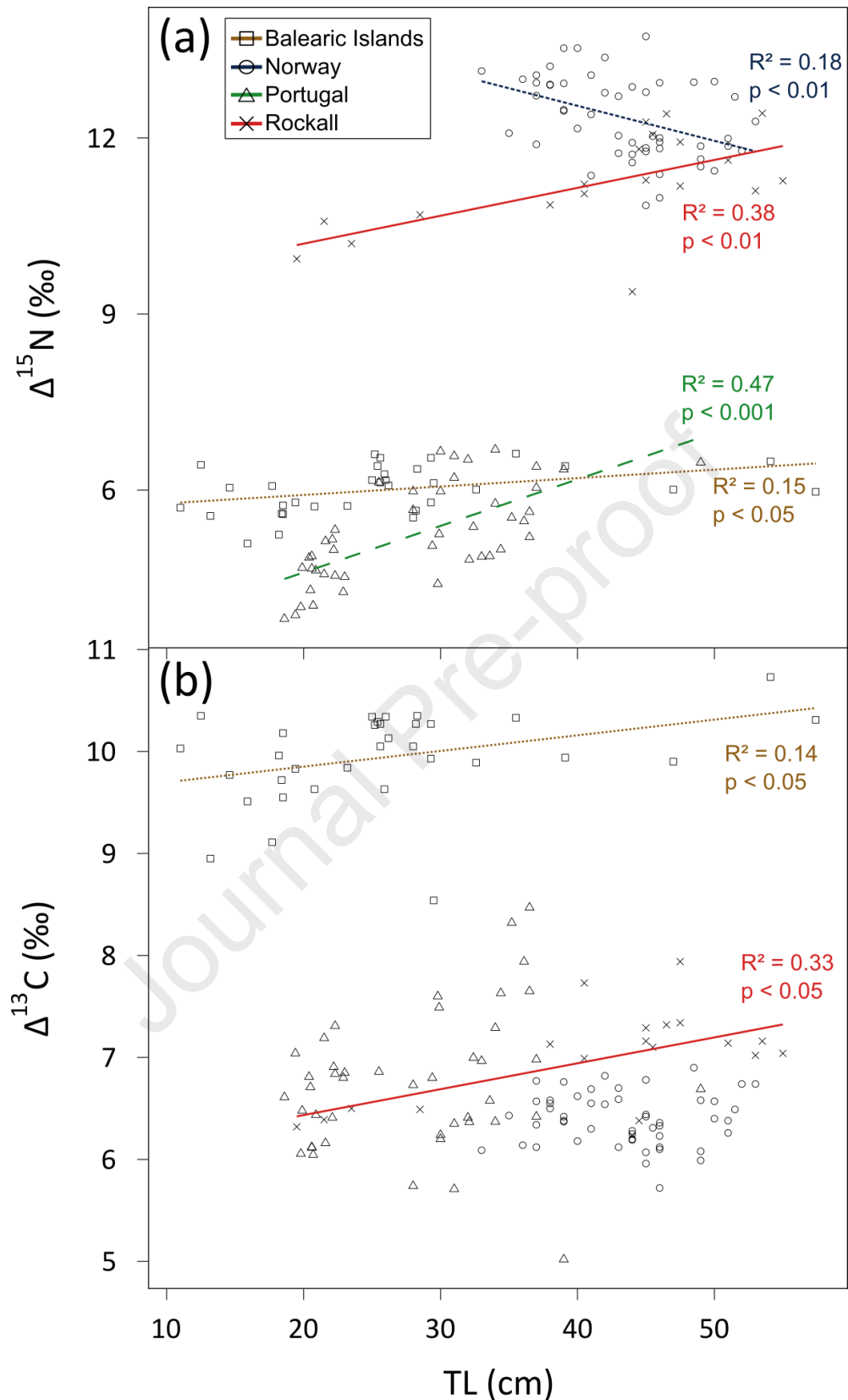


Figure 4: Relationships between individual $\Delta^{15}\text{N}$ (a)/ $\Delta^{13}\text{C}$ (b) values and total length (TL) of *E. spinax*. Pearson linear regressions were applied for each location with their corresponding R^2 and p-value reported in the figure.

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:

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