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.

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 (δ^{13}C) and

53   nitrogen (δ^{15}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   δ^{15}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 ichtyofauna 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 shelfs 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) × %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 $\delta^{13}C$ 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 $\delta^{13}C$ values) and in 2017 (i.e. $\delta^{13}C$ 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: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$

131   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

132   reference to the Vienna Pee Dee Belemnite and $\delta^{15}N$ 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,

8

137 Germany). The certified substances, provided by the International Atomic Energy Agency IAEA

138 (Vienna) were IAEA-CH-6 (sucrose) for δ^{13}C and IAEA-N-1 (ammonium sulfate) for δ^{15}N. Cod

139 (*Gadus morhua*) muscle was used as a natural replicate showing precision of ± 0.05 ‰ for δ^{13}C

140 and ± 0.23 ‰ for δ^{15}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 Elemtex (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 Elemtex 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 δ^{13}C (Magozzi et al., 2017) and δ^{15}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: $\Delta X = \delta X_{shark} - \delta X_{phyto}$ where X is ^{13}C or ^{15}N. Modelled δ^{15}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 Δ^{13}C and Δ^{15}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 (Δ^{13}C rg and Δ^{15}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 Δ^{13}C/Δ^{15}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 δ^{13}C/δ^{15}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 Δ^{13}C, Δ^{15}N and TL.

182   Finally, an analysis of covariance (ANCOVA) was performed to test for slope differences

10

183   between linear regressions. For all statistical analyses, the significance threshold was set at

184   p<0.05.

3. RESULTS

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.

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 $\delta^{13}C_{phyto}$; $\chi^2_{146,3}$ = 142.5, $p<0.001$ for $\delta^{15}N_{phyto}$). $\delta^{13}C_{phyto}$ was significantly lower in the

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 $\delta^{15}N_{phyto}$, 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. $\delta^{13}C$ and $\delta^{15}N$) 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%). $\Delta^{15}N$ values differed between locations

218 ($\chi^2_{146,3}$ = 118.3, $p<0.001$; Figure 3a). Norway individuals exhibited the highest $\Delta^{15}N$ and

219 individuals sampled in Portugal the lowest (C-I test, $p<0.001$ for all pairs of comparison).

220 Rockall $\Delta^{15}N$ value was also significantly higher than in Portugal (C-I test, $p<0.01$). $\Delta^{13}C$ 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 $\Delta^{13}C$ 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 $\Delta^{13}C$ (C-I test, $p>0.05$). At each location, there was no depth-related or

225 sex differences in $\Delta^{13}C$ and $\Delta^{15}N$ 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 Δ^{13}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 Δ^{13}C and Δ^{15}N rg. While displaying intermediate

230 TA and CD, *E. spinax* sampled in Rockall exhibited the highest Δ^{15}N rg.

231 For all sampling sites, significant linear relations were established between Δ^{15}N and TL (Figure

232 4a). Δ^{15}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 Δ^{15}N values

236 with TL. Δ^{13}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.

13

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

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 ($\Delta^{15}N$ and $\Delta^{13}C$)**

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). $\delta^{13}C$ 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 $\delta^{13}C$ values

284 measured by Elemtex. There were no observed differences in $\delta^{15}N$ 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 $\delta^{13}C$, Atmospheric air for $\delta^{15}N$).

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. $\Delta^{15}N$ and $\Delta^{13}C$) 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.

15

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 $\Delta^{15}N$ differences. Moreover, the suspected $\Delta^{15}N$ switch with TL was

300 not observed at all sites. The relevance of $\Delta^{15}N$ 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 $\delta^{15}N$ 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 $\delta^{15}N$ or $\Delta^{15}N$ values.

319   However, differences in *E. spinax* vertical segregation of maturity stages or bathymetric

320   constraint among sites could explain $\Delta^{15}N$ 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   $\Delta^{13}C$ 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* $\Delta^{13}C$ 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 $\Delta^{13}C$ 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 $\Delta^{13}C$ 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 $\delta^{13}C$ 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 $\Delta^{15}N$ variations and high redundancy index (Table

357   3). Still, their broad $\Delta^{13}C$ 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 δ^{13}C and δ^{15}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. Δ^{15}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 δ^{15}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* Δ^{15}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 Δ^{15}N values with length, as modelled δ^{15}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 $\Delta^{15}N$ 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).

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**
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)

Table 3: Summary of Layman metrics calculated on *E. spinax* isotopic niches (Δ^{13}C/Δ^{15}N values) and based on convex hull areas. Δ^{13}C rg and Δ^{15}N rg represent both isotopic ranges, TA the total area, CD the mean distance to centroid, NND (as mean ± standard deviation) the nearest neighbor distance (details of Layman metrics calculation can be found in Materials and Methods). All values are presented in ‰ except for TA (in ‰^{2}).

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

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.
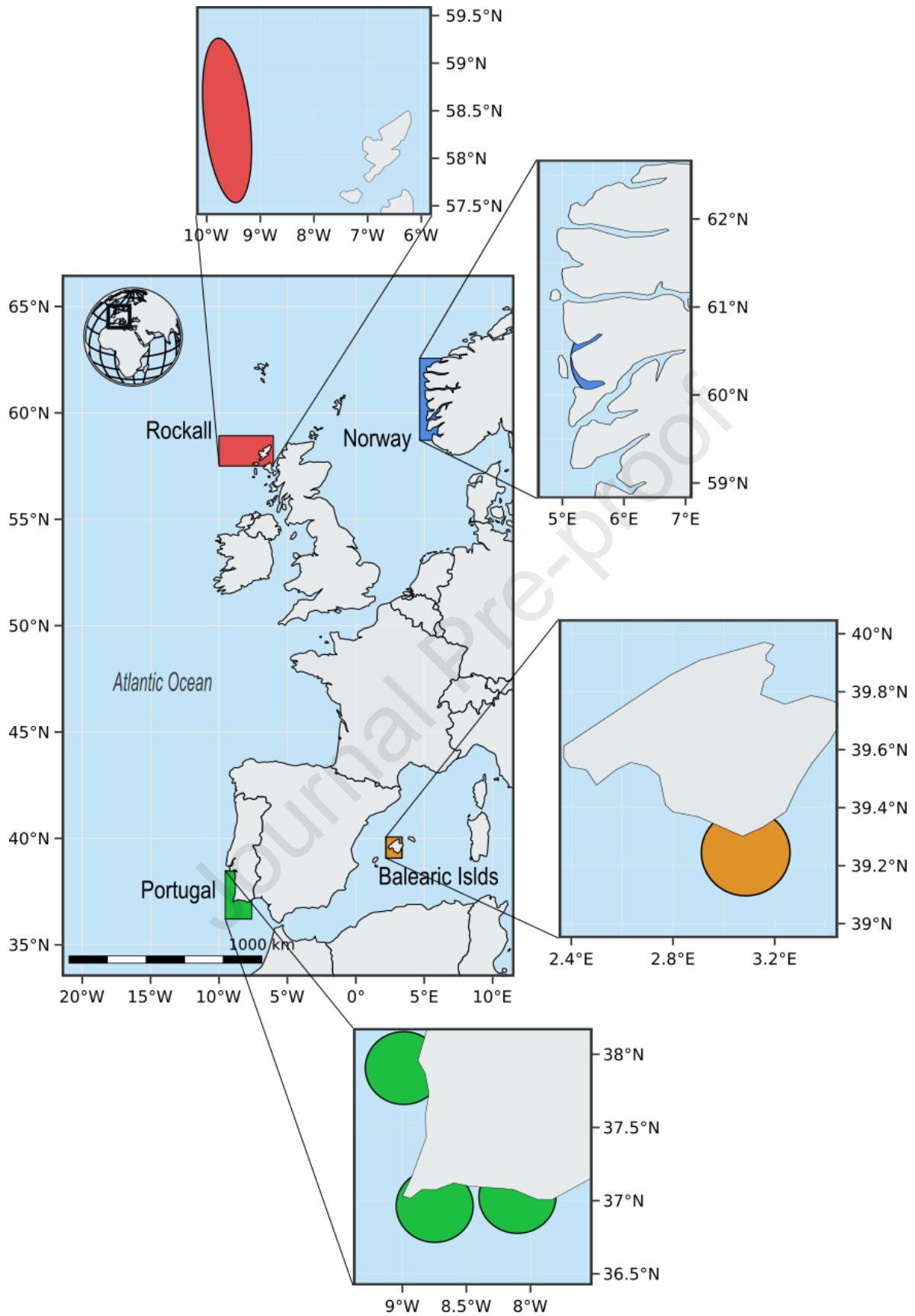
Figure 1: Sampling locations of velvet belly lantern sharks, *Etmopterus spinax*. Sampling area in Norway both corresponds to specimens analysed for stomach content and stable isotopes analysis.
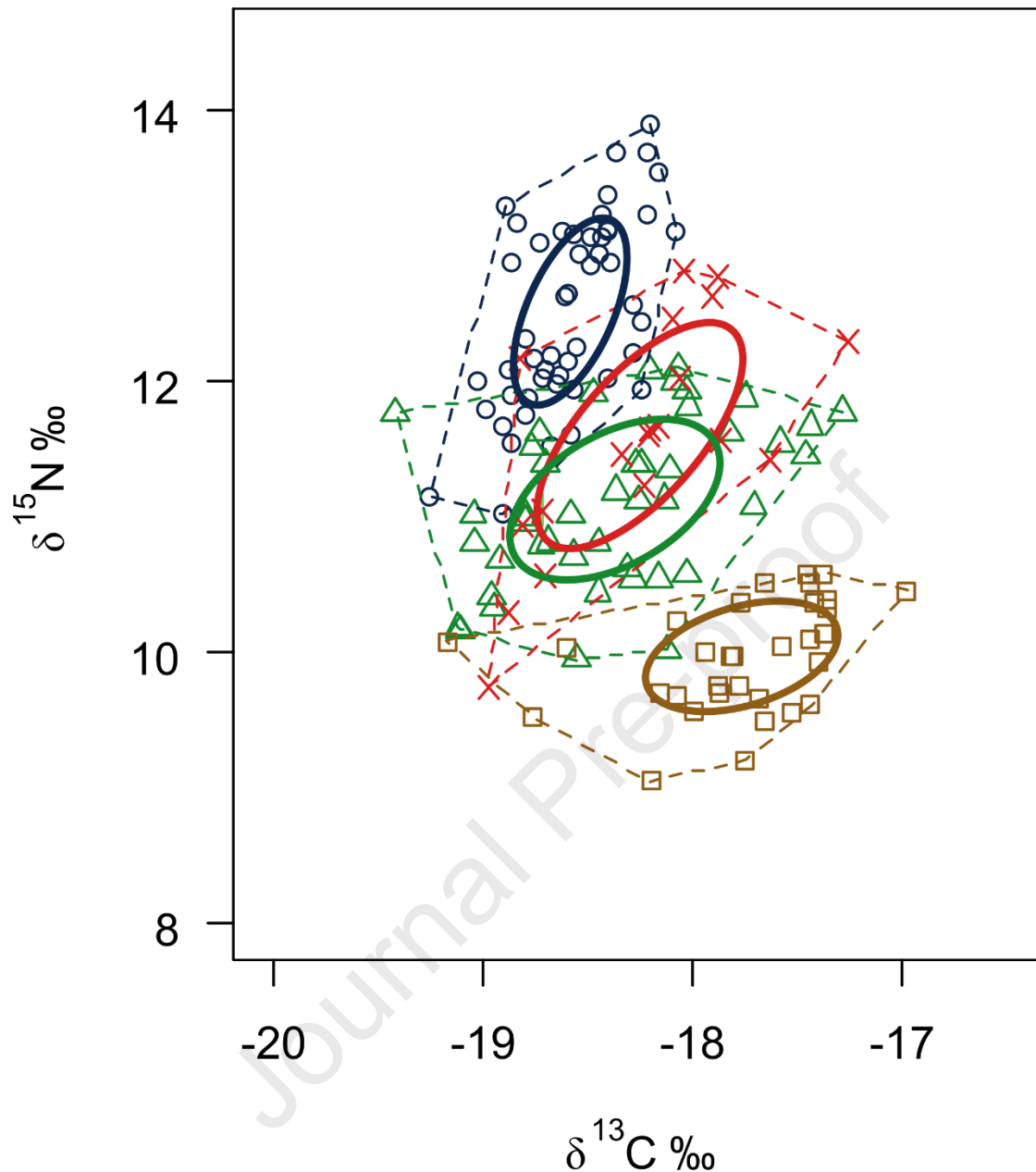
Figure 2: Muscle δ^{13}C and δ^{15}N values of *E. spinax*. Brown square points correspond to the Balearic Islands, blue circle points to Norway, green triangle points to Portugal and red cross points to Rockall samples. Solid lines delimit the standard ellipse areas (SEA) and dashed lines the convex hull areas for each sampling location. The only overlapping regions between SEA occurs between Portugal and Rockall individuals (39.89%).
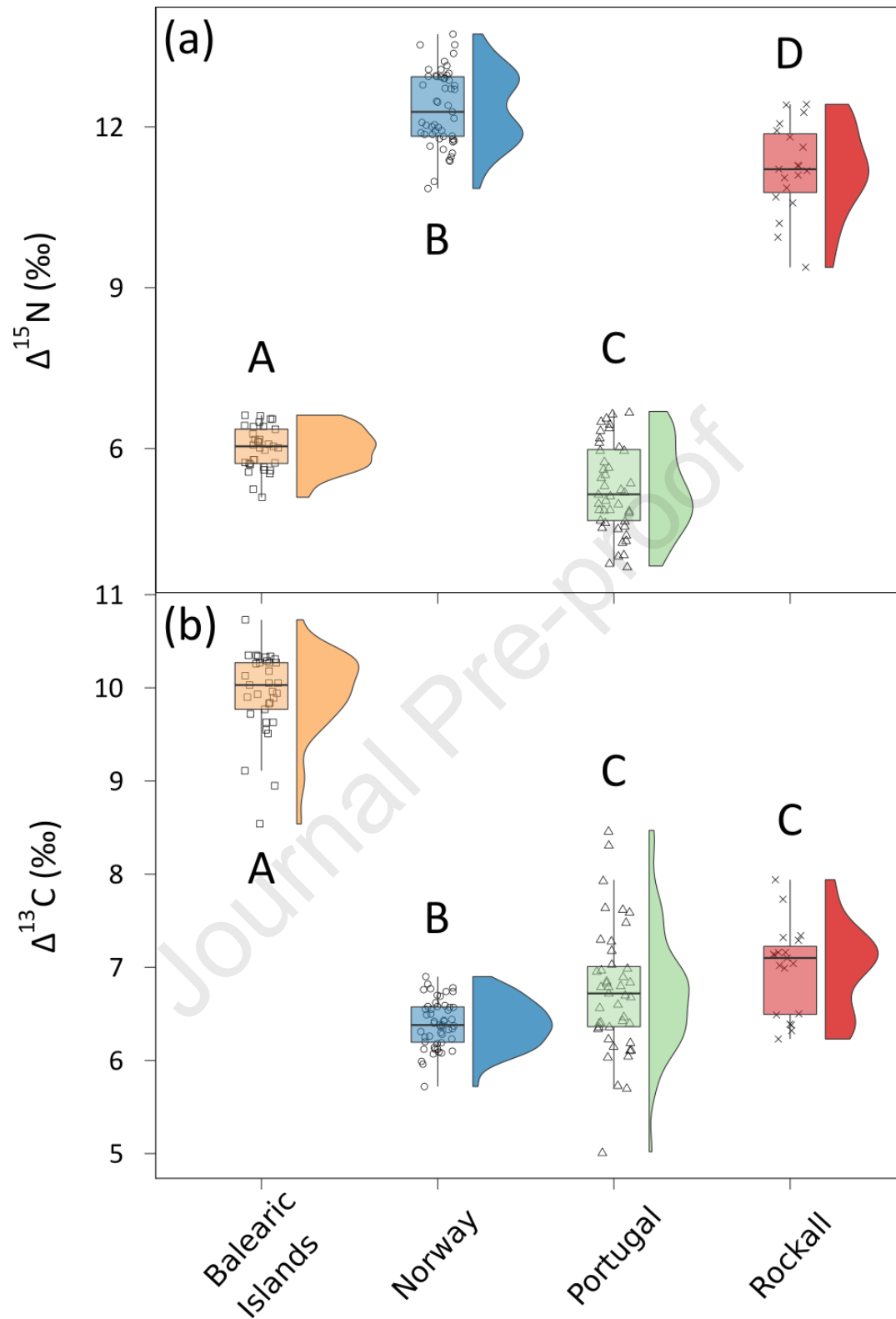
Figure 3: Boxplots of Δ^{15}N (a) and Δ^{13}C (b) values of *E. spinax* at each location. Significant differences are indicated by letters (p < 0.05).

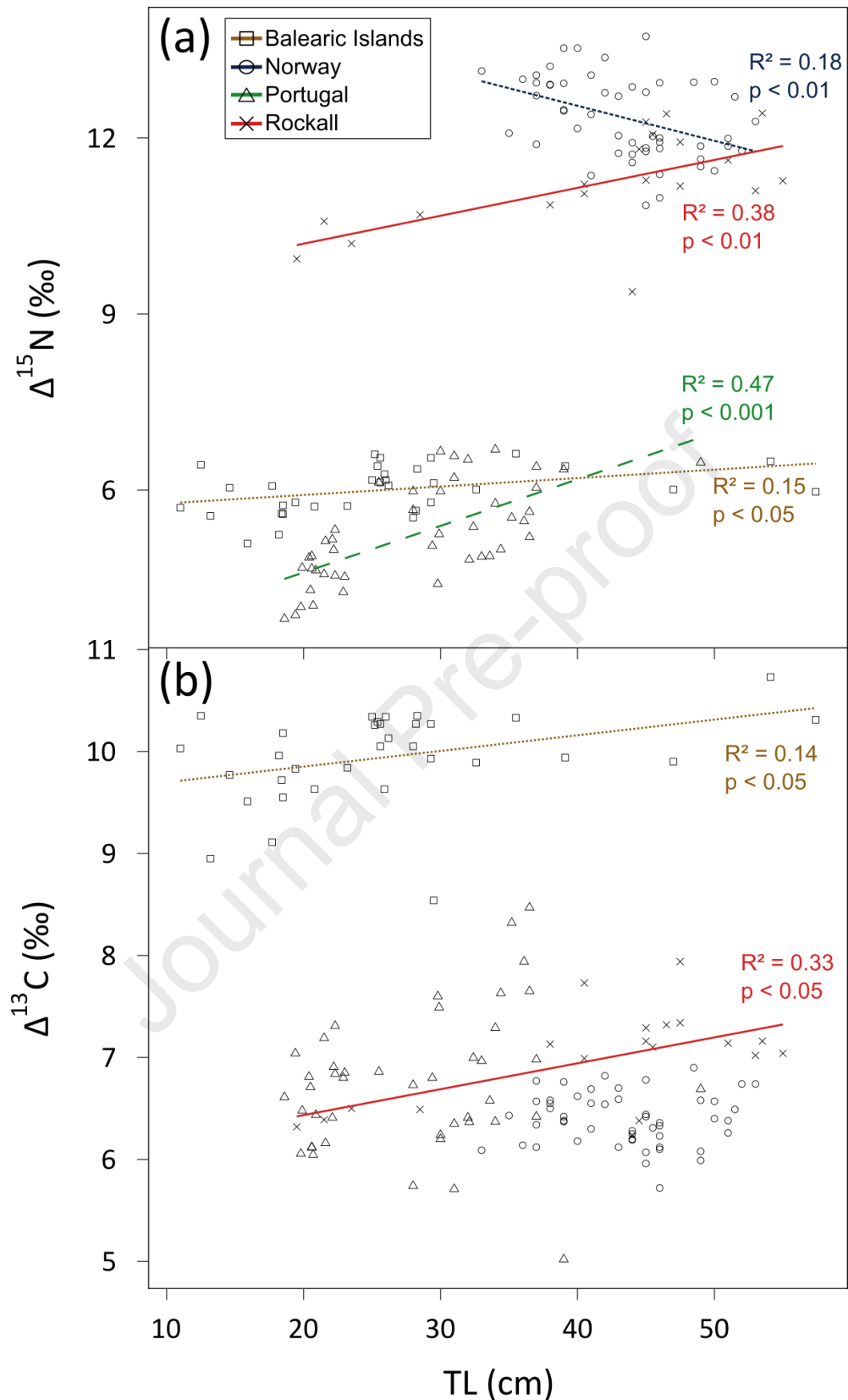**Figure 4:** Relationships between individual Δ^{15}N (a)/Δ^{13}C (b) values and total length (TL) of *E. spinax*. Pearson linear regressions were applied for each location with their corresponding R^2 and p-value reported in the figure.

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: