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1 **Stable isotope patterns in micronekton from the Mozambique Channel**

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14

15 **ABSTRACT**

16 We measured the stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic composition of tissues of
17 micronektonic organisms (fishes, squids, crustaceans and gelatinous organisms) collected in
18 the Mozambique Channel during two scientific cruises in 2008 and 2009. The oceanic
19 circulation in the Mozambique Channel is dominated by mesoscale cyclonic and anticyclonic
20 eddies which play a key role in biological processes of less-productive deep-sea ecosystems.
21 We investigated the potential impact of mesoscale features on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of
22 32 taxa of micronekton. Fishes, squids, crustaceans and gelatinous organisms encompassed
23 a wide range of isotopic niches, with large overlaps among species. Our results showed that
24 mesoscale features did not really influence the isotopic signatures of the sampled organisms,
25 although cyclonic eddies can occasionally impact the nitrogen signatures of micronekton.
26 We show that $\delta^{13}\text{C}$ values were intermediate between standard offshore and nearshore
27 signatures, suggesting that pelagic production in the Mozambique Channel could be partly
28 supported by the transport and export of inorganic and organic particles from the
29 Mozambican coast toward the offshore area. Trophic levels calculated from $\delta^{15}\text{N}$ values
30 ranged from 2.6 to 4.2, showing that micronekton taxa can be tertiary consumers in the
31 Mozambique Channel. Our findings evidenced clusters of micronektonic organisms
32 according to their $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ isotopic signatures, but variations in stable isotope values
33 reflect a complex set of embedded processes linked to physical mesoscale dynamics
34 (rotational dynamics of eddies) and basic biology and ecology of micronektonic organisms
35 (vertical habitat, migration pattern, dietary habits, body length) that are discussed with
36 regard to the stable isotope method based on time-integrated assimilated food.

37

38 **KEYWORDS:** Micronekton, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, Mesoscale, Oceanic eddies, Diel vertical migration,
39 Trophic level, Mozambique Channel.

40

41 **1. INTRODUCTION**

42 The circulation in the Mozambique Channel (south-west Indian Ocean) is ruled by an
43 important mesoscale activity (de Ruijter et al., 2002). Mesoscale rotating eddies propagate
44 southwards along the western edge of the channel (Quartly and Srokosz, 2004; Schouten et
45 al., 2003). These mesoscale features contribute to ocean mixing processes and consequently
46 impact the biological activity at different scales. Cyclonic eddies (clockwise rotating in the
47 southern hemisphere) generate vertical pumping of nutrients in their centres (Bakun, 2006;
48 Chelton et al., 2011; McGillicuddy Jr et al., 1998), enhancing local primary production
49 (Benitez-Nelson et al., 2007; Mizobata et al., 2002; Tew-Kai and Marsac, 2009). On the
50 opposite, anticyclonic eddies (counter-clockwise rotating) are usually associated with low
51 chlorophyll levels (Bakun, 2006; Chelton et al., 2011). However, phytoplankton enrichment
52 has also been associated with the upward movement of nutrient rich waters at the edges of
53 either cyclonic or anticyclonic eddies (Mizobata et al., 2002; Quartly and Srokosz, 2004). In
54 addition, coastal primary production produced on the western side of the channel can be
55 horizontally advected by continuous contra-rotating eddy pairs, referred to as dipoles and
56 propagating southwards (Roberts et al., this issue; Ternon et al., this issue). By influencing
57 the horizontal and vertical distribution at the base of the food web (nutrients, phytoplankton
58 and zooplankton), these features have been suggested to alter the distribution of
59 intermediate trophic links such as micronekton, and thus the distribution of upper-trophic
60 level organisms.

61 Biological responses to mesoscale eddies have been documented for mesozooplankton and
62 fish larvae (Bakun, 2006; Muhling et al., 2007), for tunas and swordfish (Young et al.,
63 2001);(Seki et al., 2002), for turtles (Lambardi et al., 2008; Polovina et al., 2004), for seabirds
64 (Hyrenbach et al., 2006; Nel et al., 2001; Weimerskirch et al., 2004), or for marine mammals
65 (Bailleul et al., 2010). In spite of their importance, the impact of mesoscale features on
66 micronektonic organisms remains fragmented and is still poorly quantified (see Potier et al.,
67 this issue). Recent investigations showed that eddies can shape the distribution and the
68 aggregation patterns of micronekton through bottom-up processes (Drazen et al., 2011;
69 Sabarros et al., 2009). Micronekton refers to small, but actively swimming, organisms (*ca.* 1
70 to 20cm), mainly crustaceans, fishes, and squids, that form the link between zooplankton
71 and large fish predators in open-sea ecosystems (Brodeur and Yamamura, 2005; Potier et al.,
72 2007). Most of micronekton performs large diel vertical migrations during the crepuscular
73 periods (dawn and dusk), from depths below 400m during the day to the surface layers at
74 night (Benoit-Bird et al., 2009).

75 In this work, we analyzed the ratios of stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes in
76 the tissues of micronektonic organisms collected in the Mozambique Channel within the
77 framework of the MESOBIO programme (Ternon et al., this issue). Carbon and nitrogen
78 isotopes have often successfully been applied to investigate foraging ecology and trophic
79 relationships in marine ecosystems (Cherel et al., 2010; Fanelli et al., 2011; Ménard et al.,
80 2007; Olson et al., 2010; Revill et al., 2009; Stowasser et al., 2012). Stable isotope ratios of
81 carbon and nitrogen in consumer tissues reflect those of their prey in a predictable manner,
82 and depend on the isotopic signature at the base of the food web (Fry, 2006; Post, 2002).
83 The $\delta^{15}\text{N}$ values mainly estimates the relative trophic position of an animal thanks to
84 predictable enrichment of ^{15}N with increasing trophic level (Vanderkluft and Ponsard, 2003).

85 Thus, $\delta^{15}\text{N}$ has been used for quantifying and comparing trophic levels of consumers (Cherel
86 et al., 2008). By contrast, $\delta^{13}\text{C}$ variations are used to determine the sources of primary
87 production, inshore versus offshore or pelagic versus benthic contribution to food intake
88 (Rubenstein and Hobson, 2004). Different processes affect isotopic baselines of $\delta^{13}\text{C}$ and
89 $\delta^{15}\text{N}$, including nutrient source, primary productivity, depth and ocean mixing processes (Fry,
90 2006). The present work aims (1) to investigate the potential impact of mesoscale features
91 on the ratios of stable carbon and nitrogen isotopes of micronektonic organisms, and (2) to
92 interpret the isotopic niches and the trophic levels of micronektonic species in the
93 Mozambique Channel.

94

95 **2. MATERIAL AND METHODS**

96 **2.1. Sample collection**

97 Micronekton samples were collected from two scientific cruises during December 2008 on
98 board R/V Fridtjof Nansen (2008 ASCLME survey n°4, called hereafter MC08A) and during
99 November 2009 on board R/V ANTEA (referred to as MC09B). A Young Gadoid Pelagic Trawl
100 (YGPT) was used during MC09B with a cod-end lined with 5mm knotless nylon delta mesh
101 netting, while an Akrahamn pelagic trawl with cod-end 10mm was used during MC08A.
102 Trawls were conducted during the day on aggregations detected by acoustics, and during the
103 night at the surface on sound scattering layers (0-200m). Night trawl depth was selected
104 according to highest acoustic detections. Each trawl was towed for 30 min at a speed of 3 to
105 4 knots. A total of 16 and 18 trawls were performed during MC08A and MC09B, respectively
106 (from which 2/3 were carried out at nighttime). The whole catch was sorted and soft tissues
107 of selected micronekton species were removed for further isotopic analyses: dorsal muscle
108 for fishes, mantle for squids, abdomen for crustaceans and body wall for pelagic gastropods

109 molluscs, siphonophorans, leptocephali larvae and salps. Body length of each individual was
110 measured except for salps: standard length (SL) for fishes, dorsal mantle length (DML) for
111 squids, cephalothorax length (CT) for crustaceans, and total length for the other taxa.

112

113 **2.2. Stable isotope analysis**

114 Samples were freeze-dried and ground to a fine homogeneous powder. Since lipids are
115 depleted in ^{13}C , lipids were removed using dichloromethane on an accelerated solvent
116 extraction system (ASE[®], Dionex;(Bodin et al., 2009). This method does not alter $\delta^{15}\text{N}$
117 signatures. The extent of lipid extraction was checked through the C/N mass ratio of the
118 samples (Post et al., 2007). Lipid-free samples were dried at 50°C before processing, and
119 then 300 to 400 μg of homogenized powder were packed into 8 \times 5mm tin containers.
120 Isotopic ratios were determined by a continuous flow mass spectrometer coupled on line to
121 an elemental analyzer. Replicate measurements of internal laboratory standards indicated
122 measurement errors less than 0.15‰ and 0.20‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Triplicate
123 measurements performed on some samples confirmed that analytical reproducibility was
124 very good (0.2‰ maximum variation). Isotopic ratios are expressed in the conventional δ
125 notation as parts per thousand (‰) deviations from the international standards:
126 atmospheric nitrogen (N_2) for $\delta^{15}\text{N}$ and VPDB Belemnite for $\delta^{13}\text{C}$.

$$127 \quad \delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \quad (1)$$

128 where X is ^{15}N or ^{13}C , R is the corresponding ratio $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$.

129

130 **2.3. Data analysis**

131 Satellite altimetry allows identification of mesoscale features (Chelton et al., 2007). One
132 mesoscale feature among five classes (anticyclone, A; cyclone, C; divergence, D; front, F; and

133 shelf station, S) was assigned to each of the 34 trawling stations. The classification of each
134 individual station was processed using three explanatory variables (sea level anomaly,
135 geostrophic speed and bathymetry) and a discriminant function estimated from an extra
136 training dataset (Lamont et al., this issue). Ocean bathymetry was extracted from ETOPO1
137 Global Topography (data access: <http://www.ngdc.noaa.gov/mgg/global/global.html>). Sea
138 level anomaly and the corresponding geostrophic speed were extracted from AVISO
139 products “DT-MSLA Ref” (Delayed Time, DT; Reference, “Ref”) with $0.33 \times 0.33^\circ$ spatial
140 resolution on a Mercator grid. The predictions from the linear discriminant analysis were
141 estimated for each station using the values taken by the three explanatory variables at the
142 corresponding temporal and spatial positions.

143 Links between isotope values ($\delta^{15}\text{N}$ and/or $\delta^{13}\text{C}$), and broad categories and mesoscale
144 features were investigated using multivariate analysis of variance (MANOVA), Kruskal-Wallis
145 (KW) non-parametric tests and univariate regression tree (URT). URT is a powerful statistical
146 tool that explains the variation of a single response variable ($\delta^{15}\text{N}$ or $\delta^{13}\text{C}$) using several
147 explanatory variables by growing a tree that partitions the data set into mutually exclusive
148 groups (Venables and Ripley, 2002). The objective is to partition the response into
149 homogeneous groups. All the data are represented by a single node at the top of the tree.
150 Then the tree is built by repeatedly splitting the data. Each split is defined by a simple rule
151 based on a single explanatory variable. Splits are chosen to maximize the homogeneity of
152 the resulting two nodes. However, the splitting procedure grows an overlarge tree. To keep
153 the tree reasonably small, a prune back procedure is applied. Each final group is
154 characterized by mean values of $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$.

155 As the content of ^{15}N in animal tissues is biomagnified along the length of a food chain (Post,
156 2002), trophic levels (TL) of micronekton taxa were calculated on the basis of isotopic
157 measurements using the following equation:

$$158 \quad TL = 2.0 + \frac{\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{primary consumer}}}{3.2} \quad (2)$$

159 where $\delta^{15}\text{N}_i$ is the nitrogen isotopic composition of any given micronekton taxon i , $\delta^{15}\text{N}_{\text{primary}}$
160 consumer is the $\delta^{15}\text{N}$ reference baseline value at trophic level 2, and 3.2‰ is an estimate of the
161 average increase of $\Delta^{15}\text{N}$ per trophic level (Cherel et al., 2010; Sweeting et al., 2007). Using
162 primary consumers as a baseline might reduce error in the estimation of TL (Martínez del Rio
163 et al., 2009). Salps are known to be filter-feeders grazing on phytoplankton and other small
164 food items. They were often chosen as the primary consumer species for estimating trophic
165 levels using equation (2) (Cherel et al., 2010, 2008; Stowasser et al., 2012). Therefore, we
166 chose average $\delta^{15}\text{N}$ value of *Salpa maxima* as the reference value for the food base. The
167 mean was computed using three $\delta^{15}\text{N}$ values (5.0, 5.2, 5.2‰) from MC08A and one (5.2‰)
168 from MC09B.

169

170 3. RESULTS

171 Fig. 1 displays the location of the 34 trawls categorized in four mesoscale feature classes
172 (cyclones C, anticyclones A, fronts F, divergences D and shelf station S). A total of 545
173 organisms amongst 32 taxa were analyzed (Table 1). Not all micronekton taxa were caught
174 at all mesoscale features, in particular few individuals were collected in anticyclones and
175 cyclones (68 and 77, respectively) compared with those collected in divergences and fronts
176 (187 and 121, respectively).

177

178 3.1. Micronekton assemblage

179 Taxa were divided in four broad categories: gelatinous organisms (*Salpa maxima*,
180 siphonophorans, the pelagic gastropod molluscs *Carinaria lamarckii* and leptocephali larvae),
181 crustaceans (*Funchalia* spp., *Oplophorus* sp. and *O. typus*), squids (*Cranchia scabra*,
182 *Ornithoteuthis volatilis*, *Sthenoteuthis oualaniensis*), and fishes. Fishes represented 16
183 species, 5 genera and 1 family. The family Bramidae grouped juveniles of *Pterycombus*
184 *petersii* and of other undetermined species: they were not segregated by both $\delta^{15}\text{N}$
185 (Kruskall-Wallis, $H = 1.19$, $P > 0.27$) and $\delta^{13}\text{C}$ values ($H = 0.43$, $P > 0.50$). The *Thunnus* spp.
186 category comprised very small juvenile scombrids that were not identified. *Psenes* spp.
187 comprised 2 species (*P. cyanophrys*, *P. whiteleggii*) that were not segregated by their $\delta^{15}\text{N}$
188 signatures (Kruskall-Wallis, $H = 1.78$, $P > 0.18$), but slightly segregated by $\delta^{13}\text{C}$ (Kruskall-
189 Wallis, $H = 4.0$, $P = 0.045$). The genus *Diaphus* is taxonomically one of the most difficult in the
190 family Myctophidae. We accurately identified three species (*D. garmani*, *D. metopoclampus*,
191 *D. richardsoni*). The *Diaphus* spp. category groups other species that were not identified.
192 Juveniles were collected for Bramidae, *Decapterus* sp., *Pterycombus petersii*, *Psenes* spp. and
193 *Thunnus* spp only.

194 Means of C/N mass ratio encompassed a narrow range (between 3.0 and 3.4 for 30 taxa;
195 only *Salpa maxima* and leptocephali larvae had ratios greater than 4; Table 1). Such small
196 values indicated low lipid content after lipid removal, thus allowing accurate comparisons of
197 $\delta^{13}\text{C}$ values among sample types. Isotopic analyses revealed a considerable range of $\delta^{13}\text{C}$ and
198 $\delta^{15}\text{N}$ mean values, 3.3 and 6.9‰, respectively. The $\delta^{13}\text{C}$ mean values ranged from $-20.6 \pm$
199 0.57‰ (leptocephal larvae) to $-17.3 \pm 0.24\text{‰}$ (*Oplophorus* sp.) (Table 1). The $\delta^{15}\text{N}$ ranged
200 from $5.2 \pm 0.11\text{‰}$ (*Salpa maxima*) to $12.1 \pm 0.44\text{‰}$ (*Diaphus metopoclampus*).

201 The four broad categories (fishes, squids, crustaceans and gelatinous organisms) were
202 segregated by their isotope signatures of both nitrogen and carbon treated as a multivariate

203 response (MANOVA, Wilk's lambda, $F_{3,540} = 58.37$, $P < 0.0001$). They were also segregated in
204 their isotopic signatures in both $\delta^{13}\text{C}$ (univariate analysis, KW test, $H = 115.0$, $P < 0.0001$;
205 pairwise comparisons indicated that crustaceans and squids were not significantly different)
206 and $\delta^{15}\text{N}$ values (KW test, $H = 56.0$, $P < 0.0001$; fishes and squids did not differ significantly).
207 Fig. 2 displays a summary of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm standard deviation) of all the taxa
208 grouped by broad categories. To give a better picture of the trophic structure of the
209 assemblages, taxa of the four broad categories were placed in sequence according to their
210 nitrogen and carbon mean values (Fig. 3a and 3b, respectively). Tests were then conducted
211 by categories:

212 - The 22 taxa of fish were segregated by their overall isotopic signatures (MANOVA, Wilk's
213 lambda, $F_{21,354} = 14.99$, $P < 0.0001$), and both $\delta^{13}\text{C}$ (KW test, $H = 151.1$, $P < 0.0001$) and $\delta^{15}\text{N}$
214 values (KW test, $H = 249.6$, $P < 0.0001$). The most enriched values were found for known
215 deep migrating mesopelagic fishes such as several Myctophidae (all of the genus *Diaphus*,
216 *Lobianchia gemellarii*), the bregmacerotid *Bregmaceros macclellandii*, the notosudid
217 *Scopelosaurus hoedti*, and the sternoptychid *Argyropelecus aculeatus*. *Cubiceps*
218 *pauciradiatus* (Nomeidae) and *Decapterus* sp. (Carangidae) exhibited large standard
219 deviations of $\delta^{15}\text{N}$ thanks to a subset of specimens caught in one cyclone of MC09B with very
220 high $\delta^{15}\text{N}$ values (see below).

221 - Overall isotopic signatures differed between the three squid species (MANOVA, Wilk's
222 lambda, $F_{2,101} = 4.90$, $P < 0.001$), but only the KW test based on $\delta^{13}\text{C}$ signatures was
223 significant ($H = 10.62$, $P < 0.005$ for $\delta^{13}\text{C}$; $H = 0.85$, $P = 0.66$ for $\delta^{15}\text{N}$).

224 - For crustaceans (three taxa) and gelatinous organisms (four taxa), multi- and univariate
225 tests were all significant. Standard deviations of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for leptocephali larvae
226 were very high, while the nitrogen signatures of *Salpa maxima* varied very little ($5.2 \pm$

227 0.11‰). *Oplophorus typus* (crustacean) was the only non-fish taxa having a $\delta^{15}\text{N}$ average
228 greater than 10.0‰ (Fig. 3a), and *Oplophorus* sp. had the most ^{13}C enrichment.

229

230 **3.2. Impact of mesoscale features**

231 No clear pattern emerged from $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ bi-plots of the 545 individuals categorized by
232 broad category and by mesoscale feature (figures not shown). To investigate the structure of
233 the data and assess the influence of eddies, we conducted univariate regression tree
234 analyses (URT) on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values using cruise, broad category, mesoscale feature,
235 taxon and body length as covariates. Five groups were identified by the URT based on $\delta^{15}\text{N}$
236 values (Fig. 4a). Groups were sorted in order of increasing $\delta^{15}\text{N}$ predicted values (Fig. 4b).
237 The first splits of the pruned tree separated taxa: one group of low $\delta^{15}\text{N}$ values clustered
238 gelatinous organisms (except siphonophorans), small fishes and one crustacean (*Funchalia*
239 *spp.*); the other group put together deep migrating mesopelagic organisms (11 fish taxa and
240 the crustacean *Oplophorus typus*) with rather high $\delta^{15}\text{N}$ values. A further split separated
241 cyclonic eddies from the four other classes (anticyclones, divergences, fronts and shelf
242 stations). The non cyclonic group mixed taxa from the four broad categories. The “cyclonic”
243 branch of the pruned tree separated two groups (Fig. 4a and 4b): *Cyclonic 1* grouped 22
244 individuals (14 fishes, three specimens of the crustacean *Oplophorus* sp. and five specimens
245 of the squid *Cranchia scabra*) with intermediate $\delta^{15}\text{N}$ values (predicted value of 9.4‰);
246 *Cyclonic 2* clustered six specimens of *Cubiceps pauciradiatus* (fish) and one *Ornithoteuthis*
247 *volatilis* (squid) collected in the same cyclone sampled in November 2009 (cruise MC09B),
248 with the highest $\delta^{15}\text{N}$ values (predicted value of 14.1‰).

249 Four groups were identified by the URT based on $\delta^{13}\text{C}$ values. Taxon was the only significant
250 covariate used to develop the pruned tree (Fig. 5a and 5b). Group 2 clustered most of the

251 micronekton taxa (Fig. 5a and 5b) with a predicted average of -18.7% . Group 3 classified
252 taxa with the highest ^{13}C enrichment (predicted $\delta^{13}\text{C}$ value of -18.2%). Leptocephali larvae
253 were segregated owing to their low $\delta^{13}\text{C}$ values.

254

255 **3.3 Trophic levels and size**

256 Since size is an important factor structuring trophic links, we looked at the potential
257 relationships between body length and $\delta^{15}\text{N}$ values. However we were limited by sample
258 sizes and body length ranges, and size effect was tested for ten taxa only (Table 1). The
259 fishes Bramidae, *Cubiceps pauciradius*, *Thunnus* spp. and the squid *Sthenoteuthis*
260 *oualaniensis* showed a significant body length effect (Fig. 6 and Table 2). One outlier for *S.*
261 *oualaniensis* was removed from the linear regression (Fig. 6b). Fig. 6c reveals that a simple
262 model was not appropriate for *C. pauciradius*: the six individuals sampled in the cyclone of
263 November 2009 were cut off from the other individuals. The final model did not select two
264 separate linear regressions. The most parsimonious model retained parallel regressions
265 (same estimated slope) and different intercepts (Table 2).

266 Estimated TLs within the micronekton consumers of Mozambique Channel ranged from 2.2
267 (leptocephali larvae) to 4.2 (the fish *D. metopoclampus*), encompassing theoretically two
268 trophic levels (Table 1). Of course, estimated TLs exhibited the same patterns as $\delta^{15}\text{N}$ values
269 because the only unknown in equation (2) was the nitrogen isotopic composition of
270 micronekton taxa. The three squid species shared the same TL (3.3 to 3.4), and the deep
271 migrating mesopelagic fishes and the crustacean *O. typus* had the highest TLs.

272

273 **4. DISCUSSION**

274 To our knowledge this study is the first that investigates the potential impact of mesoscale
275 eddies on the isotopic signatures of a large assemblage of micronekton from gelatinous
276 organisms to fish. An extensive investigation conducted on two counter-rotating eddies off
277 Western Australia analyzed mainly the impact of eddies on the isotopic composition of
278 dissolved inorganic nitrogen, particulate organic matter and mesozooplankton (Waite et al.,
279 2007). Fish larvae identified at the family level were also collected with small nets, allowing
280 the analysis of eel leptocephals and of small-sized specimens of Myctophidae,
281 Sternoptychidae, Paralepididae, Phosichthyidae and Scorpaenidae only. The results of Waite
282 et al. (2007) showed no significant difference in the $\delta^{15}\text{N}$ signature between the fish larvae
283 from the two eddies, but myctophid larvae from the warm-core eddy (i.e., counter-clockwise
284 rotational sense) are significantly enriched in ^{13}C relative to those from the cold-core eddy
285 (i.e., cyclonic rotation). In our study, the fish taxa sampled covered several main open-ocean
286 micronekton fish families (juveniles and/or adults) found in the Mozambique Channel:
287 Myctophidae, Nomeidae, Bramidae, Phosichthyidae, Sternoptychidae, Notosudidae,
288 Gonostomatidae, Paralepididae, Bregmacerotidae and Carangidae. Our findings showed that
289 mesoscale features did not have any clear impact on the carbon and nitrogen signatures of
290 micronekton in the Mozambique Channel. The 32 taxa of crustaceans, squids and fishes
291 encompassed a wide range of isotopic niches, with large overlaps among species. Regression
292 trees evidenced patterns with clusters of organisms according to their $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ isotopic
293 signatures. We attempt henceforward to examine some hypotheses supported by our
294 results, taking into account the nature of our data and the stable isotope method.

295

296 **4.1 Isotopic patterns amongst mesoscale features**

297 Eddies play a key role in biological processes of less-productive deep-sea ecosystems by
298 converting physical energy into trophic energy (Bakun, 2006; Godø et al., 2012). They have
299 been suggested to impact the distribution of marine organisms through bottom-up effects
300 (Domokos, 2009; Domokos et al., 2007; Drazen et al., 2011; Muhling et al., 2007; Sabarros et
301 al., 2009; Seki et al., 2002; Tew Kai and Marsac, 2010). On the one hand few individuals in
302 our study had their $\delta^{15}\text{N}$ values directly impacted by mesoscale features which on the other
303 hand did not influence the carbon signatures of the sampled organisms. Six specimens of the
304 nomeid *C. pauciradiatus* and one *O. volatilis* (Ommastrephidae) were grouped by the
305 regression tree based on their $\delta^{15}\text{N}$ values (*Cyclonic 2*, Fig. 4). These specimens were
306 collected in the same cyclone sampled in November 2009 during the MC09B cruise, and had
307 distinctly higher $\delta^{15}\text{N}$ signatures than their congeners sampled in other mesoscale features.
308 Surprisingly, specimens from other species or taxa (leptocephali larvae, the squid *Cranchia*
309 *scabra*, the crustacean *Funchalia* spp., and the fishes *Argyropelecus aculeatus*, *Hygophum*
310 *hygomii* and *Vinciguerria nimbaria*) collected in the same cyclone did not show a similar
311 pattern. Their $\delta^{15}\text{N}$ signatures did not differ significantly from specimens collected in other
312 features (all KW test had a *p*-value much greater than 10%). This singular pattern could
313 suggest possible residency for the nomeid *C. pauciradiatus* into the eddy, while other species
314 or taxa could move among the water masses. Lamkin (1997) showed indeed that adult
315 spawning grounds and larval habitat of *C. pauciradiatus* can be tied to frontal systems along
316 eddy rings in the Gulf of Mexico. Mesoscale features impacted the nitrogen signatures of
317 *Thunnus* spp. only, with higher $\delta^{15}\text{N}$ signatures within anticyclones (KW test, $H = 15.0$, $P <$
318 0.001). Two extra individuals sampled in the same cyclone could have been added to the
319 *Cyclonic 2* group: one *Decapterus* sp. which had the highest $\delta^{15}\text{N}$ value (16.6‰) and one
320 *Lobianchia gemellarii* ($\delta^{15}\text{N} = 12.4\text{‰}$). In cyclonic eddies, vertical fluxes of nitrate can

321 dominate production leading to higher $\delta^{15}\text{N}$ signatures of the phytoplankton compared with
322 an anticyclonic eddy, where nitrate supply to the surface could be physically limited (Bakun,
323 2006; McGillicuddy Jr and Robinson, 1997; Muhling et al., 2007; Waite et al., 2007). To
324 impact the isotopic signature of pelagic consumers such as micronekton organisms, one
325 should assume that this isotopic baseline is incorporated and conserved through several
326 trophic levels trapped in the water mass of the cyclonic eddy. However this hypothesis is
327 challenged by the ecology and behaviour of micronekton organisms.

328

329 The vast majority of micronekton organisms typically occurs in the surface layer during the
330 night and migrates below 400m depth during the day (Behagle et al., this issue).
331 Micronekton ascents and descents during the crepuscular periods (dawn and dusk)
332 characterize this process of diel vertical migration (Benoit-Bird et al., 2009). In the Humboldt
333 Current system, the vertical extent of the water mass trapped in eddies has been recently
334 estimated to 240m and 530m in cyclonic and anticyclonic eddies respectively, with a global
335 decrease of the physical gradients with depth (Chaigneau et al., 2011). These estimates are
336 most likely variable from eddy to eddy and from one area to another. In eddies of the
337 Mozambique Channel, swirl velocities are weaker in deeper layers than they are at the
338 surface (Ternon et al., this issue). In addition, Kolasinski et al. (2012) showed that physico-
339 chemical characteristics of deep waters (including carbon and nitrogen isotopic values of
340 POM) from cyclonic and anti-cyclonic eddy of the Mozambique Channel were alike.
341 Consequently, the diel vertical migration causes micronekton to stay half of the time in
342 water masses weakly impacted by eddies. Contrary to the study of Godø et al. (2012) in the
343 Norwegian Sea, we believe that horizontal structure is not preserved during diel vertical
344 migration in the Mozambique Channel: migration did not take place in accordance with the

345 water mass trapped in eddies. In addition, eddies are translated rather slowly in the
346 Mozambique Channel ($5.2\text{cm}\cdot\text{s}^{-1}$; (de Ruijter et al., 2002) while the average speed of a
347 mesopelagic fish was measured acoustically to be about $30\text{cm}\cdot\text{s}^{-1}$ (Torgersen and Kaartvedt,
348 2001). Therefore, fish and most likely squids would still have the ability to swim across
349 eddies at any depth. However very few studies investigated how crustaceans swim. Morris
350 et al. (1985) analyzed the swimming in a small calanoid copepod (*Pleuromamma xiphias*,
351 6mm): they estimated maximal velocities to be $0.3\text{m}\cdot\text{s}^{-1}$ during the power strokes of an
352 entire swimming cycle, and less than $0.1\text{m}\cdot\text{s}^{-1}$ during the recovery strokes. The total lengths
353 of the three crustacean taxa in our study are at least five times the size of *P. xiphias* and
354 maximal swimming velocity scales with body length. We thus believe that micronekton is
355 rarely trapped in the water mass of a particular eddy and thus does not necessarily feed on
356 concentrations of zooplankton prey found in the eddy only.

357

358 Isotopic incorporation in animal tissues is linked to turnover rates that vary according to
359 tissue, body size, growth or taxon (Martínez del Rio et al., 2009). The dynamics of isotopic
360 incorporation can then blur the interpretation of our field isotopic measurements. Indeed, a
361 sampled micronekton specimen that had recently moved into an eddy from surrounding
362 waters may have had a previous $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ signature that would have been gradually
363 modified as they fed on new food sources trapped in the eddy. Depending on tissue-specific
364 isotopic turnover, stable isotope measurements reflect average dietary records over days
365 (e.g, whole fish larvae; Herzka and Holt, 2000) to years (e.g., elasmobranch muscle; MacNeil
366 et al., 2006; Logan and Lutcavage, 2010). No clear studies estimated isotopic turnovers for
367 micronekton but several weeks seem a reasonable order of magnitude. Consequently, the

368 particular isotope baseline of an eddy is likely not conserved through these pelagic
369 consumers.

370

371 However, migration can be a multifaceted and plastic response of micronekton. Partial diel
372 vertical migration has been reported in the literature, showing that resident and migrant
373 strategies can co-exist in some populations (Mehner and Kasprzak, 2011; Olsson et al.,
374 2006). In addition several taxa in our data were clearly epipelagic (leptocephali larvae, *Salpa*
375 *maxima*, *Thunnus* sp., *Decapterus* sp.). Notwithstanding their swimming abilities and
376 assuming a passive transport, all these species would then be more sensitive to eddy
377 structure. If trapped in the water mass of the eddy, they can prey on local concentrations of
378 zooplankton propagating the baseline of the “eddy” isotopic signature. This scenario might
379 be true for the specimens of the grouping *Cyclonic 2*.

380

381 **4.2 Carbon isotope patterns**

382 There was no significant difference in $\delta^{13}\text{C}$ signatures of micronekton between mesoscale
383 features. The $\delta^{13}\text{C}$ values ranged from -20.6 to -17.3‰ suggesting that micronekton
384 organisms sampled exploit different sources of primary production, giving rise to different
385 trophic pathways. However, most of $\delta^{13}\text{C}$ mean values encompassed a narrow range
386 between -19 and -18‰ (all squids, 19 fish taxa, two crustacean genera, Fig. 4b). Only
387 gelatinous organisms and three fishes (*Psenes* spp., *Diaphus metopoclampus* and
388 *Pterycombus petersii*) were depleted in ^{13}C compared with the other taxa. Leptocephali
389 larvae which could feed on detrital materials and fecal pellets (Lecomte-Finiger et al., 2004)
390 had the most ^{13}C -depleted carbon signature with a large variance of $\delta^{13}\text{C}$ values too.
391 Surprisingly, our $\delta^{13}\text{C}$ values were intermediate between standard offshore pelagic

392 signatures and nearshore signatures measured in this region (Hill et al., 2006; Kolasinski et
393 al., 2012), suggesting that pelagic production in the Mozambique Channel could be partly
394 supported by the transport and export of inorganic and organic particles from the
395 Mozambican coast toward offshore area, through the “vacuum-cleaner effect” due to
396 rotational dynamics of eddies (Tew-Kai and Marsac, 2009).

397

398 **4.3 Trophic levels of micronekton**

399 Micronekton form a key trophic link between top predators and zooplankton (Brodeur and
400 Yamamura, 2005), and are theoretically assumed to constitute the tertiary level of pelagic
401 food webs. The lowest trophic level except salps was occupied by leptocephali larvae (TL =
402 2.2), and TLs less than 3.0 were estimated for the carnivorous heteropod *Carinaria lamarckii*,
403 the penaeids *Funchalia* spp. and juveniles of three fish taxa (*Thunnus* spp., *Pterycombus*
404 *petersii* and *Psenes* spp.). The remaining estimated TLs encompassed a continuum of values
405 between 3.1 and 4.2, very close to those obtained by Cherel et al. (2010) and Stowasser et
406 al. (2012) for myctophids in the Southern Ocean. Our results show that micronekton
407 sampled can occupy relatively high trophic positions: the high TL of the myctophid *Diaphus*
408 *metopoclampus* probably fits with a diet based on euphausiids or small fish larvae, and the
409 high TL of the crustacean *Oplophorus typus* is explained by a diet strongly dominated by
410 detritus (Karuppasamy and Menon, 2004), which are known to be ¹⁵N-enriched. However
411 our organisms were preying upon a similar range of herbivorous and omnivorous consumers,
412 mainly meso- or macrozooplankton.

413

414 Body size is known to play a crucial role in predator–prey interactions (Sheldon et al., 1977).

415 Body length can influence $\delta^{15}\text{N}$ values (then TL) of one species because larger specimens can

416 catch larger prey as they grow (e.g. Parry, 2008). However intraspecific variation in $\delta^{15}\text{N}$ with
417 body length was identified in three fish taxa and one squid species only (Fig. 6 and Table 2).
418 For these taxa, the positive significant relationships may be indicative of larger specimens
419 feeding at higher trophic levels. We probably cannot conclude for the other taxa as pelagic
420 trawls used for sampling micronekton selected limited size ranges for each species (Table 1).
421 Interestingly, a model with two intercepts and one slope was fitted to the data of the fish
422 *Cubiceps pauciradiatus*. The common slope may be indicative of consistent ontogenetic
423 variability (i.e. a similar intraspecific variation), while different intercepts can result from a
424 shift in habitat use (i.e., $\delta^{15}\text{N}$ values impacted by a baseline change in a cyclonic eddy).
425 Furthermore the linear relationship between TL and body length means of taxa was not
426 significant ($F_{1,28} = 1.95$, $P = 0.17$ for 30 taxa), showing that the structuring effect of size was
427 not depicted in our data with regard to the range of the body length averages (Table 1).
428 Leptocephali larvae were indeed an outlier in the dataset (very low TL associated with high
429 body length) and salps were unfortunately not measured onboard.

430

431 But the interpretation of trophic level estimated from $\delta^{15}\text{N}$ values presents caveats. Isotopic
432 baseline can vary from year to year and can be conserved through several trophic levels.
433 Three salp samples were collected in December 2008 (MC08A) and one in November 2009
434 (MC09B) only, preventing statistical comparison. However $\delta^{15}\text{N}$ values were very close and
435 year effect (a confounding variable with the cruise factor which was one covariate in the
436 regression tree) was never significant. In addition sources of variation of the discrimination
437 factor are numerous (Martinez del Rio et al., 2009). These biases in isotopic TL calculation
438 can alter our estimates. In addition, the basic biology and ecology of micronekton

439 (ontogenetic migration, feeding habits) remain poorly known, making interpretation
440 difficult.

441

442 **4.4. Limitations of the data**

443 The spatial and temporal resolutions of our isotope data are limited by the sampling
444 coverage of the pelagic trawls that were carried out during two cruises. The two surveys did
445 not sample the same patterns of mesoscale eddies. In 2009 (MC09B), mesoscale features
446 were very stable and well established compared to 2008 (MC08A), where eddies were in
447 their early phases (Ternon et al., this issue). Contrary to Waite et al. (2007) who investigated
448 extensively the same dipole in one area, we sampled mesoscale features at different
449 maturation phases. Eddies are characterized by their dimension, intensity (e.g., sea surface
450 height, geostrophic and rotational velocities), lifetime, origin, trajectory, and propagation
451 distance (Bakun, 2006; Chelton et al., 2011). In addition eddies develop over time scales of
452 weeks to months while biological responses such as diel vertical migration can occur within a
453 day. All these eddy properties and development phases shape biological responses and then
454 impact the stable isotope signatures of the organisms.

455

456 In summary, biogeochemical and biological responses to mesoscale dynamics along the food
457 chain up to mid-trophic levels such as micronekton are variable and the underlying
458 mechanisms are complex to disentangle. The stable isotope method, based on time-
459 integrated assimilated food, allowed us to better depict the trophic relationships in this
460 micronekton assemblage. Some species had distinct isotopic niches, but others showed
461 strong overlap. In addition isotopic differences attributed to mesoscale dynamics were
462 evidenced for individuals of the same species. Thus the variations in stable isotope values in

463 our data reflect a complex set of embedded processes linked to physical mesoscale dynamics
464 and basic biology and ecology of micronektonic organisms (e.g. vertical habitat, migration
465 pattern, dietary habits and body length).

466

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475

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637 (*Thunnus albacares*) aggregations along the shelf break off south-eastern Australia: links
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640

641 Table 1. Body lengths and ranges (standard length for fishes, dorsal mantle length for squids,
642 cephalothorax length for crustaceans, total length for gelatinous organisms; in mm), $\delta^{13}\text{C}$
643 and $\delta^{15}\text{N}$ values (per mil), C/N ratios, and estimated trophic levels of micronekton from the
644 Mozambique Channel. Species or taxa are placed in broad class. Total number n and
645 numbers per Anticyclone, Cyclone, Divergence, Front, and Shelf are indicated. Values are
646 mean \pm standard deviation. * indicates taxon for which body length effect was tested.

647

648 Table 2. Linear regression models fitted to $\delta^{15}\text{N}$ values (per mil) and body length (SL:
649 standard length in mm; DML: dorsal mantle length in mm) of four taxa of micronekton from
650 the Mozambique Channel. Models fitted to the squid *Ornithoteuthis volatilis*, and for the fish
651 taxa *Decapterus* sp., *Lestrolepis intermedia*, *Myctophum spinosum*, *Psenes* spp. and
652 *Symbolophorus evermanni* were not significant. Sample sizes and body length ranges
653 precluded model fitting for the remaining taxa.

Broad class	Species	Phase	n	Body length mean (mm)	Body length range (mm)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N	TL	Anticyclone	Cyclone	Divergence	Front	Shelf
Gelatinous organisms	<i>Carinaria lamarckii</i>	adults	5	33.0	30-40	-19.7 ± 0.28	7.4 ± 0.61	3.4 ± 0.19	2.7 ± 0.2		5			
	Leptocephali larvae	larvae	10	217.6	170-260	-20.6 ± 0.57	5.8 ± 1.55	4.2 ± 0.37	2.2 ± 0.5		5			5
	<i>Salpa maxima</i>	solitary zooid	5	-	-	-19.4 ± 0.38	5.2 ± 0.11	4.1 ± 0.21	2				1	4
	<i>Siphonophora</i>		5	42.3	40-45	-19.3 ± 0.47	8.5 ± 0.63	3.2 ± 0.11	3.1 ± 0.2	3				2
Squids	<i>Cranchia scabra</i>	juveniles	9	40.1	35-47.1	-18.6 ± 0.49	9.4 ± 0.44	3.1 ± 0.21	3.3 ± 0.1	4	5			
	<i>Ornithoteuthis volatilis</i> *	juveniles & adults	18	102.3	63.8-179	-18.5 ± 0.4	9.5 ± 0.8	3.1 ± 0.07	3.4 ± 0.2		1	7	5	5
	<i>Sthenoteuthis oualaniensis</i> *	juveniles & adults	77	92.8	21.7-360	-18.2 ± 0.35	9.4 ± 0.77	3.1 ± 0.08	3.3 ± 0.2	19		38	14	6
Crustaceans	<i>Funchalia</i> spp.	adults	22	16.4	13.8-18.4	-18.6 ± 0.27	7.8 ± 0.8	3 ± 0.07	2.8 ± 0.3		8	3	7	4
	<i>Oplophorus</i> sp.	adults	8	13.0	12.7-13.5	-17.3 ± 0.24	9.3 ± 0.94	3 ± 0.04	3.3 ± 0.3		3		5	
	<i>Oplophorus typus</i>	adults	10	13.0	11.6-14.4	-18.1 ± 0.38	10.2 ± 0.32	3.3 ± 0.15	3.6 ± 0.1	5		5		
Fishes	<i>Argyropelecus aculeatus</i>	adults	23	56.8	42-77	-18.5 ± 0.46	10.5 ± 0.88	3.1 ± 0.08	3.7 ± 0.3		3	10	10	
	<i>Bramidae</i> *	juveniles	6	82.2	43-152	-18.9 ± 0.61	9.2 ± 0.86	3.1 ± 0.03	3.3 ± 0.3		2	3	1	
	<i>Bregmaceros macclellandii</i>	adults	5	77.6	71-82	-18.6 ± 0.15	10.9 ± 0.44	3.1 ± 0.02	3.8 ± 0.1				5	
	<i>Ceratoscopelus warmingii</i>	adults	5	59.6	53-65	-18.9 ± 0.26	9.4 ± 0.57	3.1 ± 0.02	3.3 ± 0.2	5				
	<i>Cubiceps pauciradiatus</i> *	juveniles & adults	55	98.1	23-140	-18.2 ± 0.4	9 ± 2.23	3.1 ± 0.06	3.2 ± 0.7		6	37	7	5
	<i>Decapterus</i> sp.*	juveniles	13	83.1	35-116	-18.5 ± 0.23	9.2 ± 2.23	3.1 ± 0.07	3.3 ± 0.7		10		3	
	<i>Diaphus garmani</i>	adults	5	56.2	40-75	-18.4 ± 0.35	10.4 ± 0.94	3.3 ± 0.03	3.7 ± 0.3				5	
	<i>Diaphus metopoclampus</i>	adults	6	57.7	54-62	-19.3 ± 0.19	12.1 ± 0.44	3.3 ± 0.04	4.2 ± 0.1			5	1	
	<i>Diaphus richardsoni</i>	adults	39	47.0	36-59	-18.9 ± 0.23	10.8 ± 0.52	3.2 ± 0.1	3.8 ± 0.2	5			14	20
	<i>Diaphus</i> spp.	adults	16	62.7	50-80	-18.5 ± 0.29	10.5 ± 0.62	3.1 ± 0.04	3.7 ± 0.2	5			5	6
	<i>Gonostoma elongatum</i>	juveniles & adults	5	108.8	96-120	-18.9 ± 0.12	9.7 ± 0.39	3 ± 0.02	3.4 ± 0.1			5		
	<i>Gymnoscopelus</i> sp.	adults	5	68.6	60-76	-18.6 ± 0.19	10.2 ± 0.38	3.1 ± 0.02	3.6 ± 0.1				5	
	<i>Hygophum hygomii</i>	adults	15	52.1	37.3-62	-18.8 ± 0.2	9.9 ± 0.66	3.1 ± 0.02	3.5 ± 0.2	5	5	1	4	
	<i>Lestrolepis intermedia</i> *	juveniles & adults	17	127.1	75-171	-18.8 ± 0.48	9.7 ± 0.83	3.2 ± 0.09	3.4 ± 0.3		2	4	3	8
	<i>Lobianchia gemellarii</i>	adults	5	50.0	45-70	-18.4 ± 0.18	11.1 ± 0.73	3.1 ± 0.01	3.9 ± 0.2		1			4
	<i>Myctophum spinosum</i> *	juveniles & adults	33	65.7	40-86	-18.8 ± 0.24	8.9 ± 0.38	3.2 ± 0.05	3.2 ± 0.1	2		16	10	5
	<i>Psenes</i> spp.*	juveniles	8	47.4	36-76	-19.2 ± 0.65	7.6 ± 0.34	3.2 ± 0.24	2.8 ± 0.1	2	6			
	<i>Pterycombus petersii</i>	juveniles	5	58.2	35-77	-19.6 ± 0.2	8.2 ± 0.66	3 ± 0.03	2.9 ± 0.2		3	2		
	<i>Scopelosaurus hoedti</i>	adults	6	123.7	112-126	-18.9 ± 0.04	11.4 ± 0.33	3.1 ± 0.01	3.9 ± 0.1		1			5
<i>Symbolophorus evermanni</i> *	adults	57	77.4	42-108	-18.6 ± 0.24	9.3 ± 0.69	3.2 ± 0.07	3.3 ± 0.2	5		30	12	10	
<i>Thunnus</i> spp.*	juveniles	33	43.0	23-84	-18.3 ± 0.51	7 ± 0.8	3.1 ± 0.06	2.6 ± 0.2	8	6	16		3	
<i>Vinciguerria nimbaria</i>	adults	14	39.9	32-46	-18.8 ± 0.29	10 ± 0.43	3.1 ± 0.03	3.5 ± 0.1		5	5	4		

657 Table 2

Taxon	Regression equation	r ² (%)	p	n
Bramidae	$\delta^{15}\text{N} = 7.77 + 0.0179 \times \text{SL}$	87.4	0.006	6
<i>Thunnus</i> spp.	$\delta^{15}\text{N} = 6.05 + 0.0226 \times \text{SL}$	19.9	0.01	33
<i>Sthenoteuthis oualaniensis</i>	$\delta^{15}\text{N} = 8.27 + 0.0122 \times \text{DML}$	46.4	< 0.0001	76
<i>Cubiceps pauciradiatus</i> (not Cyclone)	$\delta^{15}\text{N} = 6.04 + 0.0242 \times \text{SL}$			6
<i>Cubiceps pauciradiatus</i> (Cyclone)	$\delta^{15}\text{N} = 11.80 + 0.0242 \times \text{SL}$	90.24	< 0.0001	49

658

659

660 Fig. 1. Map showing the 34 sampling stations carried out in 2008 (cruise MC08) and 2009
661 (cruise MC09B) in the Mozambique Channel. Stations are categorized according to
662 mesoscale features (no cyclone was sampled in MC08A).

663

664 Fig. 2. Summary of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope signatures (mean \pm standard deviation in per mil)
665 of micronekton taxa sampled in the Mozambique Channel. Set diagrams group the four
666 broad categories (fishes, squids, crustaceans and gelatinous organisms).

667

668 Fig. 3. $\delta^{15}\text{N}$ (a) and $\delta^{13}\text{C}$ (b) isotope signatures (mean \pm standard deviation in per mil) of
669 micronekton taxa sampled in the Mozambique Channel. Taxa are placed in broad class and
670 then isotope signatures of both nitrogen and carbon are sorted in order of decreasing
671 depletion.

672

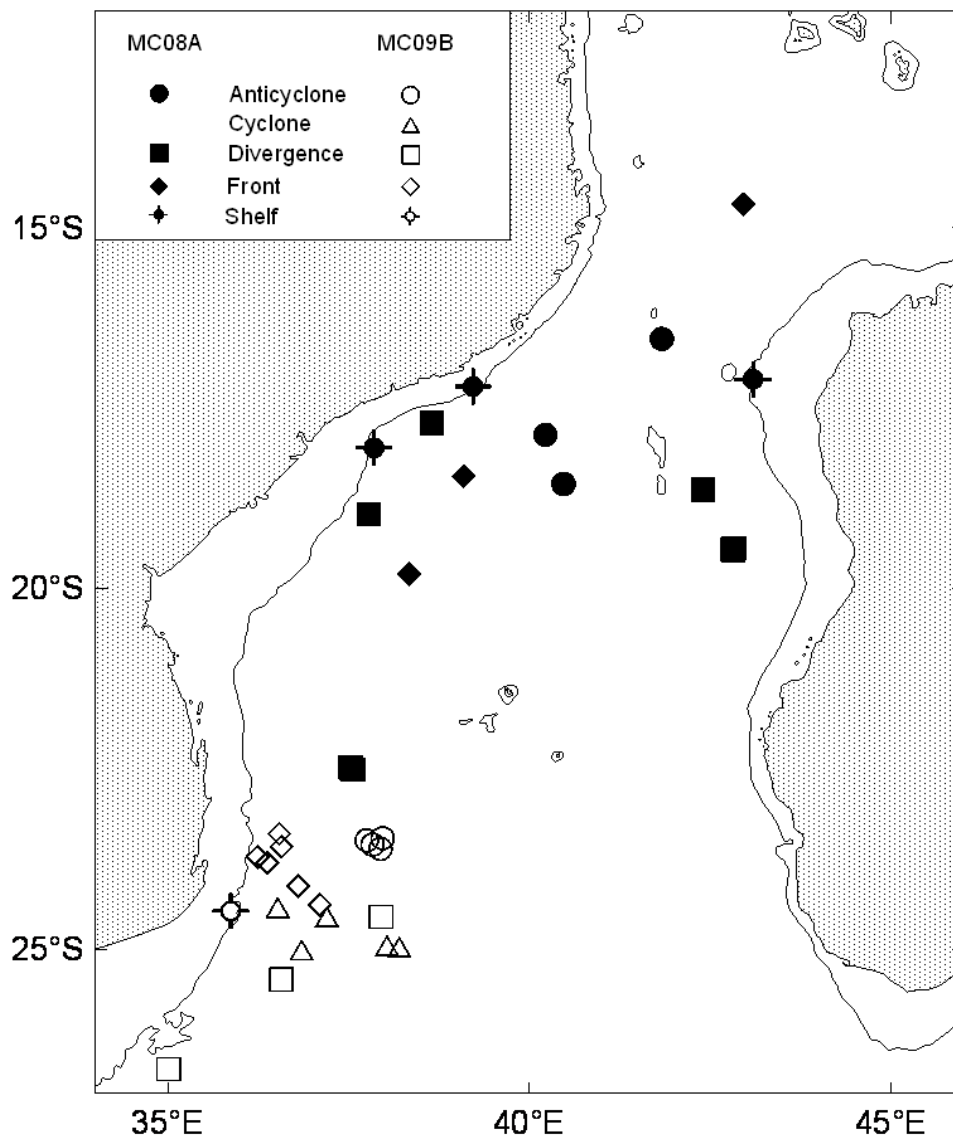
673 Fig. 4. Pruned regression tree that predicts the $\delta^{15}\text{N}$ signatures of five groups of micronekton
674 organisms. Each terminal node is characterized by $\delta^{15}\text{N}$ value (per mil), number of
675 individuals, corresponding taxa and mesoscale feature (A – Anticyclonic, C – Cyclonic, D –
676 Divergence, F – Frontal, S – Shelf). Covariates used to develop the tree are taxon and
677 mesoscale features.

678

679 Fig. 5. Pruned regression tree that predicts the $\delta^{13}\text{C}$ signatures of four groups of micronekton
680 organisms. Each terminal node is characterized by $\delta^{13}\text{C}$ value (per mil), number of
681 individuals, corresponding taxa and mesoscale feature (A – Anticyclonic, C – Cyclonic, D –
682 Divergence, F – Frontal, S – Shelf). Covariate used to develop the tree is taxon.

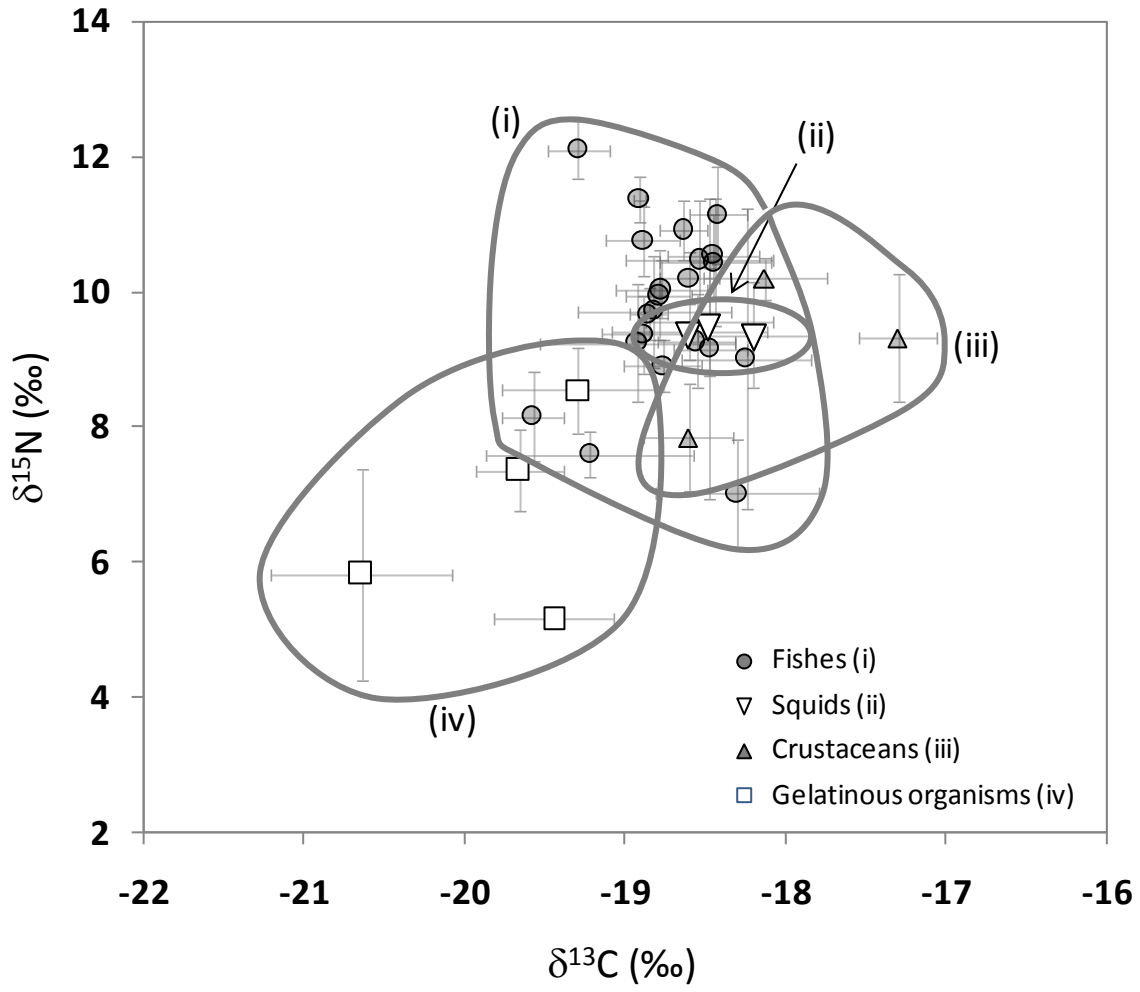
683

684 Fig. 6. $\delta^{15}\text{N}$ values (per mil) from (a) Bramidae (b) *Sthenoteuthis oualaniensis* (c) *Cubiceps*
685 *pauciradiatus* (d) *Thunnus* spp. plotted versus body length (standard length in mm for (a), (c)
686 and (d); dorsal mantle length in mm for (b)). Simple linear regressions for $\delta^{15}\text{N}$ values versus
687 body length are plotted (see text and Table 2).



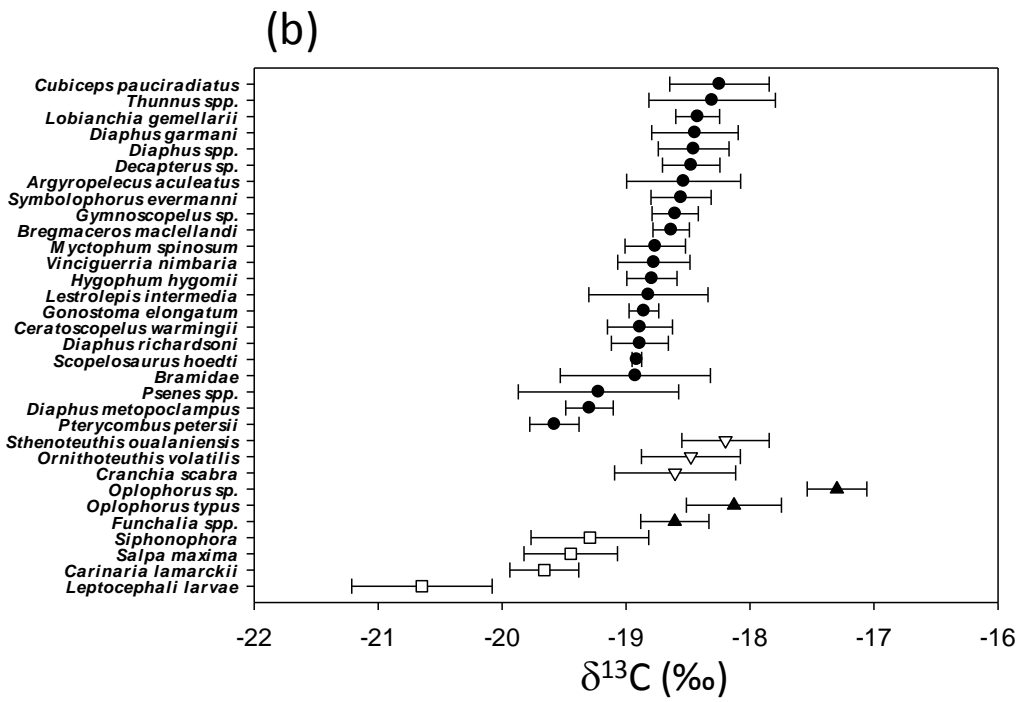
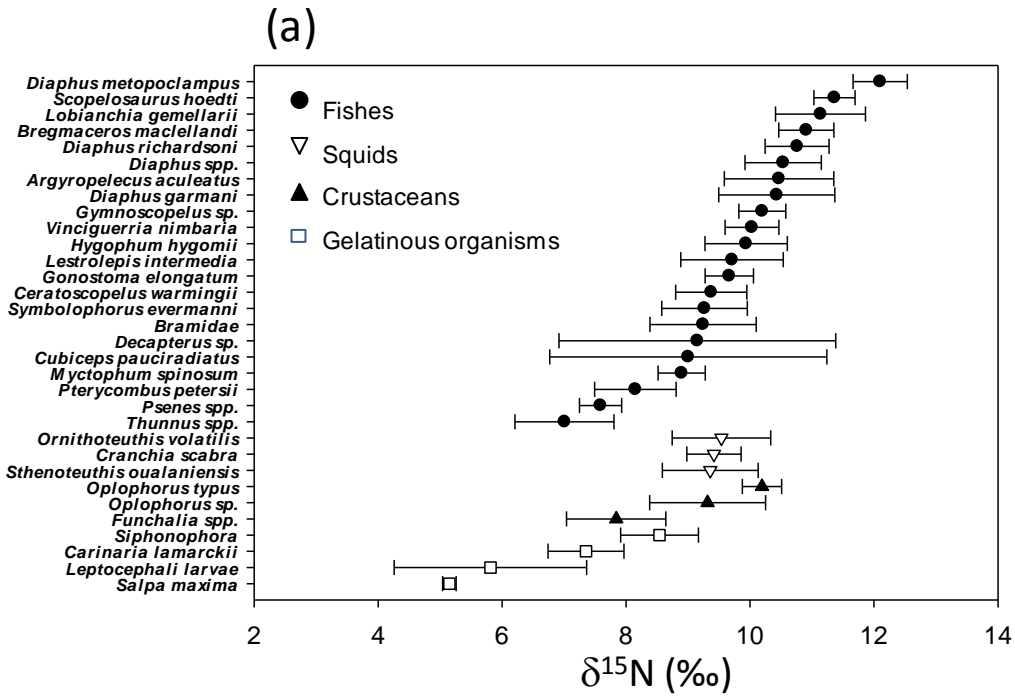
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689 Fig.1



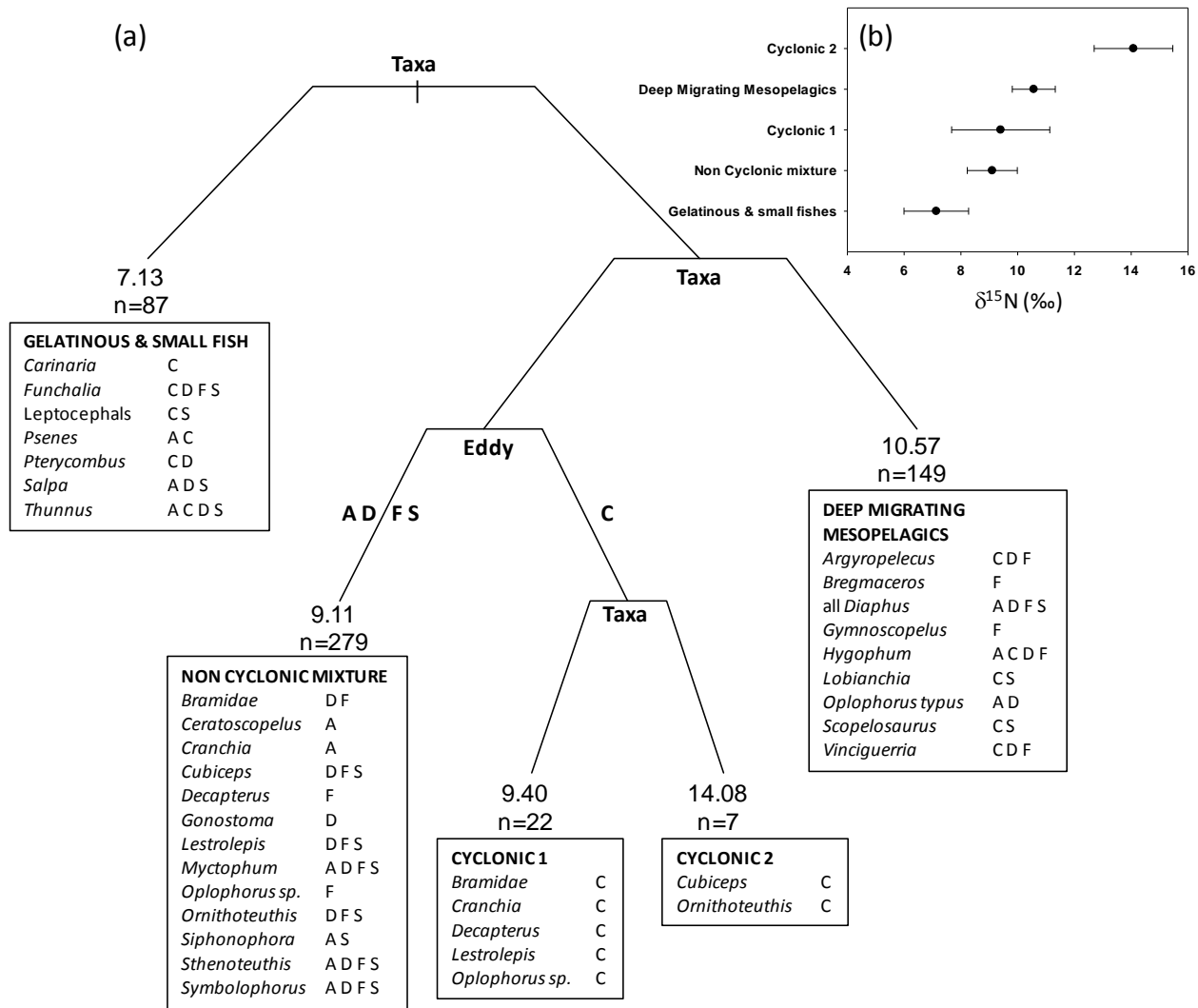
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691 Fig. 2



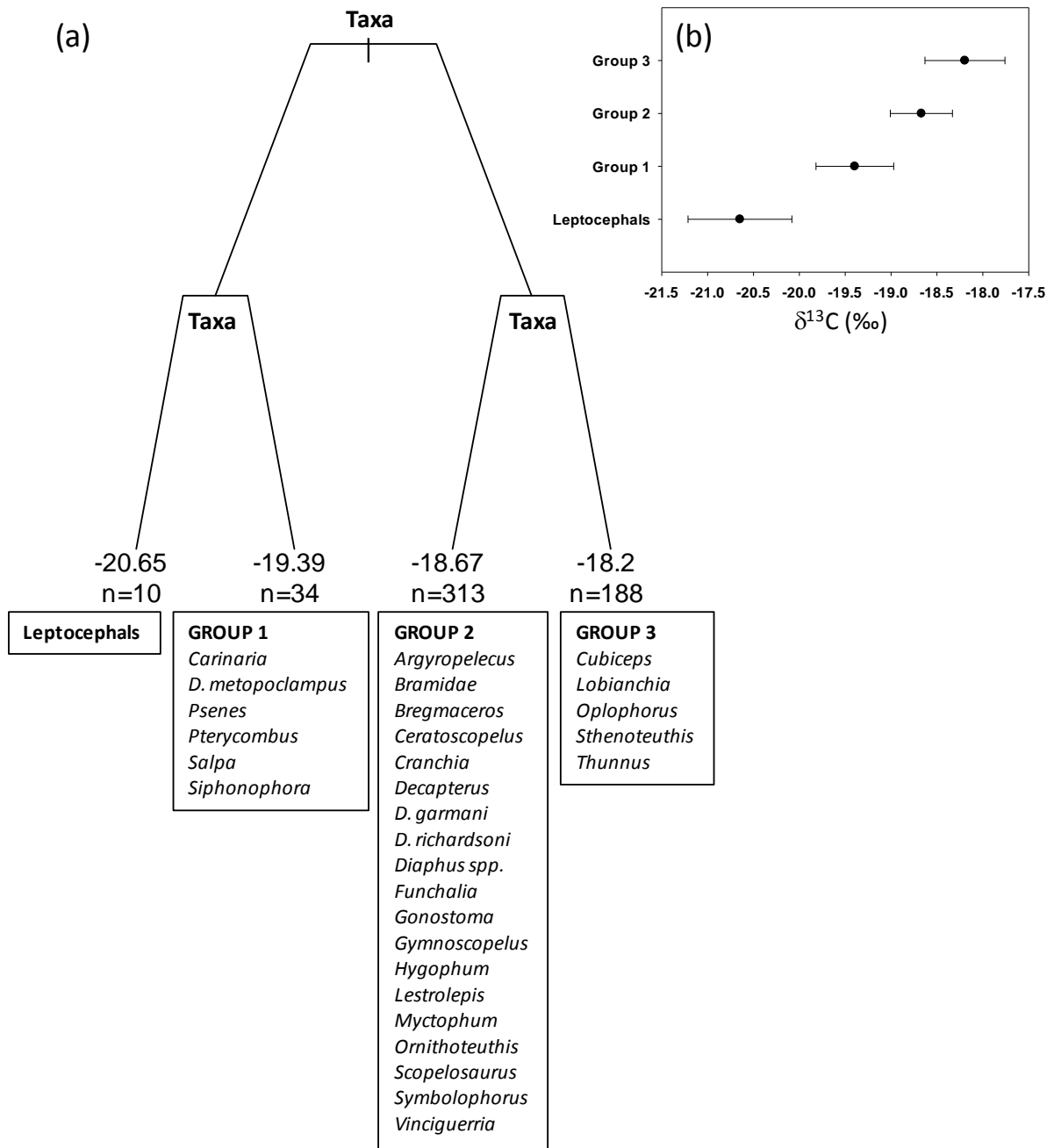
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693 Fig.3



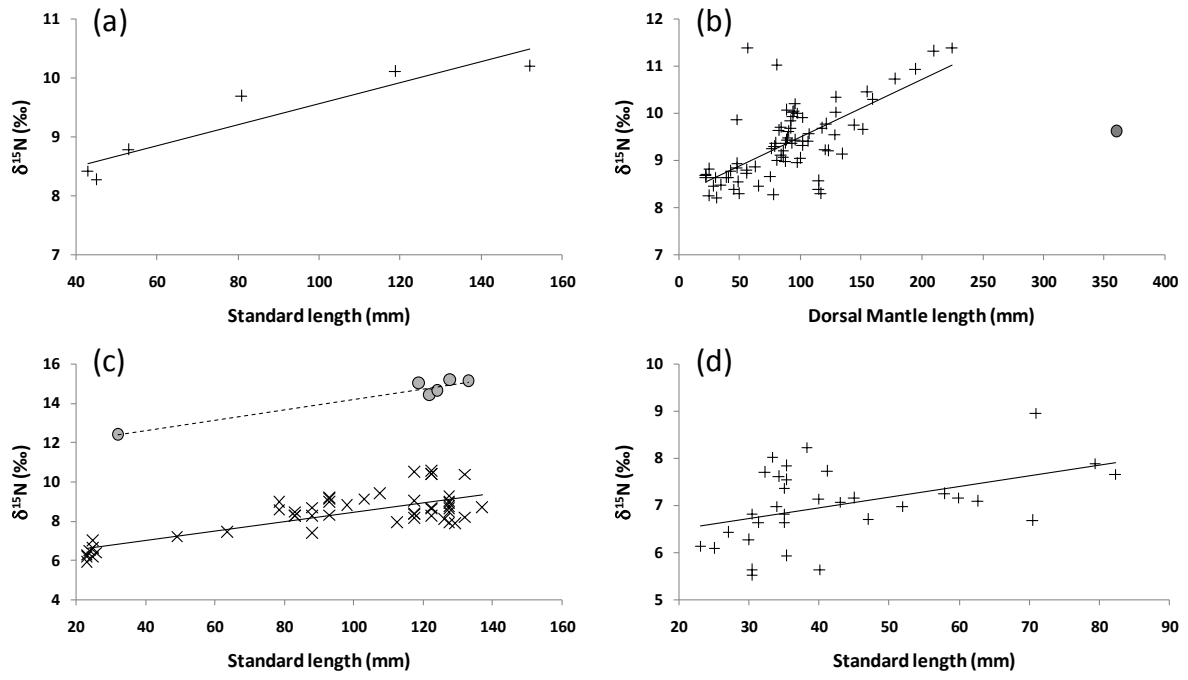
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695 Fig.4



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697 Fig. 5



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699 Fig.6