
Trophic niche overlap of sprat and commercial small pelagic teleosts in the Gulf of Lions (NW Mediterranean Sea)

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Abstract :

Increasing abundance of non-commercial sprats and decreasing biomass and landings of commercial anchovies and sardines justify the need to study the feeding ecology and trophic niche overlap of these planktivorous species in the Gulf of Lions. Their diet has been investigated on the basis of stomach content and stable isotope analyses in 2011 and 2012 according to different depths and regions in the study area. The main prey were Corycaeidae copepods, Clauso/Paracalanus, Euterpina acutifrons and Microsetella, for sprats and small copepods, such as Microsetella, Oncaea and Corycaeidae, for anchovies and sardines. This is the first time that the diet of sprats is described in the Gulf of Lions. Sprats fed on a larger size spectrum of prey and seem to be more generalist feeders compared to anchovies and sardines. Ontogenetic changes as well as spatial and temporal variations of the diet occurred in the three species. Stable isotope analysis revealed mobility of sardines and sprats among feeding areas while anchovies exhibited preferred feeding areas. Sprats showed a higher relative condition assessed by C/N ratios than sardines and anchovies. Our results showed an overlap of the trophic niches for the three species, indicating a potential trophic competition in the Gulf of Lions.

Highlights

► Sprats' diet was described for the first time in the NW Mediterranean Sea. ► There was a high trophic overlap for sardines, anchovies and sprats. ► Spatio-temporal and ontogenetic variations of their diet were described. ► Sprats were more generalist than sardines and anchovies and fed on larger prey. ► Diet particularities may explain the better relative condition of sprats.

Keywords : Anchovies, Sardines, Sprats, North-western Mediterranean sea, Stomach contents, Stable isotopes

1. Introduction

Small pelagic teleosts are key species in ecological systems as they ensure the transfer of organic matter from zooplankton to higher trophic levels (Banaru et al., 2013). They may exert different types of control in marine systems such as bottom-up (Cury et al., 2011), top-down (Köster and Möllmann, 2000; Verheye and Richardson, 1998) or wasp-waist control (Cury et al., 2000).

Traditionally, anchovies (*Engraulis encrasicolus*; Linnaeus, 1758) and sardines (*Sardina pilchardus*; Walbaum, 1792) were the two main pelagic teleosts in the Gulf of Lions (North-West Mediterranean Sea) in terms of biomass and represent target and commercial species for the fishing industry (Banaru et al., 2013). However, anchovy and sardine landings have declined since 2005 and fishing activity has been reduced to an exploratory activity in 2010. Anchovies and sardines are still abundant but their biomasses and size have decreased, which lowers their commercial value. Furthermore, there has been an unusual increase of non-commercial sprat (*Sprattus sprattus*; Linnaeus, 1758) abundance since 2008 (Van Beveren et al., 2014). A recent decline was reported in body condition and growth of anchovies and sardines (Van Beveren et al., 2014) which might be linked to changes in their diet compared to past studies (Costalago and Palomera, 2014; Plounevez and Champalbert, 2000) and/or to trophic interactions with sprats. Indeed, the abundance of prey seems to be one of the main environmental drivers of body condition in these species (Brosset et al.,

58 in press). The three species are zooplanktivorous and may be competitors for food in the study area.
59 Moreover, there is significant overlap in their spatial distribution (Saraux et al., 2014) but no data
60 are available concerning their trophic interactions in this area. No qualitative or quantitative data on
61 the zooplankton community are available to show eventual changes in the availability of the
62 resources during the last period. Consequently, studies on their feeding behaviour and interactions
63 are necessary to understand the origin of the recent shifts in the pelagic ecosystem of the Gulf of
64 Lions.

65 Stomach content analysis is a well-known method to study the trophic ecology of teleosts and
66 provides a qualitative and quantitative snapshot of the diet (Hyslop, 1980). Ratios of nitrogen and
67 carbon isotopes ($^{14}\text{N}:^{15}\text{N}$, $\delta^{15}\text{N}$; $^{12}\text{C}:^{13}\text{C}$, $\delta^{13}\text{C}$) are used to determine feeding areas and primary
68 sources of carbon in food-web (Hobson, 1999; Michener and Kaufman, 2007). Stable isotope
69 analyses allow longer-term study of the diet of organisms and identification of changes in feeding
70 sources and areas. Carbon/nitrogen (C/N) ratios measured with stable isotope ratios are a proxy of
71 the lipid content of organisms (Dempson et al., 2010; Logan et al., 2008; Post et al., 2007; Sweeting
72 et al., 2006) and thus can be used as indicators of the relative condition.

73 Some studies on the trophic ecology of small pelagic teleosts of the European coasts have
74 been previously conducted using stomach content analyses (e.g. Costalago and Palomera, 2014;
75 Costalago et al., 2014; Garrido et al., 2008; Plounevez and Champalbert, 2000; Tičina et al., 2000)
76 and stable isotopes (e.g. Bode et al., 2004; Chouvelon et al., 2014; Costalago et al., 2012), but few
77 studies have combined the two approaches (Pasquaud et al., 2008) and none of them in the study
78 area. Moreover, the last diet studies based on stomach content analysis of adult anchovies and
79 sardines in the Gulf of Lions were performed in 1995-1996 by Plounevez and Champalbert (2000),
80 and in 2007 by Costalago and Palomera (2014), when these species had higher condition values
81 (Brosset et al., in press; Van Beveren et al., 2014) and before the fall of their biomass. No data on
82 the trophic ecology of *S. sprattus* is available for the North-Western Mediterranean Sea.

83 The aim of this study was to combine the methods of stomach content analysis and stable

84 isotopes to describe the trophic ecology, niche width and diet overlap of anchovies (*E. encrasicolus*),
85 sardines (*S. pilchardus*) and sprats (*S. sprattus*) in the Gulf of Lions to infer the potential
86 interactions between the three species. In addition, this is the first time that spatial variations in the
87 diet of these species related to their stable isotope ratios were described in the North-Western
88 Mediterranean Sea.

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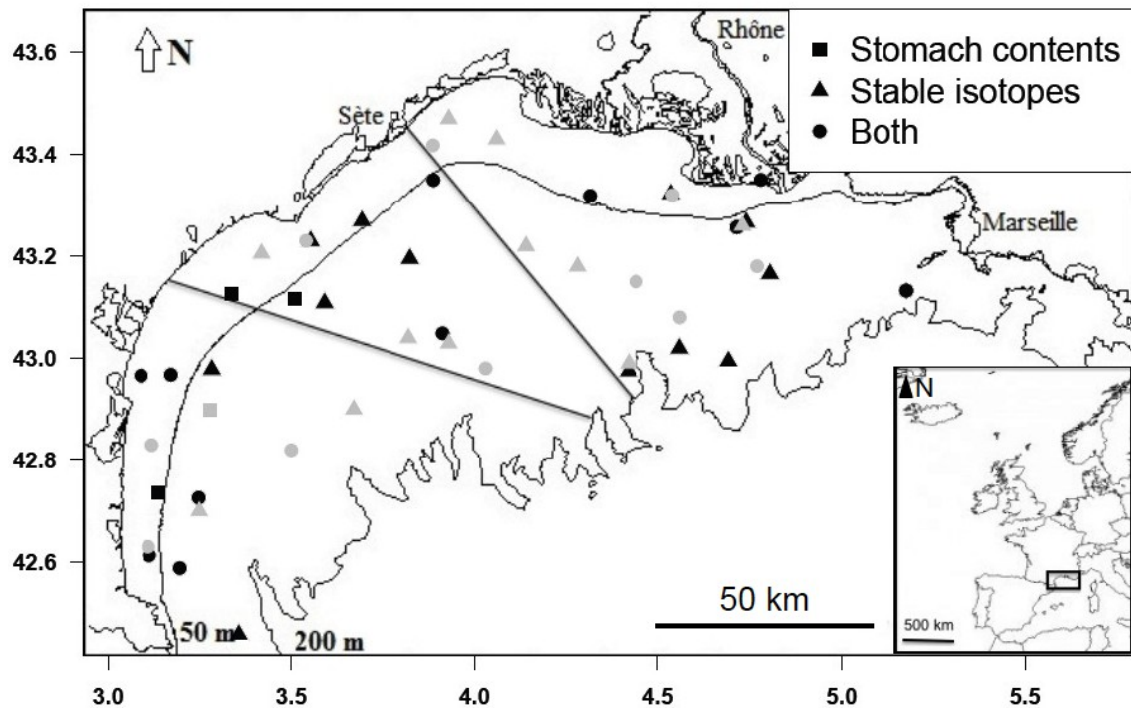
90 **2. Material and methods**

91 *2.1. Study area and sampling*

92 The Gulf of Lions has a wide continental shelf. It is a mesotrophic area influenced by Rhône
93 river inputs and the northern current flowing southwestwards along the continental slope (Espinasse
94 et al., 2014a). Consequently, concentrations of nutrients in water and sediments decrease from east
95 to west and from coast to continental shelf (Cruzado and Velasquez, 1990; Denis and Grenz, 2003;
96 Van Den Broeck and Moutin, 2002). Furthermore, river inputs influence isotopic ratios of
97 particulate organic matter and phytoplankton with higher $\delta^{15}\text{N}$ and lower $\delta^{13}\text{C}$ in waters influenced
98 by the Rhône plume (Harmelin-Vivien et al., 2008). Espinasse et al. (2014a) divided the gulf into
99 three habitat types: the western part of the coast, most of the eastern area of the gulf influenced by
100 Rhône river (the coast and a part of the continental shelf), and the continental shelf (except in
101 eastern areas where river inputs are high). In the present study, the gulf has been divided into two
102 depth zones (coastal areas and continental shelf) separated by the 50 metres isobath and three
103 regions (west, centre and east) according to the spatial changes of environmental conditions
104 (Espinasse et al., 2014a; Harmelin-Vivien et al., 2008 Fig. 1).

105 Teleosts were sampled in June and July 2011 and 2012 during the IFREMER MEDITS and
106 PELMED campaigns aboard the IFREMER R.V. 'l'Europe'. In addition, small juvenile sardines
107 were sampled in May 2011 by beach seining near the Rhône estuary. Sampled teleosts were
108 immediately frozen to avoid digestion. In the laboratory, the following measurements were taken on
109 each teleost: total length (TL) to the nearest 1 mm and total body weight (TW). Stomachs were

110 extracted and preserved in 95° alcohol. Eviscerated body weight (EW) was measured. Anterior
111 dorsal muscles of teleosts were sampled and freeze-dried for subsequent stable isotope analyses.
112



113
114 **Fig. 1.** Location of sampling stations in the Gulf of Lions selected for stomach content analysis
115 and/or stable isotope analysis in 2011 (black) and 2012 (grey). The 50 metre isobath separates
116 coastal areas and the continental shelf. The lines separate the regions west, centre and east.

117

118 2.2. Stomach content analysis

119 We chose individuals of the different available size classes (1 cm interval) for each depth and
120 region. Selected stomach contents (117 anchovies, 145 sardines, 166 sprats) (Fig. 1; Table 1.a) were
121 weighted. In each stomach, ingested organisms were identified to genus level (if possible) and
122 counted. Dry weight (DW) of ingested organisms was obtained from the literature (Table A.1).
123 Food composition was expressed by frequency of occurrence (%O; percentage of non-empty
124 stomachs containing a given prey item), numerical percentage (%N; mean percentage per stomach
125 of the number of a given prey item as a proportion of the total number of all prey in each stomach),
126 weight percentage (%W; mean percentage per stomach of the weight of a given prey item as a

127 proportion of the total weight of all prey in each stomach). The index of relative importance (IRI)
128 (Pinkas et al., 1971) was then calculated according to the formula:

$$129 \quad \text{IRI} = \%O \times (\%N + \%W)$$

130 IRI was then transformed in percentage by dividing it by the sum of IRI for each prey item
131 (%IRI; Cortés, 1997). Niche width (B_G) and diet overlap (%T; Schoener, 1970) were calculated
132 according to formulas:

$$133 \quad B_G = e^{H'} \text{ with } H' = -\sum (\text{IRI}_{xi} \times \log_2 \text{IRI}_{xi})$$

$$134 \quad \%T = (1 - 0.5 \sum |\% \text{IRI}_{xi} - \% \text{IRI}_{yi}|) \times 100$$

135 where $\% \text{IRI}_{xi}$ and $\% \text{IRI}_{yi}$ are %IRI for the prey item i in the teleost species x and y . Overlap is
136 considered as significant if %T exceeds 60% (Arculeo et al, 1993). %T was also calculated using
137 %W.

138 Prey were measured for subsamples of the three studied species (82 anchovies, 64 sardines,
139 58 sprats) for different size classes. Predator/prey size ratios were also estimated for each species.

140

141 *2.3. Stable isotope analysis*

142 For each species, depth and region, stable isotope ratios were studied in muscle samples of
143 fish collected in various sampling stations (104 anchovies, 101 sardines, 116 sprats) (Fig. 1; Table
144 1.b). Selected muscle were freeze-dried and then ground into a fine powder. Subsamples were
145 weighed (0.4 to 0.5 mg) in 5×8 tin cups and analysed with a continuous-flow isotope-ratio mass
146 spectrometer (Delta V Advantage, Thermo Scientific) coupled to an elemental analyser (Flash EA
147 1112, Thermo Scientific). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were expressed in ‰ according to the formula:

$$148 \quad \delta X_{\text{sample}} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

149 where X is ^{13}C or ^{15}N , R_{sample} is the isotopic ratio of sample and R_{standard} is the isotopic ratio of
150 standards (atmospheric nitrogen for $\delta^{15}\text{N}$ and Pee Dee Belemnite for $\delta^{13}\text{C}$).

151 $\delta^{13}\text{C}$ values were corrected for the effects of lipids when the C/N ratio was higher than 3.5
152 according to the formula developed by Post et al. (2007):

153
$$\delta^{13}\text{C}_{\text{normalised}} = \delta^{13}\text{C}_{\text{sample}} - 3.32 + 0.99 \times \text{C/N}$$

154 In order to study isotopic niches of the three species, standard ellipses were generated and the
 155 Standard Ellipse Areas (SEA) were corrected for sample size (SEA_C) using the SIAR package
 156 (Stable Isotope Analysis in R, Parnell et al., 2010). The overlap between the ellipses was then
 157 determined. Isotopic niche of the three species was estimated by determining areas of the ellipses
 158 using the bayesian method (SEA_B) (Jackson et al., 2011).

159 The relative condition factor was estimated using C/N ratios related to the lipid content.

160

161 **Table 1**

162 Number and size range (in brackets, cm) of the analysed individuals in the study area for a) stomach
 163 content and b) stable isotopes samples.

a)

Species	West		Centre		East	
	Coast	Shelf	Coast	Shelf	Coast	Shelf
<i>E. encrasicolus</i>	26 (9.4-12.5)	18 (8.5-12.3)	22 (8.4-11.6)	7 (9.8-12.7)	15 (8.5-11.7)	29 (9.4-14.0)
<i>S. pilchardus</i>	20 (10.5-14.2)	16 (7.5-14.2)	28 (9.3-12.5)	0	47 (3.9-13.1)	34 (10.4-16.5)
<i>S. sprattus</i>	56 (6.3-10.8)	20 (7.4-10.5)	15 (7.1-10.0)	10 (9.3-10.8)	23 (7.3-10.2)	42 (7.3-11.2)

b)

Species	West		Centre		East	
	Coast	Shelf	Coast	Shelf	Coast	Shelf
<i>E. encrasicolus</i>	11 (8.0-10.3)	16 (8.5-11.6)	9 (3.5-10.3)	12 (9.5-11.1)	15 (8.6-10.3)	41 (8.7-14.0)
<i>S. pilchardus</i>	16 (11.0-13.1)	12 (11.2-15.0)	8 (9.3-12.5)	8 (11.6-14.1)	24 (3.8-14.2)	33 (9.3-16.5)
<i>S. sprattus</i>	11 (6.3-10.7)	24 (8.0-10.2)	15 (7.5-10.3)	12 (9.3-10.1)	18 (6.3-10.0)	36 (8.0-11.0)

164

165

166 *2.4. Data analyses*

167 All data analyses were performed with the R statistical software (version 2.15.0).

168 Classifications (based on Bray-Curtis dissimilarity index) were performed on %IRI in each
 169 total length class (1 cm interval) to study ontogenetic shifts in the diet of each species. The same
 170 classifications were also applied on %IRI in each zone (defined by region, depth and year of
 171 sampling) for each species to study spatial and temporal variations in their diet.

172 Normality of residuals and homoscedasticity were checked by Shapiro tests, Q-Q plots and
 173 Levene tests. Ontogenetic changes in the size classes of prey consumed by anchovies, sardines and

13

14

174 sprats were studied with Spearman rank correlation tests (ρ) between teleosts total length and
175 individual prey length for each of the three species. Predator/prey size ratios were compared
176 between the three species by Kruskal-Wallis tests (H).

177 Stable isotope and C/N ratios were compared between the three species by Kruskal-Wallis
178 tests. For each species, Student's t-tests (t), or Wilcoxon tests (W) if data did not fit to a normal
179 distribution pattern, were performed to compare isotopic and C/N ratios between the years 2011 and
180 2012. Subsequent analyses were performed on separate years or the pooled two years if the year
181 factor was not significant.

182 Type III analyses of covariances (ANCOVA; F) were performed with the factors length,
183 region, depth and their interaction on isotopic and C/N ratios. The teleosts total length covariate was
184 deleted from the models if its effect on the isotopic and C/N ratios was non-significant. Scheffé
185 post-hoc tests were performed when the region significantly influenced isotopic or C/N ratios.

186

187 **3. Results**

188 *3.1. Diet composition*

189 Proportions of empty stomachs were 11.11% for anchovies, 18.62% for sardines 30.72% for
190 sprats. Fifty-five prey items were identified in the stomachs (anchovies: 43, sardines: 33, sprats:
191 37). The three species fed mainly on copepods (%IRI = 93.91 for anchovies, 92.08 for sardines and
192 97.29 for sprats, diet detailed in Table A.2).

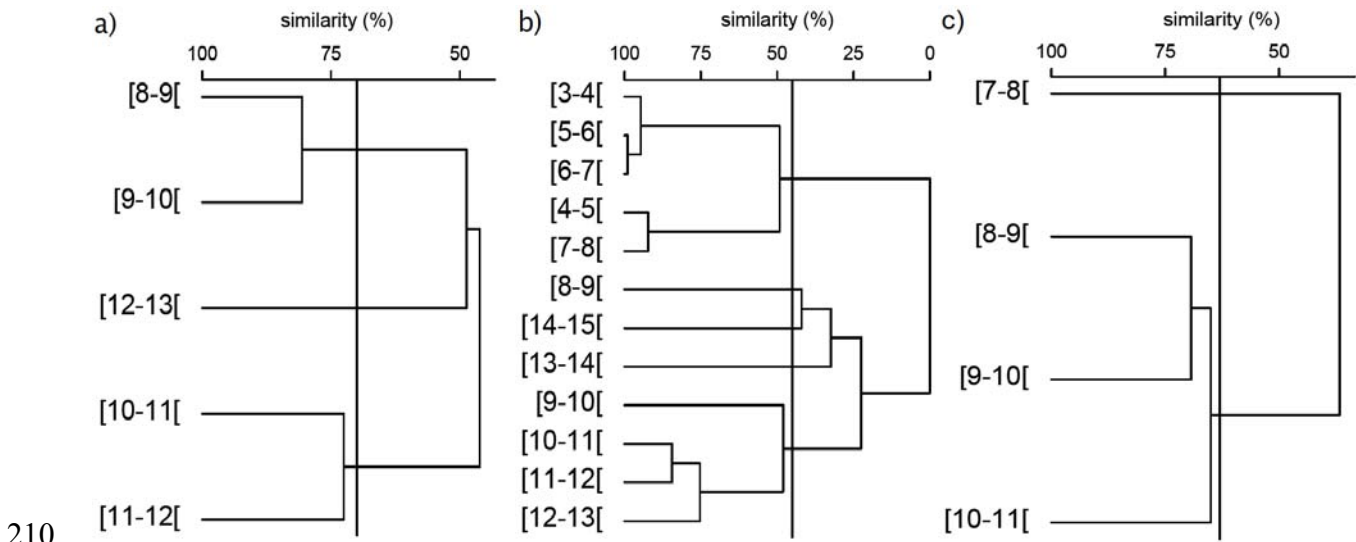
193 Anchovies had the lowest niche width ($B_G = 15.52$) and their diet was dominated by the
194 copepods *Microsetella* (%IRI = 32.06), *Oncaea* (%IRI = 25.25) and the Corycaeidae family (%IRI
195 = 16.62). *Microsetella* (%IRI = 28.63), *Oncaea* (%IRI = 23.70) and the Corycaeidae family (%IRI
196 = 20.25) also dominated the diet of sardines. Sardines had a higher niche width ($B_G = 16.67$) than
197 anchovies. Sprats had a more diversified diet ($B_G = 17.87$) dominated by *Clauso/Paracalanus*
198 (%IRI = 23.41), the Corycaeidae family (%IRI = 19.04), *Euterpina acutifrons* (%IRI = 14.61) and
199 *Microsetella* (%IRI = 10.08).

200

201 3.2. Ontogenetic variations in diet

202 Cluster analyses of teleosts diets (based on %IRI) by size classes are shown in Fig. 2.

203 Stomach contents show that *Oncaea* was the main prey for 8-10 cm long anchovies, which
204 also fed on *Microsetella*, Corycaeidae copepods and on some unidentified copepods. Anchovies
205 with a 10-12 cm body size consumed mainly *Microsetella*, but also Corycaeidae copepods and
206 *Oncaea*. Larger anchovies (12-13 cm) consumed mainly copepods from the Corycaeidae family
207 (%IRI = 23.05), but also large diatoms (%IRI = 14.67) and the copepod species *Centropages*
208 *typicus* (%IRI = 12.40). In fact, contribution of diatoms and *Centropages typicus* increased with
209 body length while that of *Oncaea* decreased.



210

211 **Fig. 2.** Cluster analyses of diet similarities (based on %IRI) among size classes (cm) in a)
212 anchovies, b) sardines, c) sprats. The vertical line separates the clusters.

213

214 Sardines between 3 and 8 cm consumed mainly suprabenthic mysids (genus *Paramysis*).
215 Unidentified copepods were also consumed by 4-5 and 7-8 cm sardines. Sardines between 9
216 and 13 cm fed on *Microsetella* and *Oncaea*. Among those sardines, 9-10 cm individuals fed also on
217 *Euterpina acutifrons* (%IRI = 24.48) and bivalve larvae (%IRI = 12.26) while 10-13 cm sardines
218 fed on Corycaeidae. The size classes 8-9 cm, 13-14 cm and 14-15 cm had unusual diets. The first

219 size class fed on *Microsetella* (%IRI = 36.01) but had high contribution of *Acartia* (%IRI = 16.40)
220 and unidentified copepods (%IRI = 37.06) in its diet. The second size class fed on Corycaeidae
221 (%IRI = 18.85) but also on *Acartia* (%IRI = 25.46), diatoms (%IRI = 21.47) and unidentified
222 copepods (%IRI = 12.24). The last size class fed on *Microsetella* (%IRI = 50.00) but also on
223 diatoms (%IRI = 37.09).

224 The main prey of small sprats (7-8 cm) were unidentified copepods (%IRI = 48.09).
225 Nevertheless, *Euterpina acutifrons* (%IRI = 16.13), *Oncaea* (%IRI = 11.82) were the most
226 important identified prey items for this body size. Sprats between 8 and 11 cm had a diet dominated
227 by two prey: *Clauso/Paracalanus* and the Corycaeidae. Among 8-11 cm sprats, *Euterpina*
228 *acutifrons* was also an important prey for sprats between 8 and 10 cm. In fact, the contribution of
229 the Corycaeidae copepods (%IRI from 4.33 to 33.95) increased for larger sprats while that of
230 *Oncaea* decreased (%IRI from 11.82 to 3.51).

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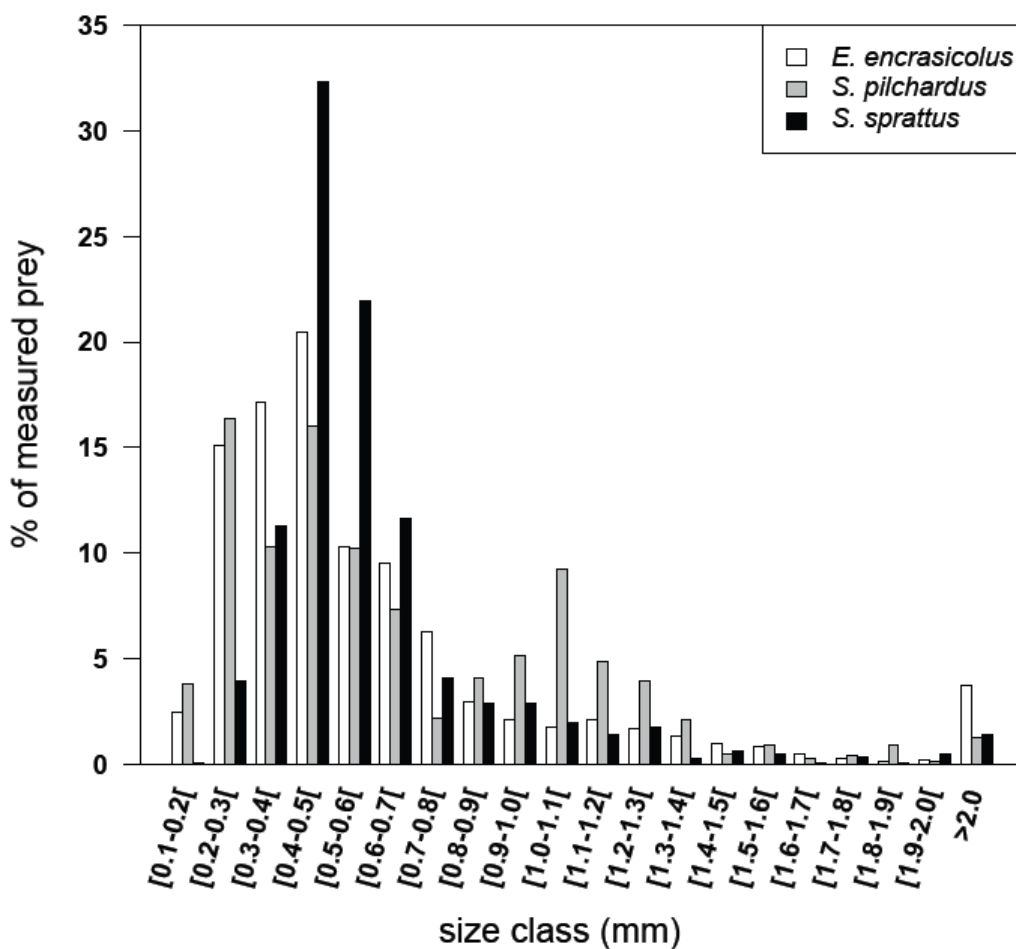
232 3.3. Class lengths of the consumed prey

233 Anchovies and sardines consumed mainly 0.2-0.6 mm prey (62.97% of all measured prey for
234 anchovies and 52.93% for sardines), the most consumed size class being the 0.4-0.5 mm (20.45% of
235 all measured prey for anchovies and 15.99% for sardines). Sprats fed on slightly larger prey as they
236 consumed mainly 0.3-0.7 mm prey (77.22% of all measured prey) (Fig. 3). The 0.4-0.5 mm size
237 class was once again the most consumed one, but this size class was consumed in larger proportions
238 by sprats than by the two other species (32.31% of all measured prey). Furthermore, the 0.5-0.6 mm
239 size class was also more strongly represented in the diet of sprats (21.94% of all measured prey)
240 than in that of anchovies (10.29%) and sardines (10.23%). There was a peak of occurrence in
241 sardines for the 1.0-1.1 mm size class (9.24% of measured prey) (Fig. 3). Nevertheless, only 11
242 sardines fed on this size class and the peak resulted from a high number of anchovy eggs (more than
243 10) in stomachs of 4 sardines in one sampling site. No ontogenetic changes of prey length
244 consumed by anchovies ($\rho = -0.008$, $P = 0.738$) and sprats ($\rho = 0.008$, $P = 0.791$) occurred for

245 the analysed individuals. In contrast, size classes consumed by sardines slightly decreased when
 246 sardines were larger ($\rho = -0.276$, $P < 0.001$).

247 Sprats had the lowest predator/prey size ratios (mean \pm SD = 176.45 ± 71.14) followed by
 248 anchovies (236.67 ± 133.66) and sardines (259.47 ± 191.69) ($H = 135.458$, $P < 0.001$) (Table 2).
 249 Anchovies consumed the largest prey compared to their own size and sardines the smallest.
 250 Sardines showed the highest variation between the minimum and the maximum predator/prey size
 251 ratios (Table 2).

252



253

254 **Fig. 3.** Proportions of the prey size classes in the stomach content of anchovies, sardines and sprats.

255

256 **Table 2**

257 Predator/prey size ratios in anchovies, sardines and sprats (N = number of individuals, SD =
 258 standard deviation).

Species	Predator lengths (cm)	N predators	N prey	Mean \pm SD	Range
<i>E. encrasicolus</i>	Total	82	1604	236.67 \pm 133.66	7.15-806.22
	[8-10[27	640	223.40 \pm 123.79	31.92-700.14
	[10-12[50	865	245.50 \pm 137.21	7.15-806.22
	[12-13[5	99	245.26 \pm 156.24	41.52-773.51
<i>S. pilchardus</i>	Total	64	1007	259.47 \pm 191.69	13.00-1621.29
	[3-8[6	33	34.23 \pm 26.67	13.00-138.24
	[8-15[58	974	267.10 \pm 190.24	33.87-1621.29
<i>S. sprattus</i>	Total	58	1080	176.45 \pm 71.14	21.47-517.05
	[7-8[6	170	150.91 \pm 45.41	21.47-359.45
	[8-11[52	910	181.22 \pm 74.02	26.88-517.05

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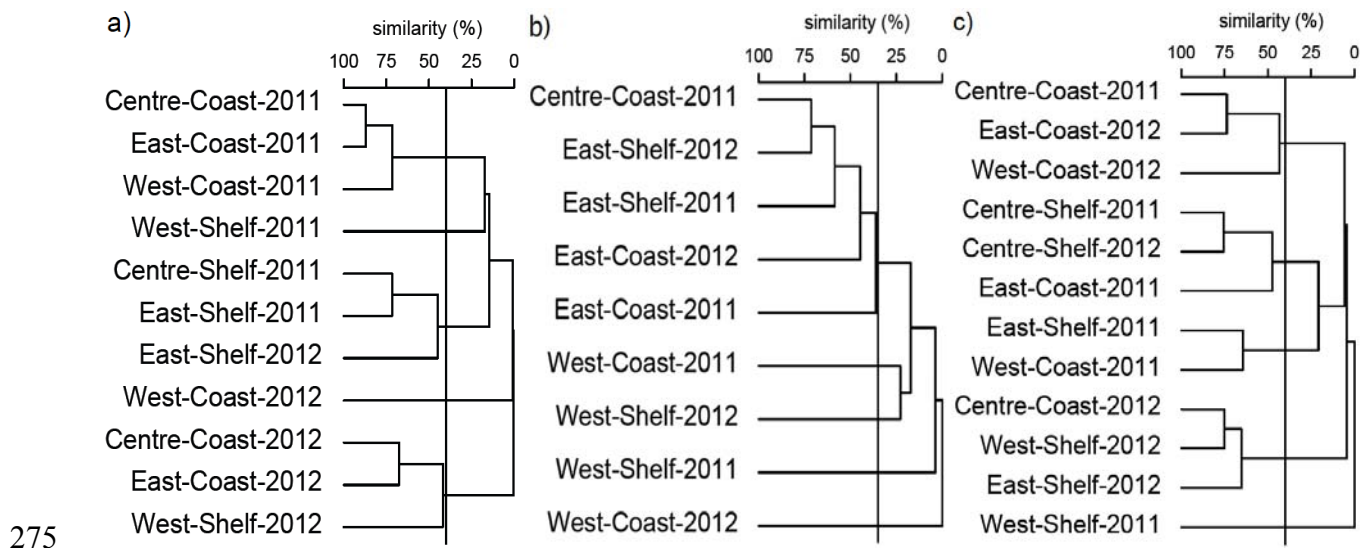
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261 3.4. Spatial and temporal variations in diet

262 Dendrograms resulting from hierarchical clustering on teleosts diet similarities (based on
263 %IRI) among region, depth and year are shown in Fig. 4.

264 Five clusters appeared for anchovies. The first cluster contained all the coastal stations
265 sampled in 2011 and depicted a diet dominated by *Oncaea* (%IRI > 40). The second cluster
266 contained anchovies only sampled in the west, on the shelf in 2011, feeding on Euphausiacean
267 larvae (%IRI = 58.48), *Microsetella* (%IRI = 12.43) and *Clauso/Paracalanus* (%IRI = 11.48). The
268 third cluster contained only zones sampled on the shelf, in 2011 and 2012, and where the diet was
269 dominated by *Microsetella* (and Corycaeidae in the zone Centre-Shelf-2011). The fourth cluster
270 contained anchovies sampled in the west, on the coast in 2012, feeding almost exclusively on
271 diatoms (%IRI = 97.26). The fifth cluster had stations sampled in 2012 but unidentified copepods
272 were the main prey. These results show that year and depth were the most important parameters
273 influencing diet.

274



275
 276 **Fig. 4.** Cluster analyses of diet similarities (based on %IRI) among region, depth and year in a)
 277 anchovies, b) sardines, c) sprats. The vertical line separates the clusters.

278

279 For sardines, five clusters appeared. The first cluster contained all sardines sampled at the
 280 centre and east of the gulf. The other clusters contained the zones sampled in the west. These results
 281 show that the region has influenced the diet, sardines sampled in the west feeding on various
 282 dominating (but there is only one sardine in the cluster West-Shelf-2011) prey among zones (eggs
 283 on the coast in 2011, diatoms on the coast in 2012 and unidentified copepods on the shelf in 2012),
 284 while sardines of the other regions fed mainly on the copepods usually observed in this study of
 285 their diet (*Microsetella*, *Oncaea* and *Corycaeidae*).

286 Five clusters appeared for sprats. The first contained sprats only sampled on the coast with a
 287 diet characterised by *Euterpina acutifrons* and diverse secondary prey (*Oncaea* at the centre in
 288 2011, *Clauso/Paracalanus* in the east in 2012 and Diatoms and *Oncaea* in the west in 2012). The
 289 second contained two zones on the shelf and one on the coast where the diet was characterised by
 290 *Corycaeidae* copepods and *Microsetella*. The third cluster contained two zones on the coast and on
 291 the shelf and in the west and the east. Sprats of this cluster fed on *Clauso/Paracalanus* and on
 292 *Corycaeidae*. The fourth cluster contained two zones on the shelf and one on the coast but the diet
 293 was characterised by unidentified copepods. The last cluster contained the zone West-Shelf-2011

294 where sprats fed on decapod larvae (%IRI = 98.24). These results suggest that depth may have
295 influenced sprat diet, with *Euterpina acutifrons* being a widely consumed prey in coastal zones.

296

297 3.5. Stable isotope analysis

298 Isotopic values were significantly different among the three species ($H = 64.028$, $P < 0.001$
299 for $\delta^{15}\text{N}$, $H = 44.843$, $P < 0.001$ for $\delta^{13}\text{C}$). Anchovies had the lowest $\delta^{15}\text{N}$ value (mean \pm SD = $7.5 \pm$
300 0.5‰), followed by sprats ($7.8 \pm 0.4\text{‰}$) and sardines ($8.1 \pm 0.5\text{‰}$). Anchovies had the highest $\delta^{13}\text{C}$
301 value ($-19.4 \pm 0.3\text{‰}$) while sprats and sardines had similar $\delta^{13}\text{C}$ values ($-19.8 \pm 0.6\text{‰}$ for both
302 species). Nevertheless, sprats had a wider range of $\delta^{13}\text{C}$ (from -21.1 to -17.2‰) than sardines (from
303 -21.2 to -19.0 , Fig. 5). Anchovies had the smallest isotopic niche (mean $\text{SEA}_B = 0.60$) while
304 sardines and sprats had similar isotopic niche width (mean $\text{SEA}_B = 0.75$ for sardines and 0.79 for
305 sprats).

306 The influence of the different factors on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ are detailed in Table A.3a and b. In
307 anchovies, $\delta^{15}\text{N}$ ($t = 5.919$, $P < 0.001$) and $\delta^{13}\text{C}$ ($t = 6.398$, $P < 0.001$) were dependent on the year of
308 sampling. In 2011, the highest $\delta^{15}\text{N}$ was observed in the west ($7.5 \pm 0.4\text{‰}$), the lowest in the centre
309 ($7.1 \pm 0.4\text{‰}$) and the intermediate value in the east ($7.3 \pm 0.5\text{‰}$). $\delta^{13}\text{C}$ slightly increased when the
310 body length increased and was higher in the centre ($-19.4 \pm 0.3\text{‰}$), lower in the east ($-19.6 \pm 0.3\text{‰}$)
311 and intermediate in the west ($-19.5 \pm 0.3\text{‰}$). The interaction between depth and region showed that
312 offshore anchovies had a higher $\delta^{13}\text{C}$ than coastal anchovies except in the east where coastal
313 anchovies had a higher $\delta^{13}\text{C}$. In 2012, depth had an effect on $\delta^{15}\text{N}$, with higher $\delta^{15}\text{N}$ for individuals
314 caught in coastal areas ($8.1 \pm 0.5\text{‰}$) than on the shelf ($7.7 \pm 0.4\text{‰}$) and the interaction between
315 depth and region also influenced $\delta^{15}\text{N}$ (greater difference between coastal $\delta^{15}\text{N}$ and offshore $\delta^{15}\text{N}$ in
316 the centre region). No factor had a significant effect on $\delta^{13}\text{C}$.

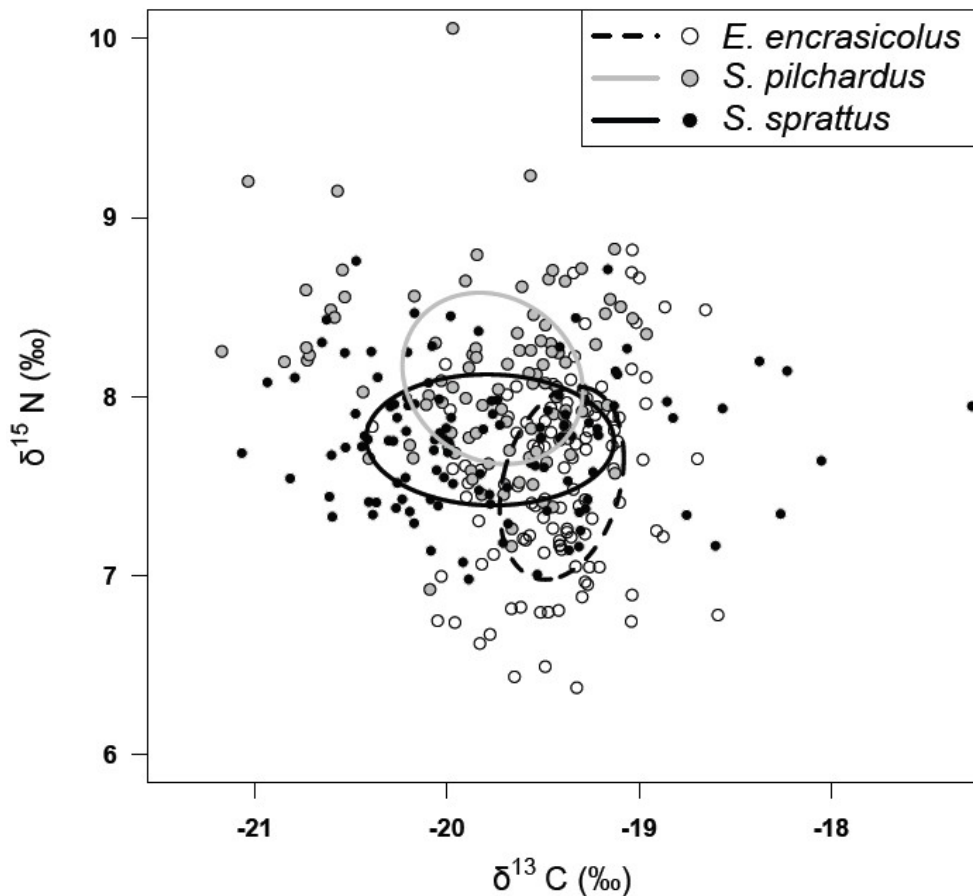
317 In sardines, the year of sampling had no effect on $\delta^{15}\text{N}$ ($W = 1123.5$, $P = 0.428$) but
318 influenced $\delta^{13}\text{C}$ ($W = 702$, $P < 0.001$). $\delta^{15}\text{N}$ decreased when body length increased. In 2011, $\delta^{13}\text{C}$
319 increased when the body length increased. In 2012, no factor had a significant effect on $\delta^{13}\text{C}$.

320 In sprats, the year of sampling influenced $\delta^{13}\text{C}$ ($W = 458$, $P < 0.001$) but not $\delta^{15}\text{N}$ ($t = 0.080$, P
321 $= 0.936$). $\delta^{15}\text{N}$ slightly increased when the body length increased. $\delta^{13}\text{C}$ slightly decreased when
322 body length increased in 2011 but influence of body length on $\delta^{13}\text{C}$ was weak in 2012.

323

324 3.6. Interactions between species

325 Diet overlap estimated on %IRI and %W was significant for anchovies and sardines (%T =
326 83.91 for %IRI and 76.92 for %W). For sprats and anchovies (%T = 55.06 for %IRI and 65.34 for
327 %W) and for sprats and sardines (%T = 58.51 for %IRI and 64.00 for %W), the overlap was nearly
328 significant when estimated using %IRI and was significant when using %W. Diet overlap between
329 length classes is detailed in Table A.4. Anchovies share only 17.12% of their isotopic niche with
330 sardines (and sardines 12.92% with anchovies) and 48.46% with sprats (and sprats 34.48% with
331 anchovies). Sardines share 48.28% of their isotopic niche with sprats (and sprats 45.50% with
332 sardines) (Fig. 5).



333

29
30

334 **Fig. 5.** Isotopic values in muscles of anchovies, sardines and sprats and depiction of their niche area
335 using standard ellipses.

336

337 *3.7. Relative condition factor*

338 Sprats had the highest C/N ratios (mean \pm SD = 4.38 ± 1.12), followed by sardines ($3.31 \pm$
339 0.14) and anchovies (3.20 ± 0.09) ($H = 148.931$, $P < 0.001$). The C/N ratios of anchovies were only
340 influenced by the interaction between depth and region (Table A.3c) while C/N ratios of sardines
341 were not dependent on any factor. For anchovies, C/N ratio did not differ between coastal and
342 offshore regions except in the centre where coastal C/N is higher than offshore C/N. For sprats, C/N
343 ratios differed between 2011 and 2012 ($W = 1093.5$, $P = 0.002$), C/N ratios being higher in 2012
344 (4.83 ± 1.36) than in 2011 (4.03 ± 0.74). The C/N ratios of sprats in 2011 and 2012 were higher
345 when body length increased but the other factors were not significant.

346

347 **4. Discussion**

348 *4.1. Diet composition and ontogenetic shifts*

349 Anchovies fed mainly on *Microsetella*, *Oncaea* and Corycaeidae copepods. Consumption of
350 *Microsetella* has been previously observed in the Gulf of Lions during summer (Plounevez and
351 Champalbert, 2000), *Oncaea* is a usual prey in other regions of the Mediterranean Sea during other
352 seasons (Bacha and Amara, 2009; Borme et al., 2009; Tudela and Palomera, 1997) and high
353 Corycaeidae copepods consumption has been reported near the Gironde estuary (Plounevez and
354 Champalbert, 1999). Our results contrast with those of Costalago et al. (2012) based on stable
355 isotope analysis where adult anchovies sampled in summer 2008 fed on cladocerans and
356 appendicularians. This contrast suggests that anchovies' summer diet changed between 2007 and
357 2011-2012. Nevertheless, results on stomach contents of adult anchovies sampled in the 2007-2008
358 period have not been published yet to confirm the qualitative change in the diet of this age class.
359 Thus, this interpretation should be taken with caution as stomach contents and stable isotopes do

360 not provide the same information.

361 Anchovies had the lowest $\delta^{15}\text{N}$ and the highest $\delta^{13}\text{C}$. As detritus discharged by the Rhône
362 reduces $\delta^{13}\text{C}$ and increases $\delta^{15}\text{N}$ of phytoplankton and particulate organic matter in eastern and
363 coastal areas (Harmelin-Vivien et al., 2008), this result indicates that anchovies fed primarily on the
364 continental shelf or in western regions of the Gulf of Lions, far from the Rhône outflow, similarly to
365 what was found in the Bay of Biscay (Chouvelon et al., 2014). The study of the spatial distribution
366 of anchovies in the Gulf of Lions (Saraux et al., 2014) confirms this hypothesis. Anchovies
367 consumed more diatoms and *Centropages typicus* and less *Oncaea* when their body length
368 increased. Consumption of *Oncaea* by small anchovies is in accordance with Costalago et al. (2014)
369 where juveniles sampled in the Gulf of Lions during summer 2007 fed on some *Oncaea*, even if the
370 dominant prey groups in their study were cladocerans and copepods such as Clauso/Paracalanidae
371 and *Centropages typicus*. It is the first time that a high contribution of diatoms in the diet of large
372 anchovies was observed in the Gulf of Lions but this has been observed in the Baltic Sea (Schaber
373 et al., 2010). Nevertheless, high diatom consumption has been only observed in one sampling
374 station in 2012 and thus cannot be considered as a general phenomenon. Furthermore, copepods
375 remained the main prey items for anchovies of all length classes. No changes of stable isotope ratios
376 with body length have been detected in anchovies except a slight increase for $\delta^{13}\text{C}$ in 2011,
377 suggesting few ontogenetic changes in the preferred feeding area.

378 *Microsetella*, *Oncaea* and the Corycaeidae family were also the main prey of sardines. The
379 *Oncaea* genus was an important prey of adult sardines in the Gulf of Lions during summer 2007
380 (Costalago and Palomera, 2014) and in other regions (e.g. Garrido et al., 2008; Sever et al., 2005).
381 Our stomach contents results are similar with those of Costalago and Palomera (2014) but
382 cladocerans were an important prey in adult sardines in 2007 (highest %IRI), which suggests that
383 the dominant prey in the summer diet of sardines might have changed between 2007 and 2011-
384 2012.

385 Sardines had the highest $\delta^{15}\text{N}$ and a low $\delta^{13}\text{C}$, indicating that this species fed mainly on

386 coastal or eastern areas of the Gulf of Lions (Harmelin-Vivien et al., 2008), similarly to what was
387 found in the Bay of Biscay (Chouvelon et al., 2014). The study of the spatial distribution of sardines
388 in the Gulf of Lions (Saraux et al., 2014) confirms this hypothesis. High consumption of benthic
389 mysids *Paramysis* by small sardines in our study shows that juveniles of this species may feed in
390 coastal and benthic habitats. Nevertheless, small juvenile sardines have been sampled only at one
391 station near the Rhône plume and consumption of *Paramysis* cannot be considered as a general
392 phenomenon in the Gulf of Lions. Costalago and Palomera (2014) and Costalago et al. (2014) have
393 reported that juvenile sardines of the Gulf of Lions fed mainly on cladocerans and decapod larvae
394 during summer 2007. Like anchovies, sardines consumed more diatoms when their body length
395 increased but this observation is limited to one sampling station. A high contribution of
396 photosynthetic organisms in the diet of adult sardines has been previously observed (e.g. Garrido et
397 al., 2008) but these prey are poorly assimilated (Bode et al., 2004; Costalago and Palomera, 2014;
398 Nikolioudakis et al., 2012). Copepods remained the main prey items for large juvenile and adult
399 sardines. High consumption of *Paramysis* by small sardines and consumption of diatoms by large
400 sardines explain the decrease of the size of the prey when the sardines are growing and may be
401 linked to the acquisition of filter feeding ability thanks to gill rakers development (Costalago and
402 Palomera, 2014). $\delta^{13}\text{C}$ increased while $\delta^{15}\text{N}$ decreased when body length increased in 2011,
403 indicating that juvenile sardines fed in areas influenced by the Rhône inputs while adult sardines fed
404 in more oligotrophic areas with marine phytoplankton being the main carbon source.

405 Sprats were more generalist and fed on *Clauso/Paracalanus*, the Corycaeidae family,
406 *Euterpina acutifrons* and *Microsetella*. By contrast, adult sprats feed mainly on the copepods
407 *Calanus* and *Temora* in the Adriatic Sea (Tičina et al., 2000) but important consumption of
408 *Microsetella* was detected in term of number in a Norwegian fjord (Falkenhaug and Dalpadado,
409 2014). Sprats also had the lowest predator/prey ratios compared to sardines and anchovies,
410 indicating that they fed on the largest prey relative to their size. The consumption of larger prey
411 compared to its own size may be explained by the fact that sampled sprats are mostly juveniles (de

412 Silva, 1973) and thus have a lesser filter-feeding capacity. The absence of changes in prey sizes for
413 anchovies and sprats is thus likely the result of a lower size range available for these species.

414 Sprats had an intermediate $\delta^{15}\text{N}$ and a $\delta^{13}\text{C}$ value very similar to the $\delta^{13}\text{C}$ value of sardines but
415 with a wider range. Consequently, the mean $\delta^{13}\text{C}$ value indicates that sprats fed mainly on coastal or
416 eastern areas of the Gulf of Lions, probably in the same areas as sardines, but the range also indicate
417 that they may feed on the shelf.

418 Whatever their size, sprats fed more on larger copepods. The contribution of *Oncaea* to the
419 diet decreased with increasing body length while the contribution of Corycaeidae increased. $\delta^{15}\text{N}$
420 increased with body length, indicating increasing trophic level while growing as they fed less on
421 omnivorous *Oncaea* (Wu et al., 2004) and more on the predatory Corycaeidae copepods (Landry et
422 al., 1985; Turner et al., 1984). $\delta^{13}\text{C}$ decreased in 2011, indicating that sprats may exploit food webs
423 influenced by Rhône inputs while growing as $\delta^{13}\text{C}$ is lower in waters influenced by the Rhône
424 plume (Harmelin-Vivien et al., 2008).

425

426 4.2. *Spatial and temporal variations of diet*

427 Diet of anchovies differed between 2011 and 2012 and between coast and shelf. In 2011,
428 coastal anchovies fed mainly on *Oncaea* while *Microsetella* was the main prey on the shelf. Only
429 few anchovies were sampled in coastal areas by Plounevez and Champalbert (2000), which may
430 explain the high importance of *Microsetella* and the low importance of *Oncaea* in the general diet
431 of anchovies sampled in their study. Diet of anchovies in the western region was quite unusual, with
432 high consumption of Euphausiacean larvae on the shelf in 2011 and of diatoms on the coast in 2012.
433 Plounevez and Champalbert (2000) observed differences of feeding between west and east for
434 offshore anchovies, with Euphausiacean larvae being an important prey for western anchovies in
435 1995 and *Microsetella* being an important prey for eastern anchovies in 1995 and 1996. In 2011,
436 stable isotope ratios were dependent on the region of sampling and, in 2012, $\delta^{15}\text{N}$ was influenced by
437 depth. Anchovies sampled in 2011 in the eastern region showed higher $\delta^{13}\text{C}$ in the coastal area than

438 on the shelf. This result was not in accordance with low $\delta^{13}\text{C}$ observed in particulate organic matter
439 (Harmelin-Vivien et al., 2008) but was in accordance with high values of $\delta^{13}\text{C}$ recorded in
440 zooplankton sampled near the Rhône river as this zooplankton previously fed in an offshore area
441 characterised by higher $\delta^{13}\text{C}$ values (Espinasse et al., 2014b). No spatial pattern was found in the
442 Bay of Biscay, indicating high mobility of anchovies in this region (Chouvelon et al., 2014). In the
443 Gulf of Lions, different stable isotope ratios between regions in 2011 or between depths in 2012
444 may indicate that anchovy schools may have preferences in feeding areas.

445 Diet of sardines differs among regions of the Gulf of Lions. Sardines sampled in the centre
446 and the east fed mainly on *Microsetella*, *Oncaea* and Corycaeidae, while sardines sampled in the
447 west had a more diverse diet (eggs on the coast in 2011, diatoms on the coast in 2012). As in the
448 Bay of Biscay (Chouvelon et al., 2014), stable isotope ratios of sardines did not vary among regions
449 or depths of sampling, except in 2011 on the eastern coast where $\delta^{13}\text{C}$ was low, suggesting high
450 mobility of sardines.

451 Diet of sprats differs between coastal areas and continental shelf and diet was dominated by
452 decapod larvae on the western shelf. In 2012, diatoms are a secondary prey in the west and on the
453 coast, suggesting that sprat is more carnivorous than anchovies and sardines. This result is in
454 accordance with those of Pethybridge et al. (2014) where sprat sampled during winter 2011 had
455 higher fatty acid markers of carnivory than anchovies and sardines. No spatial variations of stable
456 isotope ratios were observed in sprats, indicating high mobility of sprat schools in the Gulf of
457 Lions. Higher diversity and variability of dominating prey in the west of the Gulf of Lions for the
458 three species may be the result of differences of habitat conditions (Espinasse et al., 2014a).

459

460 4.3. Interaction between planktivorous teleost species

461 Trophic competition has been speculated in areas where planktivorous teleost species co-
462 occur (Casini et al., 2004; Raab et al., 2012). Our stomach contents results indicate high trophic
463 interactions between anchovies, sardines and sprats in the Gulf of Lions as diet overlap occurs in

464 their general diet, notably between anchovies and sardines. $\delta^{13}\text{C}$ values indicate that sardines and
465 sprats fed in the same areas. In contrast, trophic interactions of anchovies with sardines and sprats
466 are potentially reduced considering their differences in $\delta^{13}\text{C}$. The isotopic niche of sprats based on
467 both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios highly overlapped with those of anchovies and sardines, suggesting that
468 sprats compete with the two other species, while the isotopic niches of anchovies and sardines
469 poorly overlapped, suggesting that they fed in different areas considering their distribution (Saraux
470 et al., 2014). Pethybridge et al. (2014) have also observed reduced competition between anchovies
471 and sardines by using lipid biomarkers. Consequently, contrasting results were obtained on trophic
472 interactions between anchovies and sardines with stomach content and stable isotopes, suggesting
473 overlap for the recently ingested prey but not for the previously ingested prey and/or the feeding
474 areas. However, results on stable isotope ratios should be considered with caution as these
475 potentially migratory species feed in an area subjected to high inputs and hydrological variations
476 (Espinasse et al., 2014a; Harmelin-Vivien et al., 2008). These factors may also explain the high
477 differences noticed in the trophic niche overlap when using diet indices (%IRI and %W) and stable
478 isotope ratios.

479 Differences of $\delta^{15}\text{N}$ in anchovies between coast and continental shelf in 2012 indicate that
480 some anchovies may sometimes exploit mainly coastal areas with sardines and sprats instead of the
481 continental shelf, leading to high local trophic overlap between the three species. Adult anchovies
482 of the Bay of Biscay feed primarily in offshore habitats (Chouvelon et al., 2014) but Pasquaud et al.
483 (2008) observed that small anchovies can also feed along with sprats in estuarine habitats of the
484 Gironde. If competition between the three species occurs in the Gulf of Lions, sprats should have an
485 advantage considering their larger niche width, the feeding on slightly larger, and thus, more
486 energetic prey (Gerking, 1994; van Deurs et al., 2015) than anchovies and sardines, their lowest
487 predator/prey size ratios and because they seem to recover well after the spawning period
488 (Pethybridge et al., 2014).

489 Even if studies on stomach contents and stable isotopes do not exactly provide the same

490 information, the changes in the diets of anchovies and sardines reported from 1995-1996
491 (Plounevez and Champalbert, 2000) to 2007-2008 (Costalago et al., 2012; Costalago and Palomera,
492 2014) and to 2011-2012 (this study) may have been a contributing factor to the decline of anchovies
493 and sardines. Consumption of cladocerans by the three species is variable among regions with, for
494 examples, a good representation of this group in the general diet of sardines of the Aegean sea
495 (Nikolioudakis et al., 2012) and sprats of the Baltic Sea and of the North Sea (Casini et al., 2004;
496 Raab et al., 2012) but a low importance in western Mediterranean Sea (Borme et al., 2009;
497 Plounevez and Champalbert, 2000; Tičina et al., 2000) except at local scale (Tudela and Palomera,
498 1997). Furthermore, cladocerans are considered to have lower energetic value than copepods (Bodt
499 and Haldorson, 2002). Consequently, unusual consumption of cladocerans in 2007-2008, while it
500 was rare in 1995-1996 and 2011-2012, may have had a negative impact on the body condition of
501 adult anchovies and sardines, leading to the decreasing biomass observed for these species since
502 2008. Decreasing biomass of anchovies and sardines after such events may have led to an increase
503 in sprat biomass and competition may have prevented the recovery of anchovies and sardines,
504 leading to persistence of the phenomenon. However, competition only occurs when food resources
505 are limited for the predators and no information regarding this factor exists for the study area or
506 elsewhere for these species. Furthermore, body condition of anchovies and sardines was still low in
507 2011 and 2012 despite the fact that they ate more copepods and less cladocerans than in the past
508 years (Van Beveren et al., 2014). Consequently, other environmental and/or physiological factors
509 (Cury and Roy, 1989; Takasuka et al., 2007) may have acted in interaction with the trophic one to
510 influence the body condition and/or biomass of small pelagic teleosts. However, the relationship
511 between body condition of anchovies and sardines and mesozooplankton concentration (Brosset et
512 al., in press) indicates that the decline of these species is mainly explained by the trophic ecology of
513 these species. The importance of competition may possibly vary seasonally. In the Gulf of Lions,
514 Pethybridge et al. (2014) reported that no competition of sprats with anchovies and sardines during
515 winter 2011 was apparent on the basis of lipid biomarkers. In the Bay of Biscay, Chouvelon et al.

516 (2015) hypothesised that anchovies and sardines are potential competitors for food in autumn, but
517 not in spring.

518

519 *4.4. C/N ratios as an indicator of relative condition*

520 Sprats had the highest C/N ratios, followed by sardines and anchovies, suggesting that this
521 species has the highest lipid levels and thus the best relative condition in the Gulf of Lions during
522 summer. That does not imply the good “health” of this population over the time as sprats had a
523 lower relative condition value and a small length when compared to previous years (Van Beveren et
524 al., 2014). Low fat content in anchovies was related to the spawning activity that occurs in summer
525 (Palomera et al., 2007). Higher fat content in sardines than in anchovies has been observed in
526 various seasons (Sánchez et al., 2013; Zlatanov and Laskaridis, 2007).

527 Sprats sampled during winter 2011 had also higher lipid contents than anchovies and sardines
528 (Pethybridge et al., 2014), suggesting that they had the best relative condition throughout the year
529 when compared to sardines and anchovies. Slight increase of C/N ratios occurred only in sprats
530 when they are growing, suggesting that larger sprats increase their chances of survival. As a result,
531 sprats are at an advantage when they compete with anchovies and sardines. The greater niche width
532 and the consumption of slightly larger prey may contribute to the better relative condition of sprats.

533

534 **5. Conclusion**

535 Combining stomach content analysis with stable isotopes is necessary to better understand
536 trophic ecology of small pelagic teleosts within a region subjected to variable hydrological
537 conditions, to different sources of particulate organic matter and variable plankton communities
538 (Espinasse et al., 2014a). The studied species changed their summer diet compared to past studies.
539 The trophic niche overlap between the three species sustains the hypothesis of their competition, but
540 data on the quality and quantity of zooplankton are necessary to confirm or disprove the hypothesis
541 on the limitation of food resources. However, the higher diversity and size of the consumed prey,

542 trophic niche and C/N values of sprats indicate that they probably have a competitive advantage
543 over anchovies and sardines and thus a trophic factor may be one of the explaining factors of the
544 recent changes in small pelagic teleost communities of the Gulf of Lions.

545

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555

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Supplementary material: Trophic niche overlap of sprat and commercial small pelagic teleosts in the Gulf of Lions (NW Mediterranean Sea)

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Table A.1. Dry weight (DW; μg) of prey and morphometric relationship used to calculate DW. TL = Total length (μm).

Prey		Dry weight (μg)	Reference
Protists			
Protists	Protists	DW = 30	This study
Crustaceans			
Copepods	<i>Clauso/Paracalanus</i> , <i>Pleuromamma</i> and copepods n.d.	Log DW = 2.285 log TL – 5.965	Mauchline (1998)
	<i>Calanus</i>	Log DW = 2.790 log TL – 7.370	Mauchline (1998)
	<i>Microsetella</i>	Ln DW = 1.15 ln TL – 7.79	Satapoomin (1999)
	<i>Oncaea</i>	DW = 1.34	Borme et al. (2009)
	Corycaeidae	DW = 62	Pitois & Fox (2006)
	<i>Euterpina acutifrons</i>	DW = $1.389 \cdot 10^{-8} \text{ TL}^{2.857}$	Ara (2001)
	<i>Macrosetella</i>	Ln DW = 1.59 ln TL – 10.92	Satapoomin (1999)
	<i>Centropages typicus</i>	Log DW = 2.243 log TL – 5.568	Mauchline (1998)
	<i>Centropages hamatus</i>	DW = 14.7	Pitois & Fox (2006)
	<i>Candacia</i>	DW = 106.2	Pitois & Fox (2006)
	<i>Oithona</i>	DW = 2.2	Pitois & Fox, 2006
	<i>Temora</i>	Log DW = 2.179 log TL – 5.567	Mauchline (1998)
	<i>Euchaeta</i>	Log DW = 2.62 log TL – 6.47	Uye (1982)
	<i>Acartia</i>	Log DW = 3.208 log TL – 7.644	Mauchline (1998)
	<i>Lucicutia</i>	DW = 16.9	Delpy (2013)
	<i>Clytemnestra</i>	DW = 0.3	Delpy (2013)
Cladocerans	<i>Evadne</i>	DW = $3.946 (\text{TL}/1000)^{2.436}$	Borme et al. (2009)
	<i>Podon</i>	DW = 1.6	Borme et al. (2009)
	Cladocerans n.d.	mean <i>Evadne</i> and <i>Podon</i>	This study
Ostracods	Ostracods	DW = 6.036	Borme et al. (2009)
Mysids	<i>Paramysis</i>	Log DW = 3.08 log TL + 0.236	Uye (1982) (<i>Neomysis</i>)
Amphipods	<i>Phronima</i>	DW = 40; DW = 770	This study
	Other amphipods	DW = 40	This study
Isopods	Isopods	Ln DW = 1.69 ln (TL/1000) – 11.64	Borme et al. (2009)
Chaetognaths			
Chaetognaths	Chaetognaths	Log DW = 3.24 log TL – 0.975	Uye (1982)
Larvae			
Crustaceans	Copepodids	DW = $1.10 \cdot 10^{-5} \text{ TL}^{1.89}$	Dumont et al. (1975)
	Nauplii	Log DW = 2.848 log TL – 7.265	Borme et al. (2009)
	Cirriped nauplii	DW = 0.67	Borme et al. (2009)
	Protozoa	DW = 27.798	Borme et al. (2009)
	Metazoa	DW = 27.798	Borme et al. (2009)
	Brachyurans	DW = 27.798	Borme et al. (2009)
	Decapods	DW = 27.798	Borme et al. (2009)
	Zoea	DW = 27.798	Borme et al. (2009)
	Trachelifer	DW = 27.798	Borme et al. (2009)
	Euphausiaceans	Log DW = 0.456 + 2.8 log TL	Lindley et al. (1999)
Molluscs	Gastropods	DW = 0.6	Borme et al. (2009)
	Bivalves	DW = 3.758	Borme et al. (2009)
Teleosts	Teleosts	DW = 7510	This study
Eggs			
Eggs	Anchovies eggs	DW = 30.1	Borme et al. (2009)

Table A.3. Effect of body length, depth and region of sampling on a) $\delta^{15}\text{N}$, b) $\delta^{13}\text{C}$, c) C/N in anchovies, sardines and sprats. Bold results are significant. The body length covariate was not included in the model if its effect was not significant (NC = not computed).

a)

	2011	2012	2011 and 2012	
Species	<i>E. encrasicolus</i>	<i>E. encrasicolus</i>	<i>S. pilchardus</i>	<i>S. sprattus</i>
Length	NC	NC	F_{1,94} = 7.495 P = 0.007	F_{1,109} = 4.725 P = 0.032
Depth	F _{1,56} = 2.094 P = 0.154	F_{1,30} = 16.890 P < 0.001	F _{1,94} = 0.060 P = 0.806	F _{1,109} = 0.741 P = 0.391
Zone	F_{2,56} = 4.165 P = 0.021	F _{2,30} = 1.258 P = 0.299	F _{2,94} = 0.971 P = 0.382	F _{2,109} = 0.395 P = 0.675
Depth*Zone	F _{2,56} = 1.203 P = 0.308	F_{2,30} = 3.630 P = 0.039	F _{2,94} = 0.345 P = 0.709	F _{2,109} = 0.826 P = 0.440

b)

	2011			2012		
Species	<i>E. encrasicolus</i>	<i>S. pilchardus</i>	<i>S. sprattus</i>	<i>E. encrasicolus</i>	<i>S. pilchardus</i>	<i>S. sprattus</i>
Length	F_{1,55} = 20.274 P < 0.001	F_{1,52} = 13.936 P < 0.001	F_{1,59} = 6.253 P = 0.015	NC	NC	F_{1,43} = 4.083 P = 0.050
Depth	F _{1,55} = 0.026 P = 0.873	F _{1,52} = 0.404 P = 0.528	F _{1,59} = 0.160 P = 0.691	F _{1,30} = 0.478 P = 0.495	F _{1,36} = 0.309 P = 0.582	F _{1,43} = 0.008 P = 0.929
Zone	F_{2,55} = 4.998 P = 0.010	F _{2,52} = 1.531 P = 0.226	F _{2,59} = 1.850 P = 0.166	F _{2,30} = 1.761 P = 0.189	F _{2,36} = 1.183 P = 0.318	F _{2,43} = 2.090 P = 0.136
Depth*Zone	F_{2,55} = 6.296 P = 0.003	F _{2,52} = 2.433 P = 0.098	F _{2,59} = 0.016 P = 0.984	F _{2,30} = 1.588 P = 0.221	F _{2,36} = 0.135 P = 0.874	F _{2,43} = 3.057 P = 0.057

c)

	2011	2012	2011 and 2012	
Species	<i>S. sprattus</i>	<i>S. sprattus</i>	<i>E. encrasicolus</i>	<i>S. pilchardus</i>
Length	F_{1,59} = 33.903 P < 0.001	F_{1,43} = 10.856 P = 0.002	NC	NC
Depth	F _{1,59} = 0.573 P = 0.452	F _{1,43} = 0.002 P = 0.966	F _{1,92} = 3.027 P = 0.085	F _{1,95} = 0.012 P = 0.913
Region	F _{2,59} = 0.646 P = 0.528	F _{2,43} = 1.279 P = 0.289	F _{2,92} = 1.296 P = 0.279	F _{2,95} = 0.054 P = 0.948
Depth*Region	F _{2,59} = 1.333 P = 0.271	F _{2,43} = 2.027 P = 0.144	F_{2,92} = 5.709 P = 0.005	F _{2,95} = 2.618 P = 0.078

Table A.4. Diet overlap (%T) between length class (cm) of anchovies, sardines and sprats using Schoener's formula (1970) on %IRI (upper diagonal) and %W (lower diagonal). Bold results are significant (%T ≥ 60).

		<i>E. encrasicolus</i>			<i>S. pilchardus</i>		<i>S. sprattus</i>	
		[8-10[[10-12[[12-13[[3-8[[8-15[[7-8[[8-11[
<i>E. encrasicolus</i>	[8-10[-	69.28	55.38	14.00	68.47	57.90	53.44
	[10-12[68.46	-	50.13	4.93	81.34	33.47	46.11
	[12-13[52.21	53.55	-	14.21	54.64	39.19	60.22
<i>S. pilchardus</i>	[3-8[19.19	9.03	12.48	-	3.96	13.99	14.04
	[8-15[70.06	74.44	50.75	8.12	-	37.62	58.24
<i>S. sprattus</i>	[7-8[60.49	38.24	31.80	20.85	44.33	-	52.19
	[8-11[63.84	57.13	52.50	16.06	66.49	53.42	-

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