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1 **Diet and trophic interactions of Mediterranean planktivorous fishes**

2

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21 **Highlights**

- 22 • Diets of seven Mediterranean planktivorous fishes: *Engraulis encrasicolus*,  
23 *Sardina pilchardus*, *Sardinella aurita*, *Sprattus sprattus*, *Cepola macrophthalma*,  
24 *Chromis chromis* and *Boops boops*, are detailed.
- 25 • Copepods, decapod larvae and fish eggs were their main prey.
- 26 • Prey groups, size distribution and average size differed among fish species.
- 27 • Stomach content and stable isotope compositions showed contrasted results in  
28 terms of dietary niches, overlap and prey diversity among fishes.
- 29 • Stable isotope compositions displayed more similarities in diet between studied  
30 fish species than stomach content analysis, suggesting potential trophic  
31 competition, particularly among Engraulidae and Clupeidae.
- 32 • Even in coastal zones, small pelagic fish did not seem to compete much with the  
33 main pelago-demersal planktivorous fish species for their food resources.

34

35 **Keywords**

36 Small pelagic fish; diet composition; prey-predator size-ratio; trophic niche overlap;  
37 food competition

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41 **Abstract**

42 Diet and trophic interactions of seven species of planktivorous fishes: European  
43 anchovy *Engraulis encrasicolus*, European sardine *Sardina pilchardus*, round  
44 sardinella *Sardinella aurita*, European sprat *Sprattus sprattus*, red bandfish *Cepola*  
45 *macrophthalma*, damselfish *Chromis chromis* and bogue *Boops boops*, were studied in  
46 the Bay of Marseille (North-Western Mediterranean Sea) from March to September  
47 2017. Taxonomic composition and size distribution of prey were studied using  
48 stomach content analysis, and compared to prey availability determined by continuous  
49 zooplankton sampling at a fixed point. Frequently consumed items included copepods,  
50 decapod larvae and fish eggs. Comparatively, *E. encrasicolus* consumed more  
51 calanoid copepods (i.e. *Centropages* spp.), *S. pilchardus*, *S. aurita* and *S. sprattus*  
52 consumed more harpacticoid copepods (i.e. *Microsetella/Macrosetella* spp.), *C.*  
53 *macrophthalma* consumed more decapod larvae, *C. chromis* consumed more  
54 pteropods and *B. boops* consumed more benthic polychaetes. *Sardina pilchardus*  
55 consumed the widest diversity of prey. Prey size distribution and average prey size  
56 significantly differed among species. The prey-predator size ratio (PPSR) was highest  
57 for *B. boops* and lowest for *S. aurita*. Carbon and nitrogen stable isotope composition  
58 of species overlapped, probably due to the ingestion of particulate organic matter  
59 from the same sources at the base of the planktonic food web in the Bay of Marseille.  
60 Furthermore, trophic niche overlap supported the hypothesis of potential trophic  
61 competition between Engraulidae and Clupeidae.

## 62 1. Introduction

63 Small planktivorous fish represent a fundamental trophic group in many ecosystems  
64 (Peck et al. 2020) as they feed on diverse plankton groups and are forage species for  
65 many predators including mackerel, hake and tuna (Palomera et al. 2007; Bănaru et al.  
66 2013, 2019). Small planktivorous fishes also have a high commercial value as they  
67 represent more than 50% of the annual landings in the Gulf of Lion and more widely  
68 in the Mediterranean Sea (Bănaru et al. 2013; FAO 2020).

69 Bottom-up changes in the pelagic food web induced by climate change via  
70 hydrological processes are suspected to be one of the major drivers of planktivorous  
71 fish populations, including in the North-Western Mediterranean Sea (NWMS)  
72 (Moullec et al. 2016 and references therein; Bănaru et al. 2019; Feuilloley et al.  
73 2020). Moreover, the NWMS has also been impacted by changes in the management  
74 of sewage water, leading to a reduction of nutrient inputs (Raimbault et al. 2021) that  
75 may potentially impact plankton communities, as demonstrated in other  
76 Mediterranean areas (Pagès et al. 2020). Zooplankton play a pivotal role in marine  
77 ecosystems, as they support fisheries production and mediate fluxes of nutrients and  
78 chemical elements (Banse 1995). Mesozooplankton of 200  $\mu\text{m}$  to 1000  $\mu\text{m}$  in length,  
79 mainly consisting of copepods, constitute the main prey of adult planktivorous fish,  
80 and the bottom-up control hypothesis involves changes in the quantity or quality of  
81 these prey (Le Bourg et al. 2015). In addition, recent studies have demonstrated that  
82 the quality of plankton depends on both taxonomic group and size class  
83 (Harmelin-Vivien et al. 2019; Chen et al. 2019a).

84 In coastal areas, the changes described above may have contributed to the reduction of  
85 planktivorous fish biomass and their relative proportions in fish communities  
86 (Ourgaud et al. 2015; Cresson et al. 2019). In the NWMS, it has been hypothesized

87 that changes in both taxonomic composition and individual size of zooplankton may  
88 underlie recently observed changes in the diet of some planktivorous fish species such  
89 as the European pilchard and the European anchovy (Le Bourg et al. 2015; Chen et al.  
90 2019a). A recent decline in planktivorous fish biomass, abundance, body size and  
91 relative body condition has been observed and may have led to changes in fish diet  
92 (STECF 2015; Ourgaud et al. 2015; GFCM 2019; Saraux et al. 2019; Cresson et al.  
93 2019; Chen et al. 2021). In the changing environmental context of the Mediterranean  
94 Sea, this bottom-up control hypothesis highlights the need to study the composition of  
95 zooplanktivorous fish diet and trophic interactions, and to consider zooplankton prey  
96 groups and size in order to better estimate their role in the pelagic food webs.  
97 Knowledge of dietary specialization, including potential sharing of food resources  
98 among co-occurring members of the fish community, would help determine functional  
99 roles and to identify species for which potential competitive interactions during  
100 periods of prey scarcity may occur (Burbank et al. 2019). This is essential for  
101 ecosystem management and conservation (Bachiller et al. 2021).

102 In the NWMS, previous studies on planktivorous fish diet have focused on the  
103 taxonomic composition of stomach contents (Stergiou and Karpouzi 2002; Costalago  
104 and Palomera 2014). Some of these studies were based on the isotopic composition of  
105 muscle tissue and of the prey of planktivorous fish (Cresson et al. 2014; Costalago et  
106 al. 2014; Brosset et al. 2016), and some of them also provided information on prey  
107 size structure (Le Bourg et al. 2015; Albo-Puigserver et al. 2019; Chen et al. 2021).  
108 Combining stable isotope analyses (SIA) and stomach content analyses (SCA) offers  
109 different and complementary insights into trophic relationships. While SCA provide  
110 information on recently consumed prey (hours to one day), SIA (measurement of  $\delta^{13}\text{C}$   
111 and  $\delta^{15}\text{N}$  values) of muscle tissues [provides](#) information on food sources integrated  
112 over time (weeks to months) (Vander Zanden et al. 2015). An underlying assumption

113 is that isotopic compositions accurately reflect species dietary breadths over a period  
114 of time defined by tissue-specific turnover rates.

115 The present study focused on the diet and trophic interactions of seven planktivorous  
116 fish species: European anchovy *Engraulis encrasicolus* (Linnaeus, 1758)  
117 (Engraulidae), European sardine *Sardina pilchardus* (Walbaum, 1792) (Clupeidae),  
118 round sardinella *Sardinella aurita* (Valenciennes, 1847) (Clupeidae), European sprat  
119 *Sprattus sprattus* (Linnaeus, 1758) (Clupeidae), red bandfish *Cepola macrophthalma*  
120 (Linnaeus, 1758) (Cepolidae), damselfish *Chromis chromis* (Linnaeus, 1758)  
121 (Pomacentridae) and bogue *Boops boops* (Linnaeus, 1758) (Sparidae) in the Bay of  
122 Marseille, North-Western Mediterranean Sea. The study was performed from March  
123 to September 2017. These species represent a range in body sizes, shapes, and habitat  
124 occupations (entire water column in the case of pelagic Engraulidae and Clupeidae  
125 species, benthic and pelagic environments for the demersal *B. boops* and *C. chromis*,  
126 and burrows in soft-bottoms for *C. macrophthalma* (Stergiou and Karpouzi 2002)).  
127 Several previous studies have focused on diet, notably in commercially important *E.*  
128 *encrasicolus* and *S. pilchardus*, which demonstrated diet changes and reduced prey  
129 diversity (Le Bourg et al. 2015; Brosset et al. 2016). Using a multi-proxy approach,  
130 Bachiller et al. (2020, 2021) highlighted a trophic latitudinal gradient in *E.*  
131 *encrasicolus* and *S. pilchardus* in the Western Mediterranean Sea and a trophic niche  
132 overlap between *S. pilchardus* and *S. aurita*. Information on other pelago-demersal  
133 planktivorous species from the Gulf of Lion is lacking.

134 Our aim here was to determine the food resources consumed by planktivorous fish.  
135 Our hypothesis is that competition for food resources may occur between the NWMS  
136 planktivorous species, leading to the observed changes in small pelagic fish  
137 populations. The information provided by our study will [improve food web modeling](#),  
138 which is increasingly applied to predict fish population and ecosystem dynamics. We

139 investigated the diet of pelago-demersal planktivorous fish by combining SCA and  
140 SIA. Specifically, we aimed: (1) to analyze fish diet in terms of prey taxonomic  
141 groups and prey sizes over the entire sampling period, (2) to estimate the trophic  
142 overlap among these species using SCA and SIA, and (3) to compare the dietary  
143 diversity and overlap of trophic niches using both methods, to test the hypothesis of  
144 potential trophic competition.

145

## 146 **2. Material and methods**

### 147 *2.1. Study site*

148 The Bay of Marseille (South of France) is located in the eastern part of the Gulf of  
149 Lion in the NWMS. In this bay, phyto- and zooplankton communities benefit from  
150 diverse marine and terrestrial nutrient input (Bănaru et al. 2014; Chen et al. 2019a).  
151 The Bay of Marseille is influenced from the south by the intrusions of the offshore  
152 Northern Current (Petrenko et al. 2005), and occasionally from the west by the  
153 intrusions of the Rhone River plume, and by the coastal Huveaune River, depending on  
154 wind and rain events (Cresson et al. 2012; Fraysse et al. 2014). The bay is also subject  
155 to anthropogenic and terrestrial inputs from the Marseille sewage treatment plant at  
156 Cortiou (Millet et al. 2018) (Fig. 1).

### 157 *2.2. Sampling and sample processing*

158 Fish were sampled through a partnership with local fishermen working with lampara  
159 net, gillnets and trawling (Fig. 1). Where possible, 30 individuals of each species were  
160 sampled in the early morning, each month from March 2017 to September 2017.  
161 Alongside this monthly sampling, data were also analyzed collectively - and not  
162 seasonally - because the number of individuals sampled each month widely differed  
163 between species. The potential impact of seasonality on the results is considered  
164 separately (see section 4.4.). The number of samples for body length measurements,



165 SCA and SIA are listed in Table 1.

166 Once caught, fish were immediately put on ice and kept at -20°C upon arrival at the  
167 laboratory to inhibit digestion of the stomach contents.

168 Zooplankton was collected monthly at the Solemio station (43.24°N; 5.29°E)  
169 simultaneously with the SOMLIT (Service d'Observation en Milieu Littoral)  
170 long-term national program for littoral observation (Fig. 1). Zooplankton was sampled  
171 vertically from 50 m depth (close to the bottom) to the surface with an 80- $\mu$ m mesh  
172 size net (50 cm opening diameter). Zooplankton samples were preserved in a buffered  
173 4% formaldehyde - seawater solution.

174 In the laboratory, total body length (TL) of each fish was measured to the nearest  
175 millimeter. Each individual was sexed by examination of the gonads. Digestive tracts  
176 were collected and preserved individually in a buffered 4% formaldehyde - seawater  
177 solution for later SCA. Dorsal white muscle was sampled from each fish and frozen at  
178 -20°C for later SIA.

### 179 2.3. *Analysis of fish diet and plankton composition*

180 The number of analyzed individuals for total body length measurements, the  
181 minimum, maximum and mean total body length (cm), the proportion of empty  
182 stomachs and the degree of repletion per species are displayed in Table 1. The mean  
183 degree of stomach repletion (SRD) was estimated visually using a semi-quantitative  
184 scale of prey volume in stomach: 0 = empty, 1 = > 0 – 25 % full, 2 = 25 - 50% full, 3  
185 = 50 - 75% full, 4 = 75 - 100% full. Empty stomachs were not considered in diet  
186 index calculations.

187 Zooplankton prey were identified and sorted for further taxonomic and size analyses.

188 The taxonomic groups of zooplankton found in both fish stomachs and plankton net  
189 samples were identified and the number of individuals in each group were counted  
190 using a stereomicroscope (Leica M205C) as described by Chen et al. (2021). The

191 main copepod groups were identified using the website 'Marine Planktonic Copepods'  
192 (<https://copepodes.obs-banyuls.fr/en/loc.php?loc=14>) (Razouls et al. 2005).

193 The maximum length (sum of prosome and urosome lengths for copepods) was  
194 measured on the first 30 individuals of representative prey groups found in each  
195 stomach and zooplankton net sample. Size measurement allowed the calculation of a  
196 prey-predator size ratio (PPSR) between each fish and its prey, achieved by  
197 determination of the most consumed prey size range by species and comparison with  
198 the size of the available zooplankton prey in the 80- $\mu\text{m}$  mesh size net. For graphic  
199 representation, PPSR values were multiplied by 1000. Dry weight (DW) of each  
200 organism was estimated from length-weight relations gathered from the literature  
201 (Table S1). The degree of stomach fullness (SFD) was used to assess feeding intensity  
202 (as described by Bachiller et al. (2016)). *The SFD, expressed in  $\mu\text{g}\cdot\text{cm}^{-1}$ , is defined as*  
203 *the sum of prey dry weight in the stomach divided by the total length of the fish.*

#### 204 2.3.1. *Trophic indices*

205 Diet composition based on stomach content analyses (SCA) was analyzed using several  
206 complementary indices: frequency of occurrence (O%: percentage of non-empty  
207 stomachs containing a given prey item), numerical percentage (N%: mean percentage  
208 per stomach of the number of a given prey item related to the total number of all prey in  
209 each stomach), dry weight percentage (W%: mean percentage per stomach of the  
210 weight of a given prey item related to the total weight of all prey in each stomach).  
211 These indices were used to calculate the index of relative importance (IRI) following  
212 the formula (Pinkas et al. 1971):

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

213 and then expressed as a percentage (IRI%) (Cortés 1997).

214 For consistency, IRI was also used to compute trophic niche width and dietary overlap.

215 To compare the community composition of zooplankton sampled with nets and the

216 zooplanktonic prey in fish diet, IRI% was also calculated by month for zooplankton  
217 sampled with the 80- $\mu$ m mesh size plankton net. Here, IRI% integrates information on  
218 the abundance, occurrence and biomass of zooplankton groups sampled with nets.

### 219 2.3.2. *Diversity indices*

220 The Shannon diversity index was determined to quantify the diversity of prey in fish  
221 stomachs and then for zooplankton net samples, using the formula:

$$H' = - \sum_{i=1}^s p_i \ln p_i$$

222 where  $p_i$  is the mean proportion (IRI%) of the prey group  $i$ , and  $S$  is the total number  
223 of prey groups.

224 The Pielou evenness index was computed to determine the evenness of prey group  
225 distribution in the diets of the studied species, using the formula:  $J = H' \div \ln(S)$

226 where  $H'$  is the Shannon diversity index and  $S$  is the total number of prey groups  
227 found in stomach contents per species. This index was also estimated for the 80- $\mu$ m  
228 mesh size plankton net.

229 Trophic niche breadth and prey diversity in relation to increasing fish size was  
230 analyzed following the method proposed by Bachiller and Irigoien (2015).

### 231 2.4. *Stable isotope analysis (SIA)*

232 For the SIA, where possible, at least three fish were analyzed per month and per  
233 species among those previously analyzed for SCA (Table 1). Fish muscle tissues were  
234 freeze-dried, ground into a fine powder and a subsample was packed into a 5  $\times$  8 mm tin  
235 cup. Carbon and nitrogen stable isotope analyses were performed using a  
236 continuous-flow isotope-ratio mass spectrometer (Delta V Plus, Thermo Scientific)  
237 with a ConFlo IV interface coupled to an elemental analyzer (Flash EA 1112, Thermo  
238 Scientific) equipped with the Smart EA option. Analyses were conducted at the Littoral,  
239 Environment and Societies Joint Research Unit stable isotope facility (CNRS -

240 University of La Rochelle, France). The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values are expressed in  $\delta$   
241 notation as deviations from standards (Vienna Pee Dee Belemnite for  $\delta^{13}\text{C}$  and  $\text{N}_2$  in air  
242 for  $\delta^{15}\text{N}$ ), in ‰, according to the formula:

$$243 \quad \delta X = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000$$

244 where X is  $^{13}\text{C}$  or  $^{15}\text{N}$ ,  $R_{\text{sample}}$  is the isotopic ratio of the sample and  $R_{\text{standard}}$  is the  
245 isotopic ratio of the standard. Calibration was carried out using reference materials  
246 (USGS-24, -61, -62, IAEA-CH6, -600 for carbon; USGS-61, -62, IAEA-N2, -NO-3,  
247 -600 for nitrogen). The analytical precision of the measurements was <0.15‰ for  
248 carbon and nitrogen based on analyses of USGS-61 and USGS-62 used as laboratory  
249 internal standards.

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

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

252 Individual and mean trophic level (TL) of fish species ( $TL_{\text{fish}}$ ) were calculated using  
253  $\delta^{15}\text{N}$  values according to the following formula (Vander Zanden and Rasmussen  
254 2001):

$$TL_{\text{teleost}} = \lambda + (\delta^{15}\text{N}_{\text{teleost}} - \delta^{15}\text{N}_{\text{baseline}}) \div 3.4$$

255 where  $\delta^{15}\text{N}_{\text{fish}}$  is the  $\delta^{15}\text{N}$  value of the consumer,  $\lambda$  the trophic level of the baseline  
256 and  $\delta^{15}\text{N}_{\text{baseline}}$  the  $\delta^{15}\text{N}$  value of the baseline. The mean annual  $\delta^{15}\text{N}$  value of the  
257 200-300  $\mu\text{m}$  size class of zooplankton sampled in the framework of SOMLIT (see  
258 section 2.2.) (Chen et al. 2019a) was considered as the baseline for primary  
259 consumers (i.e. trophic position  $\lambda = 2$ ) and a trophic fractionation factor of 3.4 was  
260 used for the computations (Post 2002).

## 261 2.5. Resource partitioning

262 The total dietary trophic niche width (DNW) based on stomach content analysis was

263 estimated to compare fish species trophic diversity (Schoener 1970):  $DNW = e^{H'}$

264 with  $H' = -\sum(IRI_i \times \log_2 IRI_i)$ .

265 Overlap in species diet (T%; Schoener 1970) was calculated according to the formula:

$$T\% = (1 - 0.5\sum|IRI_{xi}\% - IRI_{yi}\%|) \times 100$$

266 where  $IRI_{xi}\%$  and  $IRI_{yi}\%$  are IRI% for the prey item  $i$  in the fish species  $x$  and  $y$ .

267 In theory, T% varies from zero (when the two groups of fish feed on totally different  
268 prey items) to one (when they consume the same prey items in the same proportions).

269 Index values higher than or equal to 0.6 are considered significantly elevated (Keast  
270 1978).

## 271 2.6. Statistical analyses

272 Data normality and homogeneity were tested using Shapiro-Wilk and Levene tests.

273 Non-parametric analysis of variance Kruskal–Wallis tests were used to examine  
274 differences in total body length, average prey size, PPSR, and isotopic compositions  
275 ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) among species. Dunn's multiple non-parametric post-hoc tests were  
276 used to pinpoint which specific means significantly differed from the others.

277 Spearman's correlation was used to test the relationship between the total body length  
278 and stable isotopic compositions ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of fish species. Differences in diet

279 composition between species were tested using one-way analysis of similarity  
280 (ANOSIM). SIMPER analysis provided the average dissimilarity of their diets. The

281 prey groupings were based on Bray-Curtis mean dissimilarities. Differences of prey  
282 size distribution among species were tested with the Chi-square test. The Bray-Curtis

283 dissimilarity was also calculated for interspecific pairwise comparisons of prey size  
284 distribution. Changes in the range of the Shannon-Wiener diversity index ( $H'$ ) and

285 **PPSR** of each individual predator with increasing size were analyzed according to the  
286 methods described in Scharf et al. (2000) and Bachiller and Irigoien (2013, 2015). To

287 represent interspecific differences in dietary and isotopic compositions, non-metric

288 multi-dimensional scaling (nMDS) was carried out on the similarity matrix of the diet  
289 (IRI%) and the stable isotopic compositions ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of fishes, respectively.  
290 The differences between the isotopic niche and the dietary niche overlaps were tested  
291 with a  $\chi^2$  test and Spearman's rank order correlation. Data processing was carried out  
292 using the software R (R Core Team 2021).

293

### 294 **3. Results**

#### 295 *3.1. Prey availability*

296 Available prey were often smaller than 1.5 mm with the most abundant prey ranging  
297 in size from 0.5 to 0.8 mm (36.4%) (Fig. 2). Zooplankton was dominated by copepods  
298 (IRI% = 84.8%), especially calanoid copepods (IRI% = 72.3%) (Fig. 3). Other  
299 zooplankton groups such as Monstrilloid and Sapphirinid copepods, fish larvae,  
300 tintinnids, echinoderm and cephalopod larvae, and other microzooplankton groups  
301 were also observed in net samples and contributed to overall diversity (Shannon  
302 diversity index =  $1.00 \pm 0.25$  (mean  $\pm$  standard deviation)).

#### 303 *3.2. Biometry and stomach fullness of caught fish*

304 Body size was measured from a total of 715 fish, SCA was measured from 446  
305 individuals and SIA from 173 individuals (Table 1). Total body length (Table 2)  
306 differed significantly among species ( $H = 129.4$ ,  $P < 0.001$ ). *Cepola macrophthalma*  
307 was the longest ( $29.3 \pm 6.8$  cm), followed by *S. aurita*, *B. boops*, *S. pilchardus*, *C.*  
308 *chromis* and *E. encrasicolus*, the lowest mean total length being recorded in *S.*  
309 *sprattus* ( $11.2 \pm 1.0$  cm). The proportion of empty stomachs was lowest for *S.*  
310 *pilchardus* (2.1%) and highest for *C. chromis* (20.6%), and stomach content was  
311 about half full for most species (Table 2). The SFDs varied significantly between  
312 species ( $H = 36.64$ ,  $P < 0.001$ ), with highest values for *C. macrophthalma* and *C.*  
313 *chromis* and lowest values for *S. pilchardus* (Table 2).

314 3.3. Prey group composition

315 For each species, trophic niche breadth based on prey diversity (i.e.  $H'$ ) did not vary  
316 with fish size (Fig. S1) or between sexes (not displayed,  $P > 0.05$  for all species).

317 The average diet composition differed significantly among species (ANOSIM  $R =$   
318  $0.15$ ,  $P < 0.001$ ) (Table 3, Fig. 3).

319 *Engraulidae* and *Clupeidae* species mainly preyed on copepods ( $IRI\% > 86$ ).

320 Although small harpacticoid (*Microsetella/Macrosetella* spp. and *Euterpinidae*) and  
321 cyclopoid (*Oncaeidae* and *Corycaeidae*) copepods were not the most abundant in the  
322 environment, they were present in high proportions as prey (Fig. 3, Table S2).

323 *Engraulis encrasicolus* and *S. aurita* consumed higher proportions of calanoid  
324 copepods than *S. pilchardus* and *S. sprattus*. *Cepola macrophthalma* consumed a high  
325 proportion of decapod larvae in addition to calanoid copepods (*Acartiidae* and  
326 *Calanidae*). *Chromis chromis* and *B. boops* both consumed other prey that were not  
327 abundant in the environment during the same sampling periods. *Chromis chromis*  
328 consumed a high proportion of gastropods (pteropods), cypris larvae and ostracods,  
329 while *B. boops* consumed benthic polychaetes and cypris larvae. Both species  
330 ingested high proportions of amphipods and decapod larvae.

331 The SIMPER analysis (Table 3) showed that the  $IRI\%$  of copepods contributed the  
332 most ( $> 60\%$ ) to the dissimilarities of diet between the studied species, but the  $IRI\%$   
333 of other prey such as gastropod and decapod larvae was also high ( $> 5\%$ ).

334 Bray-Curtis dissimilarity indices on prey composition were lowest between *S.*  
335 *pilchardus* and *S. aurita* (Table 4), while the highest values were found between *S.*  
336 *sprattus* and both *C. macrophthalma* and *C. chromis*.

337 Prey diversity ( $\chi^2 = 26$ ) and evenness ( $\chi^2 = 24$ ) indices differed significantly among  
338 fish species ( $P < 0.001$  for both). *Sprattus sprattus* exhibited the highest prey diversity  
339 ( $H' = 0.95 \pm 0.08$ ) and *C. chromis* presented the highest prey evenness ( $J = 0.76 \pm$

340 0.11). *Cepola macrophthalma* showed the lowest values for both indexes ( $H' = 0.29 \pm$   
341  $0.11$ ,  $J = 0.32 \pm 0.14$ ) (Table 5). The zooplankton composition of the 80- $\mu\text{m}$  mesh size  
342 net generally showed a higher group diversity but had about the same evenness index  
343 as fish stomach content (Table 5).

#### 344 3.4. Prey size structure

345 Prey size distribution differed significantly among species ( $\chi^2 = 405.23$ ,  $P < 0.001$ ),  
346 with one or two modes of prey size between 0.1 and 2 mm (Fig. 4). *Sardina*  
347 *pilchardus* and *S. sprattus* both presented a high consumption of prey ranging  
348 between 0.5 and 1.0 mm in size, while *S. aurita*, *C. macrophthalma*, *C. chromis* and *B.*  
349 *boops* also consumed a high proportion of prey  $> 2$  mm (up to 40% for *B. boops*).

350 Average prey size and PPSR differed significantly among species ( $H = 54$  and  $H = 61$ ,  
351 respectively, with  $P < 0.001$  for both). *Boops boops* presented the highest values for  
352 average prey size ( $8.54 \pm 6.31$  mm), and *S. pilchardus* the lowest ( $0.99 \pm 0.21$  mm)  
353 (Fig. 5A). *Boops boops* also had the highest average value for PPSR, and *C.*  
354 *macrophthalma* the lowest (Fig. 5B). A significant increase of trophic niche breadth  
355 based on PPSR with increasing fish size was observed in *B. boops* (Fig. S2). For other  
356 species, no change in mean prey size or of trophic niche breadth based on PPSR and  
357 prey diversity was observed with increasing body size.

358 Prey size distribution was significantly different between *B. boops*, *S. pilchardus* and  
359 *S. sprattus* (Table 6) and the most similar between the Clupeidae ( $< 0.30$ ).

#### 360 3.5. Stable isotope composition

361 Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values and the estimated trophic level differed significantly  
362 among species ( $\delta^{13}\text{C}$ :  $H = 35.67$ ,  $P < 0.001$ ;  $\delta^{15}\text{N}$ :  $H = 61.52$ ,  $P < 0.001$ , TL:  $H =$   
363  $61.50$ ,  $P < 0.001$ ). *Sprattus sprattus* had the highest  $\delta^{13}\text{C}$  values and *B. boops* and *S.*  
364 *pilchardus* had the lowest (Table 7). *Boops boops* and *C. macrophthalma* had the  
365 highest  $\delta^{15}\text{N}$  values and estimated trophic levels, while *S. sprattus* and *E. encrasicolus*



366 presented the lowest. Spearman's correlation tests highlighted significant negative  
367 correlations between  $\delta^{13}\text{C}$  values and total body length for *S. pilchardus* (Table 7).  
368 Significant positive correlations were found between  $\delta^{15}\text{N}$  values and both estimated  
369 trophic levels and fish size for *C. chromis* and *B. boops*, while significant negative  
370 correlations were found for *E. encrasicolus*.

### 371 3.6. Dietary niche widths and diet overlaps

372 *Chromis chromis* had the highest DNW and *C. macrophthalma* the lowest (Table 8).  
373 Higher and significant dietary niche overlaps were found between *S. pilchardus*, *S.*  
374 *aurita* and *E. encrasicolus*, while overlap was also observed between *E. encrasicolus*  
375 and *C. macrophthalma*.

376 The nMDS analysis based on SCA showed no ellipse overlaps between *S. sprattus*  
377 and the other species except for *S. pilchardus*. *Sprattus sprattus* differed the most  
378 from *E. encrasicolus*, *S. aurita* and *C. macrophthalma* (Fig. 6A). *Sardina pilchardus*,  
379 *C. chromis* and *B. boops* had an intermediate position between the two groups. The  
380 nMDS analysis based on isotopic compositions displayed more extensive ellipse  
381 overlaps among all fish species, with *S. sprattus* on one side, close to *E. encrasicolus*  
382 and *S. aurita*, while the other species appeared on the other side of the biplot (Fig. 6B).  
383 With both SCA and SIA, *S. sprattus* and *C. macrophthalma* were the most distant  
384 species.

385

## 386 4. Discussion

387 This study characterized the diet of seven Bay of Marseille fish species with the  
388 complementary use of stomach content (SCA) and stable isotope (SIA) analyses, and  
389 also considered the size of prey consumed. Diet studies generally focus on  
390 composition of prey species, data on prey size tending to be rare, despite prey size being  
391 a defining factor in pelagic fish growth (Thoral et al. 2021). For planktivorous species,

392 inter-specific differences in diet and prey size depend on the gill raker density as well as  
393 the number of gill arches, whereas gape height determines the maximum size of prey  
394 ingested (Velip and Rivonker 2018). Moreover, prey energy content is generally  
395 closely linked to both species/groups composition and size (Harmelin-Vivien et al.  
396 2019; Chen et al. 2019a). We adopted this approach in the context of recently  
397 observed changes to small pelagic fish populations in the NWMS, assumed to be  
398 related to changes in the composition of zooplankton, fish diet and trophic  
399 interactions (Brosset et al. 2016; Saraux et al. 2019).

#### 400 *4.1. Prey group and prey size composition*

401 Our study shows that diets differed from ambient prey availability, suggesting  
402 differential prey selection (Karachle and Stergiou 2013; Costalago and Palomera 2014;  
403 Chen et al. 2021). Dietary differences may be related to body shape, size, jaw  
404 morphology and habitat (Karachle and Stergiou 2013; Frédérick et al. 2014). In our  
405 study, differences in prey composition and diversity, prey size structure and dietary  
406 overlaps allowed the differentiation of two main groups, which also differed in mean  
407 size, morphology and foraging habitats. The first group included the strictly pelagic  
408 Clupeidae (*S. pilchardus*, *S. aurita* and *S. sprattus*), which preyed mostly on small  
409 sized copepods. The second group contained the benthic-demersal Cephalopoda (*C.*  
410 *macrophthalma*), Pomacentridae (*C. chromis*) and Sparidae (*B. boops*), which  
411 consumed larger copepods, other zooplankton groups and varying proportions of  
412 benthic prey. The Engraulid *E. encrasicolus* was intermediate due to the wide  
413 spectrum of planktonic prey consumed.

414 *Engraulis encrasicolus*, *S. pilchardus* and *S. sprattus* consumed mainly small and  
415 medium size copepods, such as harpacticoid (*Microsetella/Macrosetella* spp.,  
416 *Euterpina acutifrons*) and cyclopoid (Oncaeidae, Corycaeidae) copepods, in  
417 accordance with previous observations from the literature (Costalago et al. 2014; Le

418 Bourg et al. 2015; Albo-Puigserver et al. 2019; Bachiller et al. 2020, 2021). *Sprattus*  
419 *sprattus*, which had the highest relative proportion of copepods in its stomach contents,  
420 fed on a higher proportion of cyclopoid copepods than the other Clupeidae species, as  
421 reported by Le Bourg et al. (2015). Bachiller et al. (2020) also observed a latitudinal  
422 gradient of diet variation in *E. encrasicolus* and *S. pilchardus* along the NWMS coast.  
423 Our results seem to confirm poorer feeding conditions previously described for  
424 northern Mediterranean populations, with smaller prey consumed compared to the  
425 southern populations which consumed high proportions of decapods, malacostracans,  
426 and euphausiids (Bachiller et al. 2020). In terms of prey size, the preferred prey size  
427 range of *E. encrasicolus*, *S. pilchardus* and *S. sprattus* was wider in the Bay of  
428 Marseille (0.4 – 0.9 mm) than in the Gulf of Lion (0.2 – 0.5 mm) (Le Bourg et al. 2015),  
429 with larger prey (1.1 – 1.5 mm) consumed in higher proportions. The larger plankton  
430 prey size in the Bay of Marseille was probably linked to the high production induced by  
431 terrestrial inputs (Frayse et al. 2014). Mean PPSR values of these three species were  
432 higher in the Bay of Marseille ( $11.50 \pm 1.94$ ,  $44.83 \pm 15.76$ , and  $11.09 \pm 3.68$ ,  
433 respectively) than in the Gulf of Lion ( $7.32 \pm 6.57$ ,  $5.20 \pm 1.86$ , and  $6.21 \pm 1.61$ ,  
434 respectively) during the summer months, possibly due to temporal variation in prey size  
435 (Chen et al. 2021). It seems important therefore that PPSR comparisons should be  
436 undertaken contemporaneously.

437 The diet of *S. aurita* was similar to that of *S. pilchardus* in the Bay of Marseille, but  
438 presented higher prey diversity and evenness. Bachiller et al. (2021) also observed  
439 more diet similarities between *S. aurita* and *S. pilchardus* than with *E. encrasicolus*.  
440 This was likely due to their similar filtering apparatus structure, with smaller gill raker  
441 spaces than in *E. encrasicolus* (Costalago and Palomera 2014). Bachiller et al. (2021)  
442 found a high proportion of salps, appendicularians, chaetognaths and polychaetes in *S.*  
443 *aurita*, but not in *S. pilchardus*. These dietary differences may suggest more

444 opportunistic feeding in *S. aurita*, as observed in the Aegean Sea (Lomiri et al. 2008).  
445 The prey size distribution of *S. aurita* observed in the Bay of Marseille was similar to  
446 that observed in the Ebro River Delta by Albo-Puigserver et al. (2019). Although *S.*  
447 *aurita* had a higher average prey size than the other Clupeidae, it presented the lowest  
448 PPSR due to its larger body size. The high consumption of *Microsetella/Macrosetella*  
449 spp. copepods by the four small sized pelagic fish (Engraulidae and Clupeidae) may be  
450 related to the high input of aggregates in the Bay of Marseille with which these  
451 copepods were associated (Chen et al. 2021 and references therein).

452 Among benthic-demersal species, *C. macrophthalma* mainly preyed on decapod larvae,  
453 calanoid (Acartiidae and Calanidae) copepods, and small proportions of gelatinous  
454 zooplankton with their associated *Phronima* spp. amphipods. *Cepola macrophthalma* is  
455 considered a benthic opportunist preying mainly on diverse zooplankton groups, but  
456 also ingesting some benthic organisms (Stergiou 1993). Similarly, *C. chromis*  
457 consumed both planktonic and benthic organisms (Mapstone and Wood 1975; Bell and  
458 Harmelin-Vivien 1983; Dulčić 2007; Pinnegar et al. 2007; Pinnegar 2018). We  
459 observed that *C. chromis* consumed high proportions of pteropods, copepods, decapod  
460 larvae, and amphipods. Pteropods are prey that contain high protein and lipid contents  
461 (Harmelin-Vivien et al. 2019), but were rare in the diet of other species in our study.  
462 The high proportion of pteropods in *C. chromis* diet may be explained by powerful jaws  
463 specialized in ram suction feeding like other phylogenetically close pomacentrid  
464 species (Frédérich et al. 2013, 2014; Chen et al. 2019b). *Boops boops* consumed a  
465 wide diversity of benthic prey in addition to zooplanktonic crustaceans, as previously  
466 observed in the Bay of Marseille (Bell and Harmelin-Vivien 1983; Cresson et al. 2014).  
467 This demersal species can be considered an opportunistic omnivore (Stergiou and  
468 Karpouzi 2002; El-Hawet et al. 2005). In the present study *B. boops* consumed mainly  
469 annelids, gelatinous zooplankton and pteropods. Despite the generally low energy

470 content of small gelatinous zooplankton (Harmelin-Vivien et al. 2019; Chen et al.  
471 2019a), this diet is reflective of its opportunistic predation behavior. *Cepola*  
472 *macrophthalma*, together with *C. chromis* and *B. boops*, but also *S. aurita*, consumed a  
473 high proportion of prey > 2 mm in size, related to both larger body, and thus a larger  
474 mouth size for *C. macrophthalma* and *S. aurita*, and to the powerful jaws for *C. chromis*  
475 (Frédérich et al. 2013, 2014; Chen et al. 2019b).

476 While Bachiller and Irigoien (2013) observed an increase in trophic niche breadth  
477 based on PPSR in *E. encrasicolus* and *S. pilchardus*, and a decrease with growth in *S.*  
478 *sprattus*, a corresponding increase with increasing fish size was observed only for *B.*  
479 *boops* in the present study, possibly reflecting the poorer feeding conditions in the Bay  
480 of Marseille compared to those of the Atlantic Sea.

#### 481 4.2. Stable isotope composition of planktivorous fish species

482 Stable isotope analysis revealed that strictly pelagic planktivorous fish (i.e. *E.*  
483 *encrasicolus*, *S. pilchardus*, *S. aurita*, *S. sprattus*) demonstrated generally higher  
484 mean  $\delta^{13}\text{C}$  and lower mean  $\delta^{15}\text{N}$  values than benthic-demersal species (*C.*  
485 *macrophthalma*, *B. boops*), excluding *C. chromis*. This is consistent with previous  
486 observations in the Gulf of Lion (Le Bourg et al. 2015) and the Ebro River Delta  
487 (Albo-Puigserver et al. 2019). Similar mean  $\delta^{15}\text{N}$  values between *E. encrasicolus* and  
488 *S. sprattus*, and between *S. pilchardus* and *S. aurita* respectively, indicate close trophic  
489 level consistency between these species (Hussey et al. 2014). However,  $\delta^{13}\text{C}$  values  
490 differed significantly between species pairs, with *S. sprattus* presenting higher  $\delta^{13}\text{C}$   
491 values than *E. encrasicolus*, and *S. aurita* presenting higher values than *S. pilchardus*,  
492 allowing some isotopic segregation of these four species in spite of high isotopic  
493 overlaps. The values reported were similar to those observed for these species in the  
494 Gulf of Lion in 2010-2014, but differed from those recorded in 2004-2005 (Brosset et  
495 al. 2016). This may be linked to changes in zooplankton community structure and/or in

496 the organic matter composition at the base of the pelagic food webs. *Sardina pilchardus*  
497 also presented higher relative  $\delta^{15}\text{N}$  values than *E. encrasicolus* and *S. aurita* in our  
498 studies, corresponding to the observations in the nearby Western Mediterranean Sea. In  
499 our study, this observation can be related to the higher proportion of eggs in the diet of  
500 *S. pilchardus*, as isotopic compositions of fish eggs are generally similar to those of  
501 adult fish (Chen 2019). The higher  $\delta^{15}\text{N}$  values and trophic levels of *B. boops* and *C.*  
502 *macrophthalma* may be related to their consumption of crustacean larvae, chaetognaths  
503 and benthic organisms. The higher dispersion of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values observed in these  
504 two benthic-demersal species may result from a higher diversity of sources of organic  
505 matter at the base of the pelagic and the benthic food webs in the Bay of Marseille  
506 (Cresson et al. 2012).

507 While no relationship was detected between fish size and diet composition, or between  
508 fish size and trophic niche breadth, changes in fish isotopic compositions occurred with  
509 size for some species. We observed a decrease of  $\delta^{13}\text{C}$  values with growth in *S.*  
510 *pilchardus* and of  $\delta^{15}\text{N}$  values in *E. encrasicolus*, while  $\delta^{15}\text{N}$  values of *C. chromis* and  
511 *B. boops* increased. These alterations may be linked to changes in diet or foraging  
512 zones, or to zooplankton community changes related to changes of primary producers,  
513 and thus of carbon food sources, as observed in the Gulf of Lion (Costalago et al.  
514 2012). The increase of  $\delta^{15}\text{N}$  values and of trophic niche breadth (i.e. PPSR) with growth  
515 of *B. boops* may be related to the higher ability of this species to capture larger prey  
516 when growing. In contrast to our observations, Bachiller et al. (2021) showed  
517 increasing  $\delta^{13}\text{C}$  values with size for *E. encrasicolus* and *S. aurita* and decreasing  $\delta^{15}\text{N}$   
518 values with size for *S. pilchardus*. This may be related to differences in foraging  
519 patterns with growth, as larger prey and better body condition were observed in the fish  
520 populations from the southern areas of the Mediterranean Sea (Bachiller et al. 2020).

521 4.3. Differences in trophic interactions revealed by SCA and SIA

522 This study highlighted differences and complementarity between SCA and SIA, as the  
523 two methods demonstrated contrasting results. We found a higher degree of dietary  
524 overlap with the SIA than with the SCA between *S. pilchardus*, *S. aurita* and *S. sprattus*.  
525 However, even if the different species ingested different zooplankton groups, these  
526 prey may have similar isotopic composition due to similar POM sources at the base of  
527 the food web and similar trophic levels (Bănaru et al. 2014). Le Bourg et al. (2015)  
528 demonstrated that in the last decade *S. pilchardus* and *E. encrasicolus* had similar diets  
529 to *S. sprattus* in the Gulf of Lion. However, *E. encrasicolus* appeared to be less in  
530 competition with the Clupeidae species in the Bay of Marseille. The results of SCA also  
531 suggested less competition among benthic-demersal fish, indicating specialization on  
532 different prey groups and sizes, despite the high similarities of their isotopic  
533 compositions. In addition, we found some species (i.e. *S. aurita*, *C. macrophthalma*, *C.*  
534 *chromis* and *B. boops*) to be highly opportunist, in agreement with the observations of  
535 other authors (El-Maremie and El-Mor 2015; Pinnegar 2018; Albo-Puigserver et al.  
536 2019; Bachiller et al. 2020, 2021). By contrast, *E. encrasicolus*, *S. pilchardus* and *S.*  
537 *sprattus* fed mainly on copepods and seemed to be less opportunist feeders. However,  
538 with sufficient food availability, dietary overlap does not necessarily imply  
539 competition for food resources (Coe et al. 2001). Our data thus tend to show a higher  
540 potential for competition between the Engraulidae and Clupeidae species than  
541 between the other species studied. Data on the quality and quantity of zooplankton  
542 available as prey remain essential to confirm or disprove the hypothesis on the  
543 limitation of food resources.

544 4.4. Methodological issues and improvements

545 [The main difficulty for multi-species fish diet studies](#) is in simultaneously obtaining  
546 both plankton prey and fish samples. Here, monthly fish and zooplankton sampling

547 was carried out several days and a few kilometers apart. However, as some of our  
548 target species consumed high proportions of large prey (> 2 mm), certain prey  
549 categories that the fish were feeding on locally may have been missed. Combining  
550 multiple nets to capture a wider range of prey size and categories would allow a more  
551 precise comparison of diet with available zooplankton (Costalago and Palomera 2014;  
552 Albo-Puigserver et al. 2019; Bachiller et al. 2020).

553 It was not possible to collect monthly data for all our study species, as not all belong  
554 to targeted fisheries, necessitating time-aggregation of data. For example, a large  
555 sample of *S. pilchardus* was compared to small samples (< 30) of *S. sprattus*, *C.*  
556 *macrophthalmia*, *C. chromis*, and *B. boops*. Planktivorous species diets may also vary  
557 monthly/seasonally (Chen et al. 2021) along with the isotopic compositions of the  
558 primary producers (i.e. baseline), as previously shown in the Bay of Marseille by  
559 Bănaru et al. (2014). For improved fisheries management, better temporal sampling  
560 would better determine whether the observed differences of fish isotopic compositions  
561 are truly related to dietary differences or to changes in the isotopic compositions of  
562 the primary food sources. Furthermore, global climate change, and associated changes  
563 in water convection, and urban and river inputs, could drastically alter the nutrient  
564 inputs at the base of the food web, thereby altering the availability of different  
565 plankton prey groups.

566 Nevertheless, our extensive survey provided the best possible results. Most previous  
567 studies in the Mediterranean Sea have focused on the feeding of *E. encrasicolus*, *S.*  
568 *pilchardus* and *S. sprattus* with samples obtained from oceanographic surveys in  
569 targeted areas and periods, and have faced similar difficulties in relating plankton  
570 availability to fish feeding (Costalago et al. 2012, 2014; Le Bourg et al. 2015;  
571 Bachiller et al. 2020). In addition, as the commercial value of species tends to define  
572 research priorities, more scientific knowledge is available for *E. encrasicolus* and *S.*



573 *pilchardus*, but remains more limited for *S. aurita*, *S. sprattus* (Palomera et al. 2007)  
574 and the other species in this study.

575 Finally, better harmonization between fish and zooplankton sampling might include  
576 the simultaneous use of acoustic systems to detect fish species at given feeding depths  
577 (prior to capture) and of multiple net stratified-horizontal tows (such as the multiple  
578 plankton sampler Hydro-Bios) to target zooplankton at the same depths. In addition,  
579 as different prey types have different digestion rates, the rapid conservation of fish  
580 samples immediately following capture could also ensure better preservation of  
581 stomach contents. The use of DNA barcoding can also improve the prey  
582 identification, especially gelatinous prey (Lamb et al. 2019; Bachiller et al. 2021).

583

## 584 **5. Conclusion**

585 Similarities in the dietary and isotopic composition revealed by this study suggest  
586 higher potential trophic competition among strictly pelagic species under conditions  
587 of scarce food resources, while little competition was evident among benthic-demersal  
588 species.

589 Our results highlight that inter-specific similarities in isotopic composition does not  
590 necessarily imply similar diets. While SCA differed significantly between species,  
591 similar inter-specific isotopic compositions may result from similar POM sources at the  
592 base of the food web. Long-term monitoring of zooplankton communities and  
593 planktivorous fish diets is necessary to improve our understanding of the variability of  
594 species interactions in the context of climate change and to underpin ecosystem-based  
595 studies for fisheries management in the NWMS.

596

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619

## 620 **Declarations**

## 621 **Conflict of interest**

622 The authors declare that they have no conflicts of interest.

## 623 **Ethical approval**

624 All applicable national and/or institutional guidelines for sampling, care, and

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626

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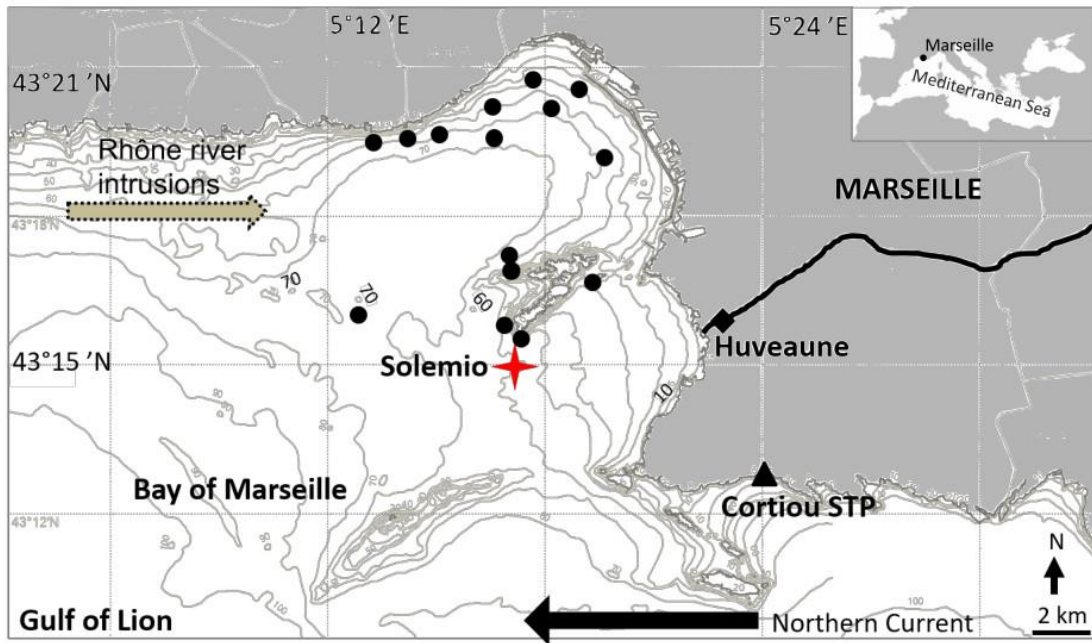
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848 Fig. 1. Planktivorous fish (black dots) and zooplankton sampling sites (Solemio, red star) in the Bay of  
849 Marseille, NW Mediterranean Sea. Huveaune river (bold line), Cortiou sewage treatment plant (black  
850 triangle).

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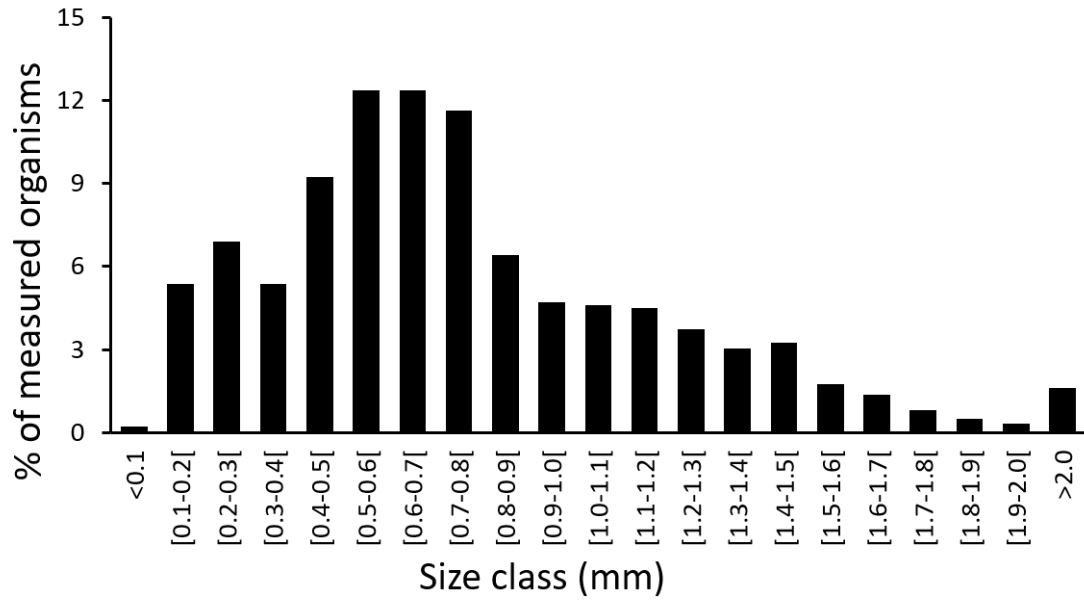


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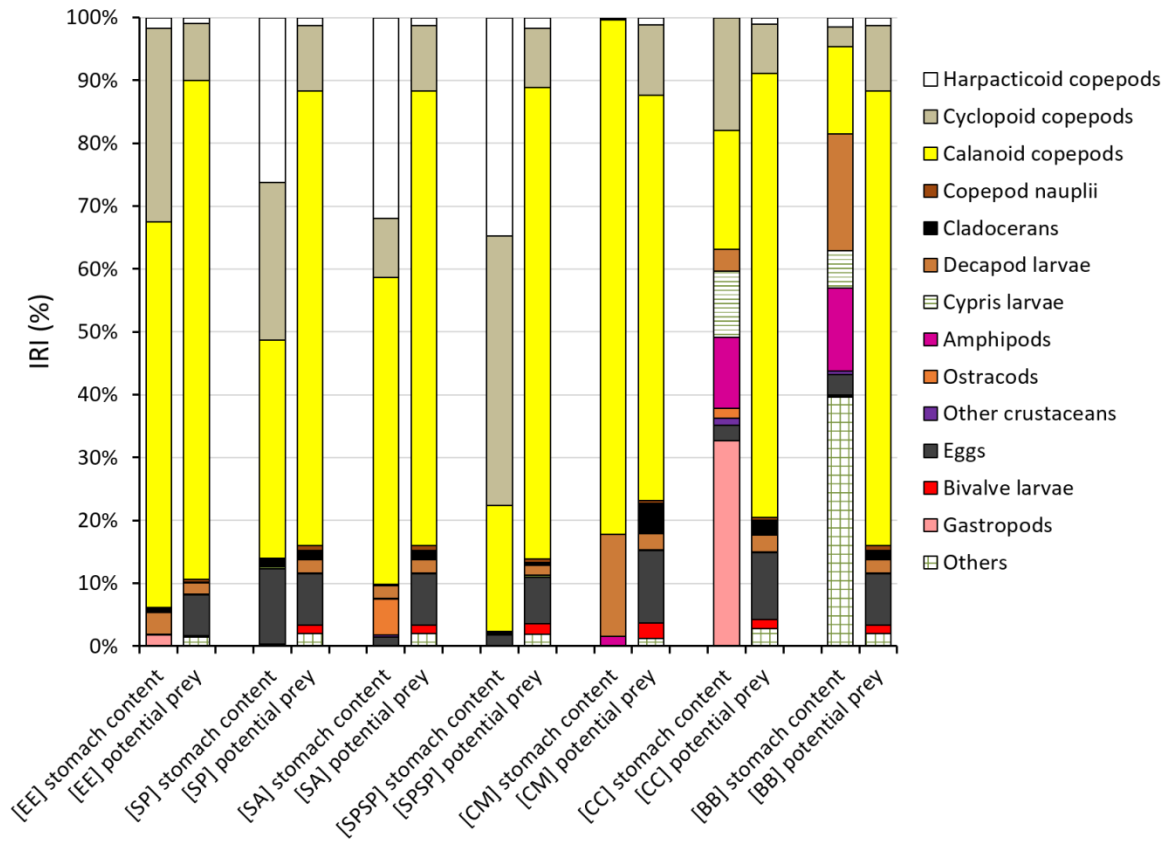
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855 Fig. 2. Size spectrum (0.1 mm size classes) of zooplankton sampled in the Bay of Marseille between  
856 March and September 2017 with an 80- $\mu$ m mesh size net. Zooplankton (N = 2394) from 14 different  
857 samples were measured.



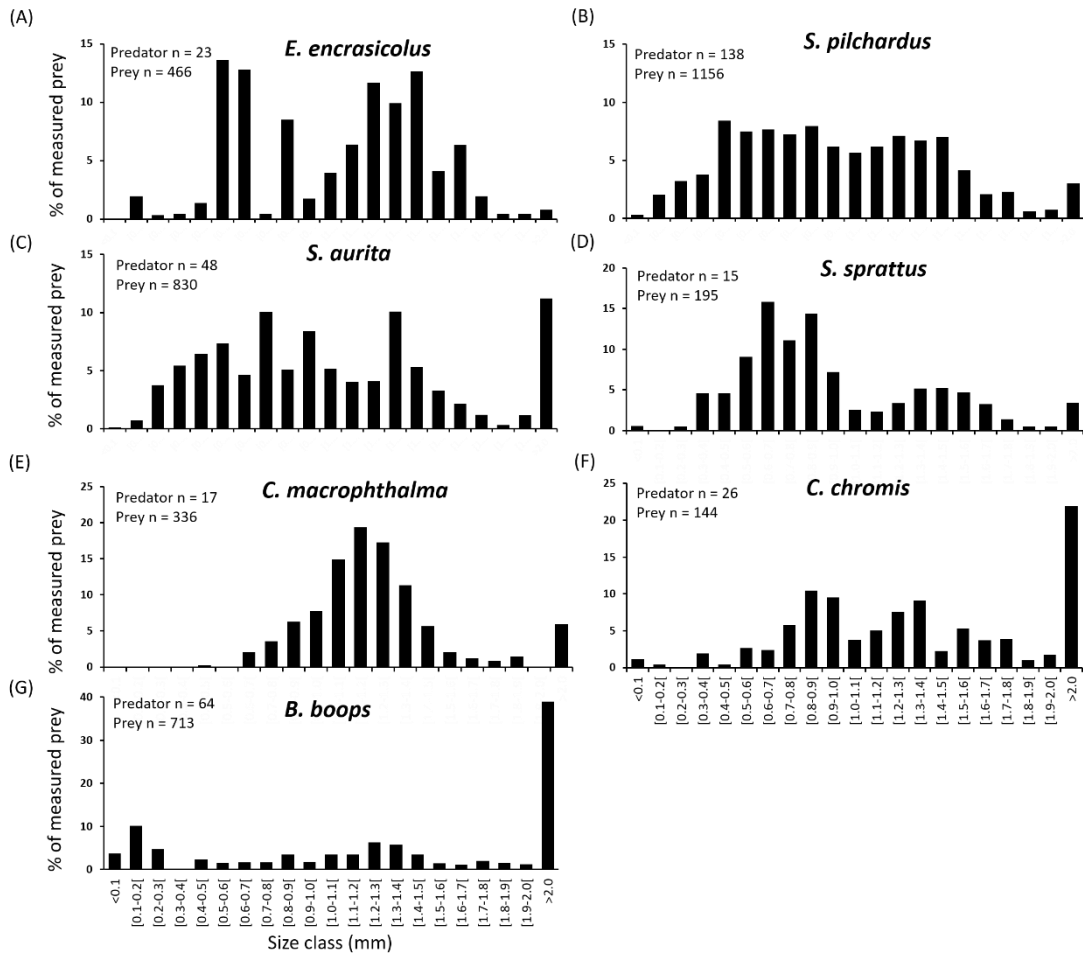
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Fig. 3. Average index of relative importance (IRI%) of zooplankton in the stomach contents of each fish species compared to the composition of zooplankton sampled with the 80- $\mu$ m mesh size net (potential prey) from March to September 2017 in the Bay of Marseille. For abbreviations of species: [EE] = *E. encrasicolus*, [SP] = *S. pilchardus*, [SA] = *S. aurita*, [SPSP] = *S. sprattus*, [CM] = *C. macrophthalma*, [CC] = *C. chromis*, [BB] = *B. boops*.



1 Fig. 4. Proportion of consumed prey by 0.1 mm size classes for the studied species (A – G) in the Bay  
 2 of Marseille (March to September 2017). “Predator n” is the number of stomachs of fish analyzed.  
 3 “Prey n” is the number of measured prey items in their stomach content.

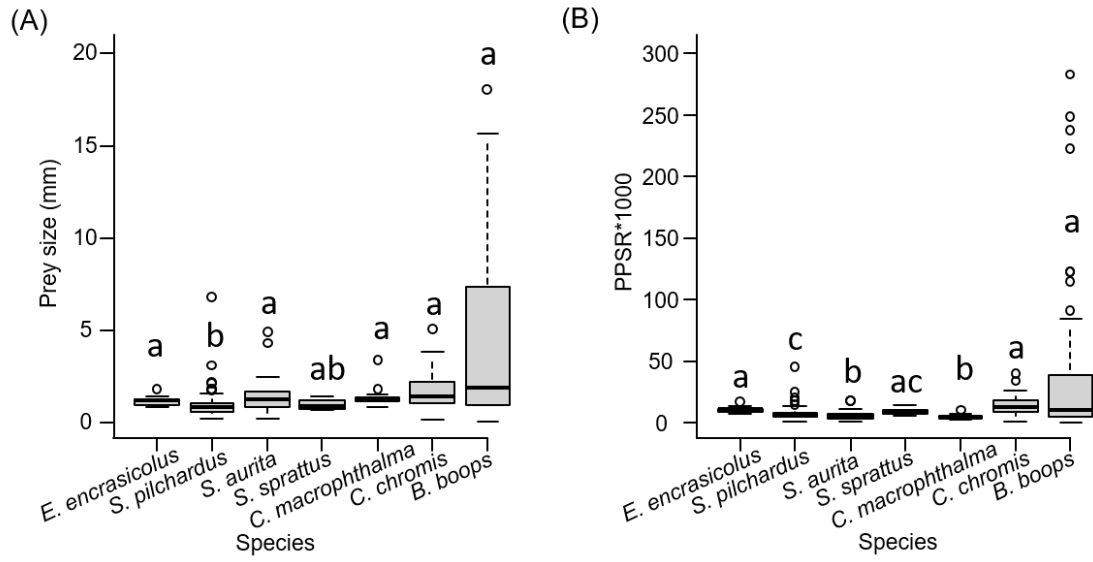
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6 Fig. 5. (A) Average prey size ( $\pm$  standard deviation) and (B) average predator-prey size  
 7 ratio (PPSR, values multiplied by 1000) by species in the Bay of Marseille (March to  
 8 September 2017). Superscript letters represent post-hoc groups and species with  
 9 same letters are not significantly different ( $P > 0.05$ ).

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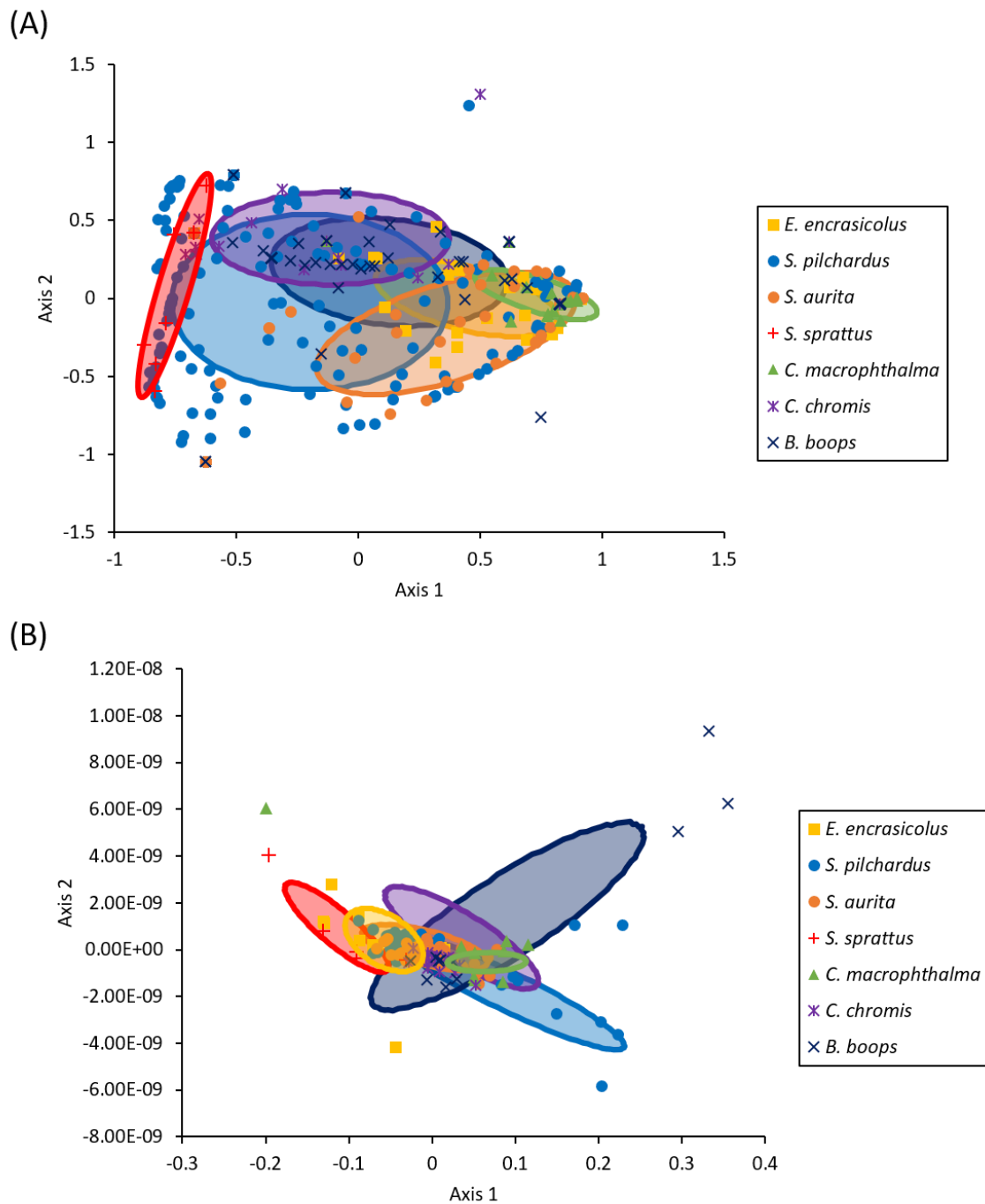


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14 Fig. 6. Non-metric multi-dimensional scaling (nMDS) plot of the diet composition similarities (A)  
15 based on stomach content analysis (IRI%, Bray-Curtis) and (B) based on isotope compositions ( $\delta^{13}\text{C}$   
16 and  $\delta^{15}\text{N}$  values, in ‰, Euclidean) of the studied planktivorous teleost species in the Bay of Marseille  
17 (March to September 2017).



20 **Table 1.** Number of samples of planktivorous fish for total length measurements (TL), stomach content  
 21 analyses (SCA) and stable isotope analyses (SIA) by month.

Month	<i>E. encrasicolus</i>			<i>S. pilchardus</i>			<i>S. aurita</i>			<i>S. sprattus</i>		
	TL	SCA	SIA	TL	SCA	SIA	TL	SCA	SIA	TL	SCA	SIA
Mar.	4	4	4	97	44	11	7	10	5	0	0	0
Apr.	0	0	0	64	44	8	6	10	4	0	0	0
May	4	4	4	45	44	6	6	7	5	7	7	4
Jun.	0	0	0	28	28	8	26	8	9	0	0	0
Jul.	31	15	9	21	21	7	36	12	10	0	0	0
Aug.	0	0	0	35	20	8	30	17	8	0	0	0
Sep.	0	0	4	44	23	9	30	13	9	8	8	4
Total	39	23	21	334	224	57	141	77	50	15	15	8

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24 **Table 1 (continued).** Number of samples of planktivorous fish for total length measurements (TL),  
 25 stomach content analyses (SCA) and stable isotope analyses (SIA) by month.

Month	<i>C. macrophthalma</i>			<i>C. chromis</i>			<i>B. boops</i>		
	TL	SCA	SIA	TL	SCA	SIA	TL	SCA	SIA
Mar.	0	0	0	0	0	0	33	11	11
Apr.	0	0	0	0	0	0	6	2	0
May	0	0	0	3	3	3	23	9	0
Jun.	17	17	9	18	18	9	16	6	0
Jul.	0	0	0	4	4	4	13	8	0
Aug.	0	0	0	1	1	1	27	22	0
Sep.	0	0	0	0	0	0	25	6	0
Total	17	17	9	26	26	17	143	64	11

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28 **Table 2.** Details of biometric measurements (n), minimum (min), maximum (max) and mean ( $\pm$  SD, standard deviation) of total length (cm), proportion of empty stomachs,  
 29 mean degree of stomach repletion (SRD) (0 = empty, 5 = full) ( $\pm$  SD) and stomach filling degree (SFD) ( $\pm$  SD) of the studied planktivorous fish species. Superscript letters  
 30 represent post-hoc groups after Kruskal-Wallis tests comparing the total body length ( $\chi^2 = 1059.90$ ,  $P = 0.002$ ). Species with the same letters have similar sizes ( $P > 0.05$ ).

31

Species	Family	n	Total length (cm)				Empty stomachs (%)	SRD	SFD
			min	max	mean	SD			
<i>E. encrasicolus</i>	Engraulidae	39	10.5	12.7	11.6 <sup>b</sup>	0.6	6.3	2.1 $\pm$ 1.2	21.1 $\pm$ 10.0 <sup>bc</sup>
<i>S. pilchardus</i>	Clupeidae	334	10.0	18.1	13.0 <sup>d</sup>	0.6	2.1	2.3 $\pm$ 1.3	13.0 $\pm$ 0.8 <sup>c</sup>
<i>S. aurita</i>	Clupeidae	141	15.5	27.5	23.4 <sup>c</sup>	1.3	19.7	2.4 $\pm$ 1.3	30.2 $\pm$ 26.4 <sup>ab</sup>
<i>S. sprattus</i>	Clupeidae	15	10.1	12.5	11.2 <sup>b</sup>	1.0	15.1	1.8 $\pm$ 1.1	50.4 $\pm$ 3.9 <sup>a</sup>
<i>C. macrophthalma</i>	Cepolidae	17	21.2	43.9	29.3 <sup>c</sup>	6.8	18.6	3.0 $\pm$ 1.3	68.9 $\pm$ 17.5 <sup>a</sup>
<i>C. chromis</i>	Pomacentridae	26	9.3	13.8	11.7 <sup>b</sup>	0.6	20.6	2.1 $\pm$ 1.1	68.6 $\pm$ 38.0 <sup>a</sup>
<i>B. boops</i>	Sparidae	143	15.1	35.0	19.9 <sup>a</sup>	1.8	13.6	2.2 $\pm$ 0.9	22.6 $\pm$ 6.9 <sup>bc</sup>

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34

35 **Table 3.** Results of SIMPER analysis of prey groups that contributed to the dissimilarities (based on Bray-Curtis distances) of the diet of the studied planktivorous teleost  
 36 species in the Bay of Marseille. Contrib. = Contribution, Cumulative % = cumulative contribution.

37

Prey groups	Average dissimilarity	Contrib. %	Cumulative %	<i>E.</i> <i>encrasicolus</i>	<i>S.</i> <i>pilchardus</i>	<i>S.</i> <i>aurita</i>	<i>S.</i> <i>sprattus</i>	<i>C.</i> <i>macrophthalmalma</i>	<i>C.</i> <i>chromis</i>	<i>B.</i> <i>boops</i>
Calanoid copepods	17.64	28.25	28.25	61.40	34.70	48.80	0.00	81.80	18.90	13.90
Cyclopoid copepods	12.05	19.30	47.55	30.80	25.10	9.36	60.70	0.10	17.80	3.09
Harpacticoid copepods	8.67	13.89	61.44	1.74	26.20	31.90	31.20	0.24	0.10	1.54
Others	5.69	9.12	70.56	0.00	0.33	0.00	0.00	0.00	0.00	39.60
Gastropods	4.84	7.75	78.31	1.74	0.00	0.01	0.00	0.00	32.70	0.19
Decapod larvae	4.27	6.83	85.14	3.44	0.08	2.01	0.00	16.20	3.49	18.60
Amphipods	3.03	4.86	90.00	0.00	0.02	0.09	0.00	1.60	11.30	13.10
Cypris larvae	2.08	3.34	93.33	0.01	0.33	0.00	0.00	0.00	10.50	5.97
Teleost eggs	2.08	3.32	96.66	0.03	12.00	1.46	2.66	0.00	2.45	3.24
Ostracods	0.97	1.55	98.21	0.00	0.00	5.71	0.00	0.00	1.60	0.03
Other crustaceans	0.65	1.04	99.25	0.00	0.01	0.30	3.59	0.00	1.16	0.55
Cladocerans	0.41	0.66	99.90	0.78	1.12	0.23	1.85	0.00	0.00	0.00
Bivalve larvae	0.03	0.05	99.96	0.10	0.00	0.01	0.00	0.00	0.00	0.17
Copepod nauplii	0.03	0.04	100.00	0.00	0.14	0.06	0.00	0.00	0.00	0.00

38

39

40 **Table 4.** Bray-Curtis' dissimilarity indices for the pairwise comparisons of the composition of stomach  
 41 content between the studied planktivorous fish species. The most significant (> 0.6) values of the index  
 42 are in bold.

43

Species	<i>E.</i> <i>encrasicolus</i>	<i>S.</i> <i>pilchardus</i>	<i>S.</i> <i>aurita</i>	<i>S.</i> <i>sprattus</i>	<i>C.</i> <i>macrophthalma</i>	<i>C.</i> <i>chromis</i>
<i>S. pilchardus</i>	<b>0.61</b>					
<i>S. aurita</i>	0.59	0.28				
<i>S. sprattus</i>	0.50	0.42	0.37			
<i>C. macrophthalma</i>	<b>0.76</b>	<b>0.78</b>	<b>0.77</b>	<b>0.83</b>		
<i>C. chromis</i>	<b>0.68</b>	<b>0.79</b>	<b>0.76</b>	<b>0.83</b>	0.54	
<i>B. boops</i>	<b>0.72</b>	<b>0.67</b>	<b>0.62</b>	<b>0.74</b>	<b>0.63</b>	<b>0.61</b>

44

45 **Table 5.** Shannon's diversity (H') and Pielou's evenness index (J) calculated according to %IRI of the  
 46 diet of the studied planktivorous fish species and for the zooplankton sampled with the 80 µm mesh  
 47 size net in the Bay of Marseille (March to September 2017). Superscript letters represent post-hoc  
 48 groups after Kruskal-Wallis tests. Values with the same post-hoc letters are not significantly different  
 49 (P > 0.05).

Species	H'	H'	J	J
	Stomach content	Zooplankton	Stomach content	Zooplankton
<i>E. encrasicolus</i>	0.69 ± 0.05 <sup>bc</sup>	0.85 ± 0.32	0.61 ± 0.15 <sup>ab</sup>	0.35 ± 0.12
<i>S. pilchardus</i>	0.61 ± 0.08 <sup>bc</sup>	1.00 ± 0.25	0.63 ± 0.11 <sup>bc</sup>	0.41 ± 0.10
<i>S. aurita</i>	0.69 ± 0.32 <sup>bc</sup>	1.00 ± 0.27	0.61 ± 0.22 <sup>ab</sup>	0.41 ± 0.11
<i>S. sprattus</i>	<b>0.95 ± 0.08<sup>c</sup></b>	1.83 ± 0.24	0.67 ± 0.07 <sup>abc</sup>	0.60 ± 0.07
<i>C. macrophthalma</i>	<b>0.29 ± 0.11<sup>a</sup></b>	1.25 ± 0.08	<b>0.32 ± 0.14<sup>a</sup></b>	0.49 ± 0.05
<i>C. chromis</i>	0.71 ± 0.33 <sup>c</sup>	1.08 ± 0.26	<b>0.76 ± 0.11<sup>c</sup></b>	0.44 ± 0.10
<i>B. boops</i>	0.47 ± 0.29 <sup>ab</sup>	1.00 ± 0.25	0.48 ± 0.21 <sup>ab</sup>	0.41 ± 0.10

50

51 **Table 6.** Bray-Curtis' dissimilarity indices for the pairwise comparisons of the prey size distribution  
 52 between the studied planktivorous fish species. The highest significant (> 0.6) values of the index are in  
 53 bold.

54

Species	<i>E.</i> <i>encrasicolus</i>	<i>S.</i> <i>pilchardus</i>	<i>S.</i> <i>aurita</i>	<i>S.</i> <i>sprattus</i>	<i>C.</i> <i>macrophthalma</i>	<i>C.</i> <i>chromis</i>
<i>S. pilchardus</i>	0.49					
<i>S. aurita</i>	0.34	0.25				
<i>S. sprattus</i>	0.44	0.20	0.26			
<i>C. macrophthalma</i>	0.44	0.53	0.35	0.53		
<i>C. chromis</i>	0.48	0.39	0.27	0.37	0.31	
<i>B. boops</i>	<b>0.63</b>	<b>0.61</b>	0.48	<b>0.62</b>	0.54	0.39

55

56 **Table 7.** Mean ( $\pm$  standard deviation)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values and trophic levels (TL) of the planktivorous fish species  
 57 in the Bay of Marseille. Spearman's rho and associated P-value testing the rank correlation between the total body  
 58 length and  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and TL are indicated. n = sample size. Superscript letters represent post-hoc groups after  
 59 Kruskal-Wallis test comparing the mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values and the TLs. Values with the same post-hoc letters are  
 60 not significantly different ( $P > 0.05$ ). Significant rho correlation values are in bold.

61

Species	n	$\delta^{13}\text{C}$ (‰)	rho	P	$\delta^{15}\text{N}$ (‰)	rho	P	TL	rho	P
<i>E. encrasicolus</i>	17	$-19.8 \pm 0.1^{ab}$	-0.12	0.639	$7.2 \pm 0.6^c$	<b>-0.66</b>	<b>0.004</b>	$2.9 \pm 0.2^c$	<b>-0.66</b>	<b>0.004</b>
<i>S. pilchardus</i>	60	$-20.0 \pm 0.3^a$	<b>-0.45</b>	<b>0.001</b>	$8.3 \pm 0.4^{bd}$	0.04	0.755	$3.2 \pm 0.1^{bd}$	0.04	0.755
<i>S. aurita</i>	50	$-19.6 \pm 0.2^{bc}$	-0.08	0.595	$8.0 \pm 0.3^d$	0.09	0.521	$3.1 \pm 0.1^d$	0.09	0.521
<i>S. sprattus</i>	5	$-19.5 \pm 0.6^c$	0.00	1.000	$6.9 \pm 1.2^{cd}$	0.00	1.000	$2.8 \pm 0.3^{cd}$	0.00	1.000
<i>C. macrophthalma</i>	9	$-21.1 \pm 2.5^{bc}$	0.37	0.169	$9.3 \pm 0.4^a$	0.33	0.211	$3.5 \pm 0.1^a$	0.33	0.211
<i>C. chromis</i>	17	$-19.7 \pm 0.1^{bc}$	0.06	0.815	$8.3 \pm 0.2^{ab}$	<b>0.49</b>	<b>0.044</b>	$3.2 \pm 0.1^{ab}$	<b>0.49</b>	<b>0.044</b>
<i>B. boops</i>	11	$-20.2 \pm 0.4^a$	-0.30	0.370	$10.6 \pm 3.8^a$	<b>0.85</b>	<b>0.001</b>	$3.9 \pm 1.1^a$	<b>0.85</b>	<b>0.001</b>

62

63 **Table 8.** Dietary trophic niche width (DNW) based on stomach content analysis of the studied planktivorous fish  
 64 species and pairwise comparisons of dietary niche overlap on the upper diagonal. The highest dietary niche width  
 65 values and the high niche overlaps ( $> 0.60$ ) are in bold.

66

Species	DNW	<i>S. pilchardus</i>	<i>S. aurita</i>	<i>S. sprattus</i>	<i>C. macrophthalma</i>	<i>C. chromis</i>	<i>B. boops</i>
<i>E. encrasicolus</i>	2.3	<b>0.62</b>	<b>0.62</b>	0.33	<b>0.65</b>	0.42	0.22
<i>S. pilchardus</i>	3.6		<b>0.72</b>	0.55	0.35	0.40	0.23
<i>S. aurita</i>	3.2			0.43	0.51	0.34	0.22
<i>S. sprattus</i>	2.6				0.00	0.22	0.08
<i>C. macrophthalma</i>	2.2					0.24	0.32
<i>C. chromis</i>	<b>5.4</b>						0.41
<i>B. boops</i>	4.1						

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68

69 **Table S1.** Regression equations of dry weight (DW) against total length (TL) used for zooplankters found in the  
 70 field and/or in *S. pilchardus* stomach content during this study.

71

Zooplankton group		DW ( $\mu\text{g}$ ) -TL ( $\mu\text{m}$ )	Reference
<b>Crustaceans</b>			
<b>Copepods</b>			
<b>Calanoids</b>			
	<i>Pleuromamma</i>	Log DW = 2.285 log TL - 5.965	Mauchline, 1998
	<i>Calanus</i>	Log DW = 2.790 log TL - 7.370	Mauchline, 1998
	Centropagidae	Log DW = 2.243 log TL - 5.568	Mauchline, 1998
	Candaciidae	DW = 106.2	Pitois and Fox, 2006
	Temoridae	Log DW = 2.179 log TL - 5.567	Mauchline, 1998
	Acartidae	Log DW = 3.208 log TL - 7.644	Mauchline, 1998
	Lucicutidae	DW = 16.9	Delpy, 2013
	<i>Isias</i>	Log DW = 2.33 log TL - 3.034	Dumont et al., 1975
	Clauso/Paracalanidae	Log DW = 2.738 log TL - 6.934	Mauchline, 1998
<b>Cyclopoids</b>			
	Oncaeidae	DW = 1.34	Borme et al. 2009
	Corycaeidae	DW = 62	Pitois and Fox, 2006
	Oithonidae	DW = 2.2	Pitois and Fox, 2006
<b>Harpacticoids</b>			
	<i>Microsetella/Macrosetella</i>	Log DW = 2.648 Log TL - 17.937	Satapoomin, 1999
	Euterpinidae	Log DW = 2.857TL - 7.857	Ara, 2001
	<i>Distiocolus</i>	Log DW = 4.400TL + 0.176	Dumont et al., 1975
	<i>Clytemnestra</i>	DW = 0.3	Delpy, 2013
<b>Cladocerans</b>	<i>Evadne</i>	Log DW = 0.033TL - 7.785	van der Lingen 2002
	<i>Podon</i>	DW = 1.6	Fonda Umani et al. 1979
<b>Ostracods</b>	Ostracods	DW = 6.036	Borme et al. 2009
<b>Amphipods</b>	<i>Phronima</i>	DW = 40; DW = 770	Le Bourg et al. 2015
	Other amphipods	DW = 40	Le Bourg et al. 2015
<b>Larvae</b>			
Crustaceans	Copepod nauplii	Log DW = 2.848 log TL - 7.265	Borme et al. 2009
	Cirriped nauplii	DW = 1.1	Borme et al. 2009
	Cirriped cypris	DW = 5.4	Hopkins, 1966
	Decapods Zoea	DW = 27.798	Borme et al. 2009
	Euphausiids	Log DW = 2.8 log TL + 0.456	Lindley et al., 1999
	Isopods	Log DW = 4.51 log TL - 11.64	Hopkins 1966
	<b>Mollusks</b>	Bivalve	DW = 3.758
	Pteropods	DW = 0.6	Borme et al. 2009
<b>Siphonophores</b>		DW = 5.0	Hopkins 1966
<b>Ophiuroids</b>		Log DW = 2.22 log TL - 2.24	Robinson et al. 2010
<b>Polychaetes</b>		Log DW = 1.92 log TL + 0.17	Galasso et al. 2018
<b>Chaetognaths</b>	<i>Sagitta</i> spp.	Log DW = 1.875- 1.442 log TL	Vergara-Soto et al. 2010
<b>Teleost eggs</b>	Anchovy eggs	DW = 30.1	Borme et al. 2009

73

74 **Table S2-1.** Mean stomach content composition of the studied planktivorous fish species in the Bay of Marseille from March to September 2017. O% =  
75 percentage of prey occurrence, N% = percentage of prey numerical abundance, W% = percentage of prey weight. IRI% = percentage of relative importance  
76 index. The highest percentages by species are in bold.

Prey category	<i>E. encrasicolus</i>				<i>S. pilchardus</i>				<i>S. aurita</i>				<i>S. sprattus</i>			
	O%	N%	W%	IRI%	O%	N%	W%	IRI%	O%	N%	W%	IRI%	O%	N%	W%	IRI%
Harpacticoid copepods	0.3	3.0	3.0	1.7	<b>0.6</b>	26.2	23.4	26.2	<b>0.7</b>	32.3	31.2	31.9	0.5	30.3	26.4	34.7
Cyclopoid copepods	0.8	28.2	29.4	30.8	<b>0.6</b>	22.8	24.1	25.1	0.3	10.4	10.5	9.4	<b>1.0</b>	15.8	19.1	<b>42.9</b>
Calanoid copepods	<b>0.9</b>	<b>57.7</b>	<b>56.5</b>	<b>61.4</b>	<b>0.6</b>	<b>32.5</b>	<b>33.4</b>	<b>34.7</b>	<b>0.7</b>	<b>42.7</b>	<b>43.6</b>	<b>48.8</b>	0.2	<b>49.1</b>	<b>49.3</b>	20.1
Copepod nauplii	0.0	0.0	0.0	0.0	0.0	0.9	1.0	0.1	0.0	0.3	0.3	0.1	0.0	0.0	0.0	0.0
Cladocerans	0.2	2.1	2.1	0.8	0.1	2.6	2.6	1.1	0.1	0.6	0.6	0.2	0.1	1.0	1.1	0.3
Decapod larvae	0.4	4.6	4.6	3.4	0.0	0.5	0.5	0.1	0.3	3.2	3.3	2.0	0.0	0.0	0.0	0.0
Cypris larvae	0.0	0.1	0.1	0.0	0.0	1.4	1.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphipods	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.5	0.6	0.1	0.0	0.0	0.0	0.0
Ostracods	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	5.7	5.7	5.7	0.0	0.0	0.0	0.0
Other crustaceans	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.1	0.5	0.5	0.3	0.1	1.0	1.1	0.3
Eggs	0.0	0.4	0.4	0.0	0.3	11.7	12.1	12.0	0.1	3.6	3.6	1.5	0.4	1.5	1.7	1.8
Bivalve larvae	0.1	0.4	0.4	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastropods	0.3	3.4	3.4	1.7	0.0	0.1	0.1	0.0	0.0	0.1	0.1	0.0	0.0	1.2	1.2	0.0
Others	0.0	0.0	0.0	0.0	0.1	1.0	1.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

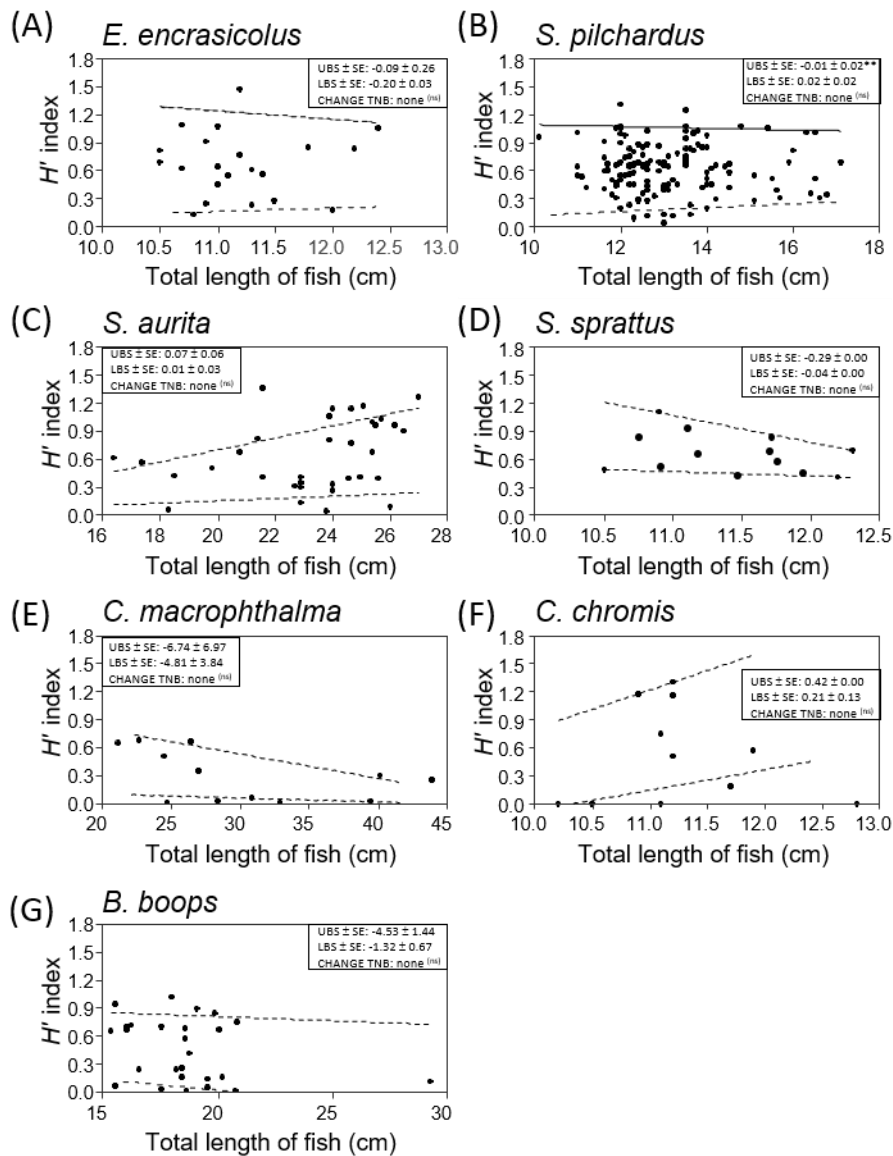
77 **Table S2-2.** Mean stomach content composition of the studied planktivorous fish species in the Bay of Marseille  
78 from March to September 2017. O% = percentage of prey occurrence, N% = percentage of prey numerical  
79 abundance, W% = percentage of prey weight. IRI% = percentage of relative importance index. The highest  
80 percentages by species are in bold.

Prey category	<i>C. macrophthalma</i>				<i>C. chromis</i>				<i>B. boops</i>			
	O%	N%	W%	IRI%	O%	N%	W%	IRI%	O%	N%	W%	IRI%
Harpacticoid copepods	0.3	0.6	0.6	0.2	0.1	0.4	0.2	0.1	0.2	4.1	1.5	1.5
Cyclopoid copepods	0.1	0.6	0.6	0.1	<b>0.7</b>	19.0	19.2	17.8	0.1	5.5	2.1	3.1
Calanoid copepods	<b>0.9</b>	<b>72.5</b>	<b>74.7</b>	<b>81.8</b>	0.6	20.3	20.3	18.9	<b>0.4</b>	13.6	4.7	13.9
Copepod nauplii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cladocerans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Decapod larvae	0.8	19.5	17.3	16.2	0.3	4.9	4.9	3.5	0.3	22.5	8.6	18.6
Cypris larvae	0.0	0.0	0.0	0.0	0.3	10.7	10.7	10.5	0.1	6.3	1.2	6.0
Amphipods	0.2	6.8	6.8	1.6	0.3	6.9	7.0	11.3	0.2	14.5	8.7	13.1
Ostracods	0.0	0.0	0.0	0.0	0.3	1.8	1.8	1.6	0.0	0.3	0.2	0.0
Other crustaceans	0.0	0.0	0.0	0.0	0.1	1.8	1.8	1.2	0.1	0.7	5.5	0.5
Eggs	0.0	0.0	0.0	0.0	0.1	4.6	4.6	2.4	0.1	5.4	2.0	3.2
Bivalve larvae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.5	0.2
Gastropods	0.0	0.0	0.0	0.0	<b>0.7</b>	<b>29.5</b>	<b>29.5</b>	<b>32.7</b>	0.1	0.6	0.4	0.2
Others	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	<b>28.8</b>	<b>64.6</b>	<b>39.6</b>

81

82 **Fig. S1.** Scatter plots illustrating Shannon-Wiener diversity index ( $H'$ ) of prey as functions of predator  
 83 total body length (cm) for the studied species in the Bay of Marseille from March to September 2017.  
 84 Each point represents the prey diversity in the stomach content of a single fish. Dotted quantile  
 85 regression lines represent changes in the range of diversity as trophic niche breadth (TNB) with  
 86 increasing predator size. Upper- (UBS) and lower-bound slopes (LBS) are quantile regressions  
 87 estimating 90<sup>th</sup> (upper) and 10<sup>th</sup> (lower) quantiles of diversity vs. predator length comparisons (\*\*  
 88 0.0001, \*\* P < 0.001, \* P < 0.01, ' P < 0.1, none = not significant). SE is the standard error of each  
 89 quantile regression. Results from quantile regressions of diversity vs. predator length comparisons are  
 90 also presented. CHANGE TNB represents decreases or increases in trophic niche breadth based on  
 91 statistically significant differences between UBS and LBS (P > 0.05 and thus no change in TNB for  
 92 all).

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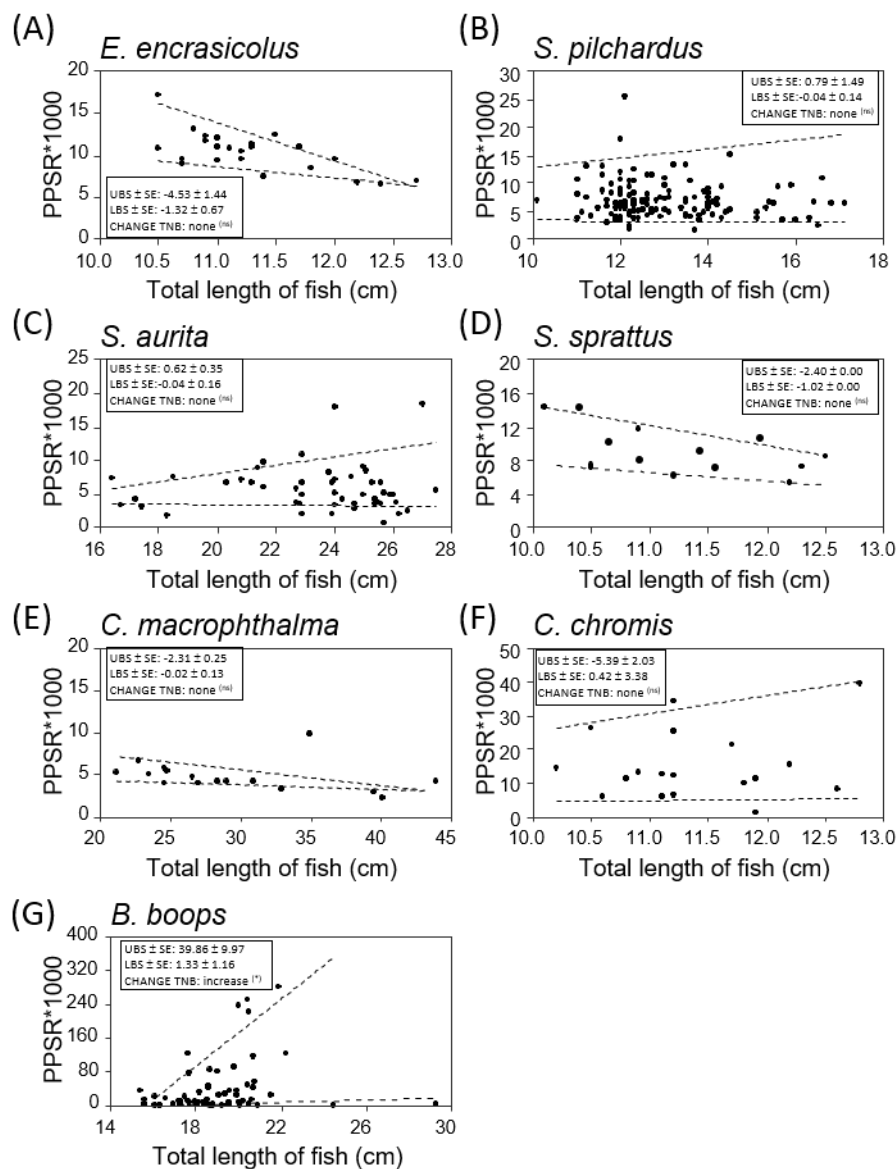


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96 **Fig. S2.** Scatter plots illustrating prey-predator size ratios (PPSR)\*1000 as functions of predator total  
 97 body length (cm) of the studied species in the Bay of Marseille from March to September 2017. Each  
 98 point represents the PPSR\*1000 in the stomach content of a single fish. Solid quantile regression lines  
 99 represent significant changes in the range of the PPSR\*1000 as trophic niche breadth (TNB) with  
 100 increasing predator size while dotted quantile regression lines represent non-significant changes.  
 101 Upper- (UBS) and lower-bound slopes (LBS) are quantile regressions estimating 90<sup>th</sup> (upper) and 10<sup>th</sup>  
 102 (lower) quantiles of PPSR\*1000 vs. predator length comparisons (\*\*\* P < 0.0001, \*\* P < 0.001, \* P <  
 103 0.01, ' P < 0.1, none = not significant). SE is the standard error of each quantile regression. Results  
 104 from quantile regressions of PPSR\*1000 vs. predator length comparisons are also presented. CHANGE  
 105 TNB represents decreases or increases in trophic niche breadth based on statistically significant  
 106 differences between UBS and LBS (P > 0.05). There was no change in TNB for all species, except for  
 107 *B. boops* (P = 0.004).

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