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## Variability of energy density among mesozooplankton community: new insights in functional diversity to forage fish

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22 **Abstract**

23 To assess one of the dimensions of mesozooplankton functional diversity, this study  
24 quantifies energy density during the springtime in the Bay of Biscay considering both  
25 taxonomic and size-classes diversity. Energy density among copepods species (*Centropages*  
26 *typicus*, *Anomalocera patersoni*, *Calanus helgolandicus*, and *Labidocera wollastoni*), as well  
27 as anchovy eggs (*Engraulis encrasicolus*) ranges from 0.5 to 6.7 kJ/g on a taxonomic basis.  
28 Considering size-classes, energy density varies from 0.74 to 1.26 kJ/g. *C. helgolandicus*  
29 exhibits with average energy density estimates generally higher in the plume of the Gironde  
30 estuary. In contrast, no spatial coherence is found in the variability of mesozooplankton energy  
31 density by size-classes. Our results show that the mesozooplanktonic resource is not  
32 homogeneous in terms of quality in the Bay of Biscay. During spring, some species and some  
33 geographical areas seems thus to be more profitable to predators than others. We argue that the  
34 energy density is a key functional trait of mesozooplankton, but the assessment of  
35 mesozooplankton quality should be preferentially based on taxonomy rather than on size-  
36 classes. We conclude that interspecific and spatial variability of energy density among the  
37 mesozooplankton community can have important implications on fish population dynamics.

38

39 **Key words:** Bay of Biscay, profitability, copepods, prey-predator relationship, fisheries

40

## 41 **Introduction**

42 Characteristics of species and environment (i.e., functional diversity) can shape  
43 population or impacts ecosystems dynamics (e.g., Hulot et al., 2000; Petchey and Gaston,  
44 2006). Prey availability and quality are central in ecosystem functioning, however studies on  
45 food webs have traditionally focused on taxonomic relationships among trophic levels, thereby  
46 downplaying the importance of prey functional traits (Spitz et al., 2014). Thus, understanding  
47 how prey characteristics drive predators' foraging strategies and shape energy fluxes is one of  
48 the current challenges to improving our knowledge of ecosystem functioning.

49

50 Profitability is the net energy intake from food less the net energy allocated for a  
51 predator to pursue, capture and consume their target prey (Pulliam, 1974). In marine ecosystem,  
52 diet composition was traditionally based on stomach content analyses (Hyslop, 1980), whereas  
53 profitability was based on prey availability and capturability (Garrido et al., 2007; Wirtz, 2012).  
54 More recently, profitability has been investigated with respect to prey functional characteristics  
55 and not only to sheer quantity of prey. Prey body size was the first functional trait to be  
56 correlated with profitability (Scharf et al., 1998). Prey quality defined here as energy content  
57 per unit of prey mass consumed, as individual prey potential energy, is another functional  
58 trait investigated to understand predators' energetic needs (Spitz et al., 2014) that can explain  
59 physiological stress at the individual level, or scale up to explain some population declines  
60 (Kitaysky et al., 2001; Rosen and Trites, 2000). A collapse of fat and energy-rich prey  
61 associated with an increase of low quality prey biomass ("junk-food", Österblom et al. 2008)  
62 has negatively impacted some populations of marine top predators (the common murre seabird  
63 or Stellers sea lions for instance) around the world (Kadin et al., 2012). The role of prey energy  
64 densities was mainly investigated on high trophic-level species such as marine mammals or  
65 seabirds (Shoji et al., 2014; Spitz et al., 2012). Hence, the quality of prey such as forage fish,  
66 cephalopods or crustaceans has been investigated (Spitz, et al., 2010; Spitz & Jouma'a, 2013;  
67 Schrimpf et al., 2012), but the variability of energy density in low trophic-level prey, such as  
68 mesozooplankton, remains largely unknown.

69 The latter, defined as zooplanktonic organisms ranging between 200 and 2,000  $\mu\text{m}$   
70 (Sieburth et al., 1978), is a key compartment of marine food webs. Mesozooplankton  
71 communities participate in carbon recycling in the ocean (Mayzaud and Pakhomov, 2014),  
72 being the main marine compartment that transfers energy from primary producers to the upper  
73 trophic levels. Mesozooplankton organisms are the major predators in the planktonic food web  
74 and constitute the main prey of many marine fish species including major commercial species,

75 such as sardines and anchovies. Moreover, due to short life cycles, mesozooplankton organisms  
76 constitute an indicator of environmental changes. Climatic variations may involve concomitant  
77 biogeographical and phenological shifts (Chiba et al., 2008; Richardson, 2008). Hence, climate-  
78 mediated changes in mesozooplankton abundance and composition can influence fish  
79 recruitment and thus impact abundance of fish stocks and fisheries management (Batchelder et  
80 al., 2012; Beaugrand et al., 2003). In temperate areas, mesozooplankton abundance peaks in  
81 spring, consecutively or simultaneous to a phytoplankton bloom (Gonzalez-Gil et al., 2015).

82

83 The Bay of Biscay (northeastern Atlantic) is a large open area, where the continental  
84 shelf narrows from North to South. It constitutes a strongly productive fishing area (Guénette  
85 and Gascuel, 2012) where several small pelagic fish rely on mesozooplankton, including  
86 pilchard, anchovy, sprat, chub and atlantic mackerel, atlantic and mediterranean horse  
87 mackerel, blue whiting. Among these small zooplanktivorous pelagic fish, European pilchard,  
88 *Sardina pilchardus*, and European anchovy, *Engraulis encrasicolus*, have a high commercial  
89 interest, but present contrasting annual patterns of their stocks (ICES, 2010; OSPAR  
90 Commission, 2000). To explain the variability in the recruitment of these forage fish, the role  
91 of abiotic characteristics have been previously studied at different spatial scales in the Bay of  
92 Biscay (Borges et al., 2003; Borja et al., 2008; Guisande et al., 2001). The influence of biotic  
93 parameters, such as the biomass of mesozooplankton (Irigoien et al., 2009) or the effect of  
94 predation on anchovy eggs by pilchards (Bachiller et al., 2015), have been also investigated,  
95 however, the quality of available food to forage fish has been never explore in the Bay of  
96 Biscay.

97

98 Our hypothesis is that mesozooplankton energy density should vary depending species  
99 assemblages or spatially, resulting in variability of the food quality to forage fish. To this end,  
100 we aimed in this study to explore the variability in mesozooplankton energy density across the  
101 Bay of Biscay. We first investigated variations of energy density -1- according to  
102 mesozooplankton sizes because prey size is crucial in trophic pattern of plankton feeders  
103 (Garrido et al., 2007); and -2- according taxonomic diversity because energy density is known  
104 to vary considerably within others species communities, such as fish or cephalopods (Doyle et  
105 al., 2007; Spitz et al., 2010). Finally, we explored some spatial patterns in energy density both  
106 for size-classes and for one major species, *Calanus helgolandicus*.

107

108

## 109 **Materials and Methods**

### 110 *Sampling*

111 Mesozooplankton samples were collected in the Bay of Biscay on the R/V Thalassa  
112 during the PELGAS surveys in spring (April-May 2013 and 2014). PELGAS are ecosystemic  
113 surveys conducted every year since 2003 by the *Institut Français de Recherche pour*  
114 *l'Exploitation de la Mer* (IFREMER - Doray et al., this issue). Size-class sampling of  
115 mesozooplankton was performed using WP2 nets along five transects covering the continental  
116 shelf from the coastline to the continental slope (Fig. 1). North *versus* South limit was the  
117 Gironde estuary. This sampling was conducted during nighttime by vertical tows (maximum  
118 100 m depth for continental shelf and slope stations, mesh size of 200 µm and mouth area of  
119 0.25 m<sup>2</sup>). Three size-classes of mesozooplankton were analyzed in 2013 corresponding to  
120 successive filtrations (washed with distilled water) on three sieves with different mesh size:  
121 200, 1000 and 2000 µm. In 2014, four size-classes were conducted with mesh size of sieves  
122 corresponding to 200, 500, 1000 and 2000 µm. In total, thirteen stations were sampled reaching  
123 28 samples in spring 2013 and 35 samples in spring 2014 (Supplemental table 1). All samples  
124 were stored frozen at -20°C until further analysis.

125 A Continuous Underwater Fish Egg Sampler (CUFES, Model C-100, Ocean  
126 Instruments Inc.) was used during daytime to collect the different taxa of mesozooplankton.  
127 The first objective of CUFES was to estimate the abundance of pilchard and anchovy eggs  
128 (Petitgas et al., 2009). CUFES samples were filtered on 315 µm and the pump was operated at  
129 -3 m under the sea surface (ICES, 2007). Immediately after their sampling, copepods (only on  
130 adult stages and non ovigerous females), fish eggs and decapod *zoea* were identified on board  
131 at the lowest taxonomic level (see Table 2) possible with a Leica M3Z stereo microscope (x 65  
132 to x100 magnifications). For abundant and large species, replicates were collected at each  
133 station. For the smallest or less abundant species (*e.g. Oithona* and *Acartia* spp), individuals  
134 were pooled and collected only with a WP2 net. Finally, the number of organisms analyzed  
135 ranged from 40 to 5,600 across 10 different taxa. Organisms were washed with distilled water  
136 and stored in Eppendorf tubes at -20°C. In total, our sampling encompassed twelve different  
137 prey items available to forage fish in the Bay of Biscay (see Table 2). WP2 net and CUFES  
138 were considered as tools enabling to acquire enough organisms for laboratory analysis. This  
139 sampling was not considered in relation to biomass or sampling layer for example.

140

### 141 *Calorimetric analyses*

142 Energy density was estimated, following Spitz et al. (2010), using a Parr<sup>®</sup> 1266 semi-  
143 micro oxygen bomb calorimeter, an adiabatic bomb-calorimetry in which gross energy was  
144 determined by measuring heat of combustion. Energy density was measured on dry samples  
145 after a 48-h freeze-drying period. They were converted to wet mass by taking into account water  
146 content (wet-weighted (ww) and dried-weighted (dw) before and after a 48h freeze-drying  
147 period). In the present study, energy density was expressed in kJ/g of fresh mass (ww mention  
148 after kJ/g unit). Energy density based on fresh mass is physiologically more relevant to  
149 investigate differences in prey quality to predators and to study energy transfer because fish  
150 forage and digest food in this form. In complement, energy density estimates of  
151 mesozooplankton size-classes, species or genus results were expressed in kJ/g of dry mass (see  
152 Supplemental figure 1 and Supplemental table 2). All measurements reported in this study were  
153 averages of technical replicates (deviation between two assays was < 5%).

154

#### 155 *Data treatment*

156 Statistical analyses were conducted with R v.3.1.2 (R Core Team, 2014). Non-  
157 parametric analyses were conducted to compare energy density by size-classes of  
158 mesozooplankton along latitudinal or longitudinal gradient and to compare energy density  
159 considering taxonomic description. Previously, normality and homogeneity of variances were  
160 respectively checked using Shapiro-Wilks tests and Bartlett tests. Then, ANOVA (followed by  
161 post-hoc Tukey tests) was applied for comparisons of more than two means in non-parametric  
162 or parametric conditions. Statistical significance was set at 5%. Details of p-value were  
163 presented in Supplemental table 3.

164 To predict energy density of *Calanus helgolandicus* (the most abundant species) at  
165 unsampled locations, ordinary kriging was performed (Wikle, 2003). The geodetic distance  
166 between pairs of locations where measurement were taken was computed and used for  
167 variogram estimation. We assumed an isotropic Matern covariance function of order  $3/2$   
168 (Juntunen et al., 2012). Model fitting was done via the software STAN v.2.5.0 (Stan  
169 Development Team, 2013) and interpolations were done with R v.3.1.2 (R Core Team, 2014).  
170 4 chains were initialized with random starting values, and run for 6 000 iterations with a warm-  
171 up of 1 000 iterations. Model convergence was assessed with the Gelman-Rubin-Brook  
172 diagnostics. Weakly informative priors (Stan Development Team, 2013) were used to help  
173 parameter estimation given the small sample size. The latter feature motivated a Bayesian  
174 approach to avoid relying on asymptotic justifications, which are unlikely to hold in small  
175 sample analyses.

## 176 **Results**

### 177 *Energy density by size-classes*

178

179 Energy densities ranged from 0.01 to 2.32 kJ/g ww across all samples (2013 and 2014,  
180 all size-classes). Energy density means were around 1.05 kJ/g ww, for all studied size-classes  
181 (see details by each size-classes in Table 1). Mean energy density of 200-1000, 1000-2000 and  
182 greater than 2000  $\mu\text{m}$  were evaluated respectively in spring 2013 at 0.82, 1.06 and 1.15 kJ/g  
183 ww (Table 1). In 2014, mean energy density of 200-500, 500-1000, 1000-2000 and greater than  
184 2000  $\mu\text{m}$  were respectively at 1.26, 1.15, 1.04 and 0.74 kJ/g ww (Table 1). No interannual  
185 differences in mean energy density were detected in spring (Fig. 2). No differences were  
186 detected within size-classes across the Bay of Biscay (Fig. 2). In both 2013 and 2014, no  
187 differences of mean energy density were observed between the Northern and Southern part of  
188 the Bay, or from coastal to continental slope areas.

189 Despite the absence of any significant difference in size-class, we observed a local  
190 variability of energy density within size-classes. For a given station, the values of energy  
191 density can largely vary within size-classes (Fig. 3). A maximum difference between two size-  
192 classes reached 1.82 kJ/g ww (*e.g.* 3.5 fold-change) and was recorded in spring 2014 at station  
193 S350 (Fig. 1) between 500-1000 and 1000-2000 $\mu\text{m}$  size-classes. No pattern in energy density  
194 of size-classes was detected across sampled stations, for instance smallest size-classes can both  
195 exhibit higher (*e.g.* R243, R253, S336 or S430) or lower values (*e.g.* R262, R190, S448 or  
196 S334) than other size-classes at the same station.

197

### 198 *Energy density by taxonomic diversity*

199

200 Energy density ranged from 0.5 to 6.7 kJ/g ww for copepods (minimum for *Temora*  
201 *longicornis*: 0.5 kJ/g ww and, maximum for *Calanus helgolandicus*: 6.7 kJ/g ww, from 0.8 to  
202 4.4 kJ/g ww for anchovy eggs and 2.7 kJ/g ww for undetermined decapod *zoea* (Table 2). No  
203 analytical measurement was obtained for *Acartia* spp. or *Oithona* spp., because analyzed  
204 samples were below the detection threshold; individuals from these genus were too small to  
205 collect enough material for the analysis. Thus, it was considered that their gross energy contents  
206 were lower than the smallest gross energy measured, (*i.e.* < 0.5 kJ/g ww). Across all organisms,  
207 average energy density in spring was  $2.6 \pm 1.3$  kJ/g ww (Fig. 4). Without consideration of items  
208 with less than two biological replicates (*e.g.* decapods *zoea*, *P. elongatus*, *A. patersoni*), a  
209 *posteriori* comparisons revealed also one significant difference between *T. longicornis* and *C.*

210 *helgolandicus* (Tuckey-HSD, p-adj=0.051). The highest variability were recorded for *C.*  
211 *helgolandicus* from 0.68 to 6.74 kJ/g and for *L. wollastoni* from 1.28 to 4.87 kJ/g ww.

212 A clear spatial pattern of energy density was highlighted for *C. helgolandicus* (Fig. 5):  
213 energy density was higher from coastline to the middle part of the continental shelf (~ isobath  
214 -50 m) of the Bay of Biscay (between 3.5 and 4.5 kJ/g ww). The energy density of *C.*  
215 *helgolandicus* was highest at river mouths (4.5 kJ/g ww in the Gironde estuary). In contrast, the  
216 energy density of *C. helgolandicus* sampled from the central part of the continental slope and  
217 from the Northern part of the Bay were halved (approx. 2.5 kJ/g ww).

218

## 219 **Discussion**

220 Previous studies on mesozooplankton quality focused mostly on *Calanus* species (Davies et al.,  
221 2012; Michaud and Taggart, 2007). Our objective was specifically to consider the sizes and the  
222 specific energy density in a diversified community (only on adult stages and non ovigerous  
223 females copepods). This study is the first to investigate mesozooplankton quality both at a broad  
224 taxonomic and at size scales across a major European fishing ground. This approach  
225 demonstrates also the importance of assessing profitability taxonomically instead of by its size.

226 Nevertheless, several limitations are inherent in the approaches used in this study.  
227 Sampling mesozooplankton at the species level and direct calorimetric analysis are time-  
228 consuming which made obtaining a large collection of samples difficult over a realistic period  
229 of time. Thus, our sampling did not cover all the taxonomic diversity of the spring  
230 mesozooplankton community in the Bay of Biscay (e.g. Valdés et al., 2007). Moreover, most  
231 copepods realize diel vertical migration for feeding on phytoplankton from the photic layer  
232 (Hays, 2003), suggesting a potential difference of species composition between night and day,  
233 even if size-classes were in the same range in this study.

234 Mesozooplankton and particularly copepods are used as climatic proxy (e.g. Beaugrand, 2004)  
235 in relation with their short life cycle involving a high metabolism (Allan, 1976) and possibly  
236 with rapid (short life species, few days from eggs to adult stages) changes of their energetic  
237 status ( Lee et al., 2006). Temporal variation of density energy exist (Hagen and Auel, 2001),  
238 our results documented only the springtime considering together two different years as a  
239 seasonal snapshot. Despite these sources of uncertainty, our study provided consistent results  
240 and the monitoring of energy densities in mesozooplankton can thus inform both on nutritional  
241 status of these organisms and on the quality of the underlying environmental conditions.

242

243 *Variability of quality among mesozooplankton communities*

244

245 Energy density of mesozooplankton in the Bay of Biscay ranges from energy density of  
246 jellyfish (<4 kJ/g ww) to lipid-rich fish such clupeids (>6kJ/g ww) ( Spitz et al., 2010). Thus,  
247 the mesozooplanktonic compartment in the Bay of Biscay can be described as low-quality  
248 resources (< 4 kJ/g ww ) if we consider energy density based on size-classes, or moderate-  
249 quality resources (from 4 to 6 kJ/g ww) if we consider the most energetic copepods *C.*  
250 *helgolandicus* (Spitz et al. 2010). However, the energy density of copepods studied at the  
251 specific level has been mainly investigated on diapausing stages species living in colder  
252 ecosystems (e.g. *Calanus glacialis*, *C. hyperboreus* or *C. finmarchicus*), which have very  
253 different metabolic activities (Davies et al., 2012; Michaud and Taggart, 2007).

254 Energy density estimates should be expressed in wet weight units to investigate energy  
255 fluxes through ecosystems because predators consume wet prey; but some previous studies only  
256 reported dry weight (dw) estimates which are of limited use in bioenergetic studies (e.g. Davies  
257 et al., 2012; McKinstry et al., 2013; Michaud and Taggart, 2007). For comparability with some  
258 other studies, we expressed our results in dry weight units (see Supplemental figure 1 and  
259 Supplemental table 2). Our estimates were also comparable to previous ones. For example, the  
260 overall average of energy content of *Calanus finmarchicus* and *C. hyperboreus* was estimated  
261 at  $27.9 \pm 5.0$  kJ/g dw in the Bay of Fundy (Davies et al., 2012), close to our estimate concerning  
262 *C. helgolandicus* of  $26.2 \pm 3.7$  kJ/g dw.

263

#### 264 *Ecological observations of mesozooplanktonic organisms and energy density*

265

266 Feeding activities, reproduction, respiration and growth are energy demanding  
267 processes (Postel et al., 2000). Large copepods species suggesting a proportion of storage  
268 volume more important, oil sac, compared to other species (Lee et al., 2006; Davies and  
269 Taggart, 2012). Size cannot be also strictly used as a proxy of quality in mesozooplankton as  
270 suggested by our results on size classes or on some large species, i.e. *A. patersoni* and  
271 *Pleuromamma* spp (Supplemental table 4). This latter genus was constituted of large copepods  
272 which showed one of the lowest energy density in copepods. *Pleuromamma* spp. seems to be  
273 the deepest copepods species of our sampling suggesting possibly that deeper mesozooplankton  
274 species could be less energetic than epipelagic species ( Zarubin et al. 2014).

275 *A. patersoni* was the largest species of our sampling but have a low energy density. *A.*  
276 *patersoni* was probably the most carnivorous species compared to herbivorous and omnivorous

277 species suggesting diet composition may influence metabolic processes and energy storage  
278 based on protein intake (Supplemental table 4). Similarly, *T. longicornis* appears to be one of  
279 the energy-poorest species. This species cannot accumulate extensive energy because of its  
280 rapid metabolic and functional responses to food limitation (Niehoff et al., 2015). In  
281 experimental conditions, *T. longicornis* exhibits a rapid loss of lipids compared to *P. elongatus*  
282 (Martynova et al., 2009). Moreover, *Acartia* spp., *T. longicornis* and *C. typicus* present high  
283 metabolic rates implicating a limited lipid accumulation and in some cases (when unflavored  
284 conditions appear) resting eggs (Arts et al., 2009). Further studies should focus on relationship  
285 between the taxonomic composition of the mesozooplankton size-classes and their energy  
286 density.

287 The breeding season of organisms could also impact the observed patterns of energy density  
288 among copepods species (Ventura and Catalan, 2005). Despite a short life-cycle due to their  
289 strong metabolic activity, it is possible that breeding cycles are synchronous among copepod  
290 species. Springtime is a highly dynamic season that can offer various and rapid change of  
291 abiotic environment allowing the establishment of diverse ecological niches.

292

### 293 *Implications on fish population dynamics*

294 Energy fluxes between organisms depend on the relationships between environmental  
295 conditions (*e.g.* temperature), food consumption (*e.g.* abundance) and biologic factors (*e.g.*  
296 metabolic processes to reproduction) (Lambert et al., 2003). Bioenergetic models consider three  
297 compartments (food reserve, growth and reproduction); the variability of energy fluxes to these  
298 compartments can explain population dynamics (Brandt and Hartman, 1993). Energy density  
299 can be obtained using direct measures (as in our study), using the proximate composition, or  
300 using calculations from the percentage of the organic constituents from carbon called the  
301 ‘calorimetric equivalent’ (Postel et al, 2000). Existing models on fish population dynamics in  
302 the Bay of Biscay used mesozooplankton as a homogenous compartment in terms of energy  
303 density (Gatti et al., 2017). Mesozooplanktivorous species like pilchards and anchovies will be  
304 constrained by the intrinsic quality of their prey at a local scale (Bachiller and Irigoien, 2013).  
305 Variations in mesozooplankton biomass fail to explain alone the recruitment variability of  
306 anchovies in the Bay of Biscay (Irigoien et al., 2009). Politikos et al., (2015) suggested that the  
307 spawning spring spatial pattern of anchovies in the Bay of Biscay “is a result of the general  
308 southward movement of the population, as well as the associated better bioenergetic conditions  
309 as compared to the individuals remaining in the North”. Our hypothesis here is that the  
310 nutritional quality of plankton contributes to recruitment efficiency. Forage fish, such as

311 anchovies and pilchards, are mechanically constrained through their filter-size features  
312 (Bachiller and Irigoien, 2013). Consequently, low quality mesozooplanktonic organisms, even  
313 if they are abundant, should negatively impact the fitness of some planktivorous consumers.  
314 Physiology and digestion rates would not compensate the ingestion of low prey quality by  
315 higher consumption rates. A lower quality food induces lower reserves and less energy to  
316 immediate swimming activity, to forage and to produce high quality gametes.

317

## 318 Conclusion

319 We showed mesozooplankton quality (measured here by the energy density) was variable  
320 among sizes, species and spatially. Mesozooplankton quality should be assessed according  
321 taxonomic diversity rather than by size classes. Mesozooplankton species cannot be considered  
322 as interchangeable to satisfy energy requirements of forage fish. Ultimately, variability of some  
323 key functional traits in some species, here energy density in mesozooplankton community, can  
324 play an important role to maintain the quality of some ecosystem services, as well as fish  
325 production to human consumption.

326

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## 339 References

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341 Allan, J.D., 1976. Life History Patterns in Zooplankton. *Am. Nat.* 110, 165–180.  
342 doi:10.2307/2459885

343 Arts, M.T., Brett, M.T., Kainz, M., 2009. *Lipids in Aquatic Ecosystems*. Springer.

344 Bachiller, E., Cotano, U., Ibaibarriaga, L., Santos, M., Irigoien, X., 2015. Intraguild predation  
345 between small pelagic fish in the Bay of Biscay: impact on anchovy (*Engraulis*  
346 *encrasicolus* L.) egg mortality. *Mar. Biol.* doi:10.1007/s00227-015-2674-0

- 347 Bachiller, E., Irigoien, X., 2013. Allometric relations and consequences for feeding in small  
348 pelagic fish in the Bay of Biscay. ICES J. Mar. Sci. 70, 232–243.  
349 doi:10.1093/icesjms/fss171
- 350 Batchelder, H.P., Mackas, D.L., O'Brien, T.D., 2012. Spatial–temporal scales of synchrony in  
351 marine zooplankton biomass and abundance patterns: A world-wide comparison. Glob.  
352 Comp. Zooplankton Time Ser. 97–100, 15–30. doi:10.1016/j.pocean.2011.11.010
- 353 Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and  
354 consequences. Prog. Oceanogr. 60, 245–262. doi:10.1016/j.pocean.2004.02.018
- 355 Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., Reid, P.C., 2003. Plankton effect on  
356 cod recruitment in the North Sea. Nature 426, 661–664. doi:10.1038/nature02164
- 357 Bellier, E., Planque, B., Petitgas, P., 2007. Historical fluctuations in spawning location of  
358 anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the Bay of Biscay  
359 during 1967–73 and 2000–2004. Fish. Oceanogr. 16, 1–15. doi:10.1111/j.1365-  
360 2419.2006.00410.x
- 361 Bonnet, D., Richardson, A., Harris, R., Hirst, A., Beaugrand, G., Edwards, M., 2005. An  
362 overview of *Calanus helgolandicus* ecology in European waters. Prog. Oceanogr. 65,  
363 1–53. doi:10.1016/j.pocean.2005.02.002
- 364 Borges, M.F., Santos, A.M.P., Crato, N., Mendes, H., Mota, B., 2003. Sardine regime shifts off  
365 Portugal: A time series analysis of catches and wind conditions. Sci. Mar. 67, 235–244.
- 366 Borja, A., Fontán, A., Sáenz, J., Valencia, V., 2008. Climate, oceanography, and recruitment:  
367 The case of the Bay of Biscay anchovy (*Engraulis encrasicolus*). Fish. Oceanogr. 17,  
368 477–493. doi:10.1111/j.1365-2419.2008.00494.x
- 369 Brandt, S.B., Hartman, K.J., 1993. Innovative approaches with bioenergetics models : Future  
370 applications to fish ecology and management. Trans. Am. Fish. Soc. 122, 731–735.  
371 doi:10.1577/1548-8659(1993)122<0731:IAWBMF>2.3.CO;2
- 372 Chiba, S., Aita, M.N., Tadokoro, K., Saino, T., Sugisaki, H., Nakata, K., 2008. From climate  
373 regime shifts to lower-trophic level phenology: Synthesis of recent progress in  
374 retrospective studies of the western North Pacific. Clim. Var. Ecosyst. Impacts North  
375 Pac. Basin-Scale Synth. 77, 112–126. doi:10.1016/j.pocean.2008.03.004
- 376 Chauvelon, T., Chappuis, A., Bustamante, P., Lefebvre, S., Mornet, F., Guillou, G., Violamer,  
377 L., Dupuy, C., 2014. Trophic ecology of European sardine *Sardina pilchardus* and  
378 European anchovy *Engraulis encrasicolus* in the Bay of Biscay (north-east Atlantic)  
379 inferred from  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of fish and identified mesozooplanktonic  
380 organisms. J. Sea Res. 277–291. doi:10.1016/j.seares.2013.05.011
- 381 Chauvelon, T., Violamer, L., Dessier, A., Bustamante, P., Mornet, F., Pignon-Mussaud, C.,  
382 Dupuy, C., 2015. Small pelagic fish feeding patterns in relation to food resource  
383 variability: an isotopic investigation for *Sardina pilchardus* and *Engraulis encrasicolus*  
384 from the Bay of Biscay (north-east Atlantic). Mar. Biol. 162, 15–37.  
385 doi:10.1007/s00227-014-2577-5
- 386 Davies, K.T.A., Ryan, A., Taggart, C.T., 2012. Measured and inferred gross energy content in  
387 diapausing *Calanus* spp. in a Scotian shelf basin. J. Plankton Res. 34, 614–625.  
388 doi:10.1093/plankt/fbs031
- 389 Doray, M., Masse, J., Duhamel, E., Huret, M., Doremus, G., Petitgas, P., 2014. Manual of  
390 fisheries survey protocols. PELGAS surveys (PELAGiques GAScogne).  
391 doi:10.13155/30259
- 392 Doyle, T.K., Houghton, J.D.R., McDevitt, R., Davenport, J., Hays, G.C., 2007. The energy  
393 density of jellyfish: Estimates from bomb-calorimetry and proximate-composition. J.  
394 Exp. Mar. Biol. Ecol. 343, 239–252. doi:10.1016/j.jembe.2006.12.010

395 Garrido, S., Mar\ccalo, A., Zwolinski, J., Van der Lingen, C.D., 2007. Laboratory  
396 investigations on the effect of prey size and concentration on the feeding behaviour of  
397 *Sardina pilchardus*. Mar. Ecol. Prog. Ser. 330, 189–199. doi:10.3354/meps330189  
398 Garrido, S., Van Der Lingen, C.D., 2015. Chapter 4: Feeding biology and ecology, in: Biology  
399 and Ecology of Sardines and Anchovies. Greece, pp. 122–190.  
400 Gatti P., Petitgas P., Huret M., *submitted*. Comparing biological traits of anchovy and sardine  
401 in the Bay of Biscay: a modelling approach with the Dynamic Energy Budget.  
402 Gonzalez-Gil, R., Gonzalez Taboada, F., Hoeffler, J., Anadon, R., 2015. Winter mixing and  
403 coastal upwelling drive long-term changes in zooplankton in the Bay of Biscay (1993-  
404 2010). J. Plankton Res. 37, 337–351. doi:10.1093/plankt/fbv001  
405 Gatti, P., Petitgas, P., Huret, M., 2017. Comparing biological traits of anchovy and sardine in  
406 the Bay of Biscay: A modelling approach with the Dynamic Energy Budget. Ecol.  
407 Model. 348, 93–109. doi:10.1016/j.ecolmodel.2016.12.018  
408 Guénette, S., Gascuel, D., 2012. Shifting baselines in European fisheries: The case of the Celtic  
409 Sea and Bay of Biscay. Spec. Issue Fish. Policy Reform EU 70, 10–21.  
410 doi:10.1016/j.ocecoaman.2012.06.010  
411 Guisande, C., Cabanas, J.M., Vergara, A.R., Riveiro, I., 2001. Effect of climate on recruitment  
412 success of Atlantic Iberian sardine *Sardina pilchardus*. Mar. Ecol. Prog. Ser. 223, 243–  
413 250. doi:10.3354/meps223243  
414 Hagen, W., Auel, H., 2001. Seasonal adaptations and the role of lipids in oceanic zooplankton.  
415 Zoology 313–326. doi:10.1078/0944-2006-00037  
416 Hays, G.C., 2003. A review of the adaptive significance and ecosystem consequences of  
417 zooplankton diel vertical migrations. Hydrobiologia 503, 163–170.  
418 doi:10.1023/B:HYDR.0000008476.23617.b0  
419 Herbland, A., Delmas, D., Laborde, P., Sautour, B., Artigas, F., 1998. Phytoplankton spring  
420 bloom of the Gironde plume waters in the Bay of Biscay: early phosphorus limitation  
421 and food-web consequences. Oceanol. Acta 21, 279–291. doi:10.1016/S0399-  
422 1784(98)80015-7  
423 Hulot, F.D., Lacroix, G., Lescher-Moutoue, F., Loreau, M., 2000. Functional diversity governs  
424 ecosystem response to nutrient enrichment. Nature 405, 340–344.  
425 doi:10.1038/35012591  
426 Huret, M., Garnier, V., Grellier, P., Petitgas, P., Sourisseau, M., (submitted for publication). A  
427 full life cycle bioenergetics model of anchovy in the Bay of Biscay calibrated with  
428 seasonal information on energy and spatial distribution. Ecol Model.  
429 Hyslop, E.J., others, 1980. Stomach contents analysis-a review of methods and their  
430 application. J. Fish Biol. 17, 411–429. doi:10.1111/j.1095-8649.1980.tb02775.x  
431 ICES, 2007. Report of the Working Group on Acoustic and Egg Surveys for Sardine and  
432 Anchovy in ICES Areas VIII and IX (WGACEGG). (No. ICES Document. CM 2007 /  
433 LRC: 16).  
434 ICES, 2010. Life-cycle spatial patterns of small pelagic fish in the Northeast Atlantic. ICES  
435 Coop. Res. Rep. 306, 290.  
436 Irigoien, X., Fernandes, J.A., Grosjean, P., Denis, K., Albaina, A., Santos, M., 2009. Spring  
437 zooplankton distribution in the Bay of Biscay from 1998 to 2006 in relation with  
438 anchovy recruitment. J. Plankton Res. 31, 1–17. doi:10.1093/plankt/fbn096  
439  
440 Juntunen, T., Vanhatalo, J., Peltonen, H., Mäntyniemi, S., 2012. Bayesian spatial multispecies  
441 modelling to assess pelagic fish stocks from acoustic- and trawl-survey data. ICES J.  
442 Mar. Sci. 69, 95–104. doi:10.1093/icesjms/fsr183

443 Kadin, M., Österblom, H., Hentati-Sundberg, J., Olsson, O., 2012. Contrasting effects of food  
444 quality and quantity on a marine top predator. *Mar. Ecol. Prog. Ser.* 444, 239–249.  
445 doi:10.3354/meps09417

446 Kitaysky, A.S., Kitaiskaia, E.V., Wingfield, J.C., Piatt, J.F., 2001. Dietary restriction causes  
447 chronic elevation of corticosterone and enhances stress response in red-legged kittiwake  
448 chicks. *J. Comp. Physiol. - B Biochem. Syst. Environ. Physiol.* 171, 701–709.  
449 doi:10.1007/s003600100230

450 Lambert, Y., Yaragina, N.A., Kraus, G., Marteinsdottir, G., Wright, P.J., 2003. Using  
451 environmental and biological indices as proxies for egg and larval production of marine  
452 fish. *J Northw Atl Fish Sci* 33, 159. doi:10.2960/J.v33.a7

453 Lee, R., Hagen, W., Kattner, G., 2006. Lipid storage in marine zooplankton. *Mar. Ecol. Prog.*  
454 *Ser.* 307, 273–306. doi:10.3354/meps307273

455 Lee, R.F., Nevenzel, J.C., Paffenhöfer, G.-A., 1971. Importance of wax esters and other lipids  
456 in the marine food chain: Phytoplankton and copepods. *Mar. Biol.* 9, 99–108.  
457 doi:10.1007/BF00348249

458 Mauchline, J., 1998. The biology of calanoid copepods. *Adv. Mar. Biol.*, In: Blaxter, J.H.S.,  
459 Southward, A.J., Tyler, P.A. (Eds.) 33, Academic Press, 710pp.

460 Mayzaud, P., Pakhomov, E.A., 2014. The role of zooplankton communities in carbon recycling  
461 in the Ocean: The case of the Southern Ocean. *J. Plankton Res.* 36, 1543–1556.  
462 doi:10.1093/plankt/fbu076

463 McKinstry, C.A.E., Westgate, A.J., Koopman, H.N., 2013. Annual variation in the nutritional  
464 value of stage V *Calanus finmarchicus*: Implications for right whales and other copepod  
465 predators. *Endanger. Species Res.* 20, 195–204. doi:10.3354/esr00497

466 Michaud, J., Taggart, C.T., 2007. Lipid and gross energy content of North Atlantic right whale  
467 food, *Calanus finmarchicus*, in the Bay of Fundy. *Endanger. Species Res.* 3, 77–94.  
468 doi:10.3354/esr003077

469 OSPAR Commission, 2000. Quality Status Report 2000 Region IV Bay of Biscay and Iberian  
470 Coast. London.

471 Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward.  
472 *Ecol. Lett.* 9, 741–758. doi:10.1111/j.1461-0248.2006.00924.x

473 Petitgas, P., Goarant, A., Massé, J., Bourriau, P., 2009. Combining acoustic and CUFES data  
474 for the quality control of fish-stock survey estimates. *ICES J. Mar. Sci.* 66, 1384–1390.  
475 doi:10.1093/icesjms/fsp007

476 Politikos, D.V., Huret, M., Petitgas, P., 2015. A coupled movement and bioenergetics model to  
477 explore the spawning migration of anchovy in the Bay of Biscay. *Ecol. Model.* 313,  
478 212–222. doi:10.1016/j.ecolmodel.2015.06.036

479 Postel, L., Fock, H., Hagen, W., 2000. Chapitre 4. Biomass and abundance, in: *ICES*  
480 *Zooplankton Methodology Manual*. London, pp. 83–193.

481 Pulliam, H.R., 1974. On the Theory of Optimal Diets. *Am. Nat.* 108, 59–74.  
482 doi:10.2307/2459736

483 Pusch, C., Schiel, S., Mizdalski, E., von Westernhagen, H., 2004. Feeding of three myctophid  
484 species at Great Meteor Seamount (NE Atlantic). *Arch. Fish. Mar. Res.* 51, 251–271.

485 R Core Team, 2014. R: A language and environment for statistical computing. R Found. Stat.  
486 Comput. Vienna Austria.

487 Richards, W.J., Lindeman, K.C., 1987. Recruitment Dynamics of Reef Fishes: Planktonic  
488 Processes, Settlement and Demersal Ecologies, and Fishery Analysis. *Bull. Mar. Sci.*  
489 41, 392–410. Richardson, A.J., 2008. In hot water: zooplankton and climate change.  
490 *ICES J. Mar. Sci. J. Cons.* 65, 279–295. doi:10.1093/icesjms/fsn028

491 Romano, G., Ianora, A., Miralto, A., 1996. Respiratory physiology in summer diapause  
492 embryos of the neustonic copepod *Anomalocera patersoni*. *Mar. Biol.* 127, 229–234.

493 Rose, M., 1933. Faune de France - Copépodes Pélagiques, Fédération française des sociétés des  
494 sciences naturelles - Office central de Faunistique.

495 Rosen, D.A.S., Trites, A.W., 2000. Pollock and the decline of Steller sea lions: Testing the  
496 junk-food hypothesis. *Can. J. Zool.* 78, 1243–1250. doi:10.1139/z00-060

497 Sargent, J.R., Gatten, R.R., Henderson, R.J., 1981. Lipid biochemistry of zooplankton from  
498 high latitudes. *Océanis* 623–632.

499 Scharf, F.S., Buckel, J.A., Juanes, F., Conover, D.O., 1998. Predation by juvenile piscivorous  
500 bluefish (*Pomatomus saltatrix*): The influence of prey to predator size ratio and prey  
501 type on predator capture success and prey profitability. *Can. J. Fish. Aquat. Sci.* 55,  
502 1695–1703. doi:10.1139/cjfas-55-7-1695

503 Shoji, A., Owen, E., Bolton, M., Dean, B., Kirk, H., Fayet, A., Boyle, D., Freeman, R., Perrins,  
504 C., Aris-Brosou, S., Guilford, T., 2014. Flexible foraging strategies in a diving seabird  
505 with high flight cost. *Mar. Biol.* 161, 2121–2129. doi:10.1007/s00227-014-2492-9

506 Sieburth, J.M., Smetacek, V., Lenz, J., 1978. Pelagic ecosystem structure: Heterotrophic  
507 compartments of the plankton and their relationship to plankton size fractions. *Limnol.*  
508 *Oceanogr.* 23, 1256–1263. doi:10.4319/lo.1978.23.6.1256

509 Spitz, J., Jouma'a, J., 2013. Variability in energy density of forage fishes from the Bay of Biscay  
510 (north-east Atlantic Ocean): Reliability of functional grouping based on prey quality. *J.*  
511 *Fish Biol.* 82, 2147–2152. doi:10.1111/jfb.12142

512 Spitz, J., Mourocq, E., Schoen, V., Ridoux, V., 2010. Proximate composition and energy  
513 content of forage species from the Bay of Biscay: High- or low-quality food? *ICES J.*  
514 *Mar. Sci.* 67, 909–915. doi:10.1093/icesjms/fsq008

515 Spitz, J., Trites, A.W., Becquet, V., Brind'Amour, A., Cherel, Y., Galois, R., Ridoux, V., 2012.  
516 Cost of Living Dictates what Whales, Dolphins and Porpoises Eat: The Importance of  
517 Prey Quality on Predator Foraging Strategies. *PLoS ONE* 7.  
518 doi:10.1371/journal.pone.0050096

519 Stan Development Team, 2013. Stan Modeling Language User's Guide and Reference Manual,  
520 Version 2.5.0. doi:http://mc-stan.org/

521 Valdés, L., López-Urrutia, A., Cabal, J., Alvarez-Ossorio, M., Bode, A., Miranda, A., Cabanas,  
522 M., Huskin, I., Anadón, R., Alvarez-Marqués, F., 2007. A decade of sampling in the  
523 Bay of Biscay: What are the zooplankton time series telling us? *Prog. Oceanogr.* 74,  
524 98–114. doi:10.1016/j.pocean.2007.04.016

525 Vandromme, P., Nogueira, E., Huret, M., Lopez-Urrutia, Á., González-Nuevo González, G.,  
526 Sourisseau, M., Petitgas, P., 2014. Springtime zooplankton size structure over the  
527 continental shelf of the Bay of Biscay. *Ocean Sci.* 10, 821–835. doi:10.5194/os-10-821-  
528 2014

529 Wanless S., Harris M. P., Redman P., Speakman J. R., 2005. Low energy values of fish as a  
530 probable cause of a major seabird breeding failure in the North Sea. *Mar. Ecol. Prog.*  
531 *Ser.* 294, 1–8.

532 Ventura, M., Catalan, J., 2005. Reproduction as one of the main causes of temporal variability  
533 in the elemental composition of zooplankton. *Limnol. Oceanogr.* 50, 2043–2056.  
534 doi:10.4319/lo.2005.50.6.2043

535 Wikle, C.K., 2003. Hierarchical models in environmental science. *Int. Stat. Rev.* 71, 181–199.

536 Wirtz, K., 2012. Who is eating whom? Morphology and feeding type determine the size relation  
537 between planktonic predators and their ideal prey. *Mar. Ecol. Prog. Ser.* 445, 1–12.  
538 doi:10.3354/meps09502

539 Zarubin, M., Farstey, V., Wold, A., Falk-Petersen, S., Genin, A., 2014. Intraspecific differences  
540 in lipid content of calanoid copepods across fine-scale depth ranges within the photic  
541 layer. *PLoS ONE* 9. doi:10.1371/journal.pone.0092935

542 Zlatanov, S., Laskaridis, K., 2007. Seasonal variation in the fatty acid composition of three  
543 Mediterranean fish - sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicolus*)  
544 and picarel (*Spicara smaris*). *Food Chem.* 103, 725–728.  
545 doi:10.1016/j.foodchem.2006.09.013

546 **List of figures**

547

548 **Figure 1:** Map of the continental shelf of the Bay of Biscay showing sampling sites where size-  
549 classes of mesozooplankton were sampled in spring 2013 and in spring 2014. Stations around  
550 500 meter isobaths were considered as continental slope stations, stations near coastline were  
551 considered as coastal stations and other stations, in the center of the shelf as continental shelf  
552 stations.

553

554

555 **Figure 2:** Boxplot of mean energy density (kJ/g ww) of mesozooplankton community along  
556 three criteria: A: along temporal scale during spring 2013 versus during spring 2014, B: along  
557 latitudinal gradient and C: along longitudinal gradient with compiled data obtained from two  
558 springs of mesozooplankton sampling in the Bay of Biscay. The box and the line represent the  
559 lower quartile, median and upper quartile of the mean energy density by station (average of all  
560 size class represented at each station). Sampling size of each box is reported using “n=”  
561 indicated the number of stations considered. Details on energy density for each spring and for  
562 each size classes are presented in Table 1.

563

564 **Figure 3:** Histograms showing variations of energetic density (square root scale - kJ/g ww) of  
565 mesozooplankton among size-classes sampled at each station sampled at springtime 2013 (A)  
566 and 2014 (B) in the Bay of Biscay. Only stations where different size-classes of  
567 mesozooplankton community was represented here.

568

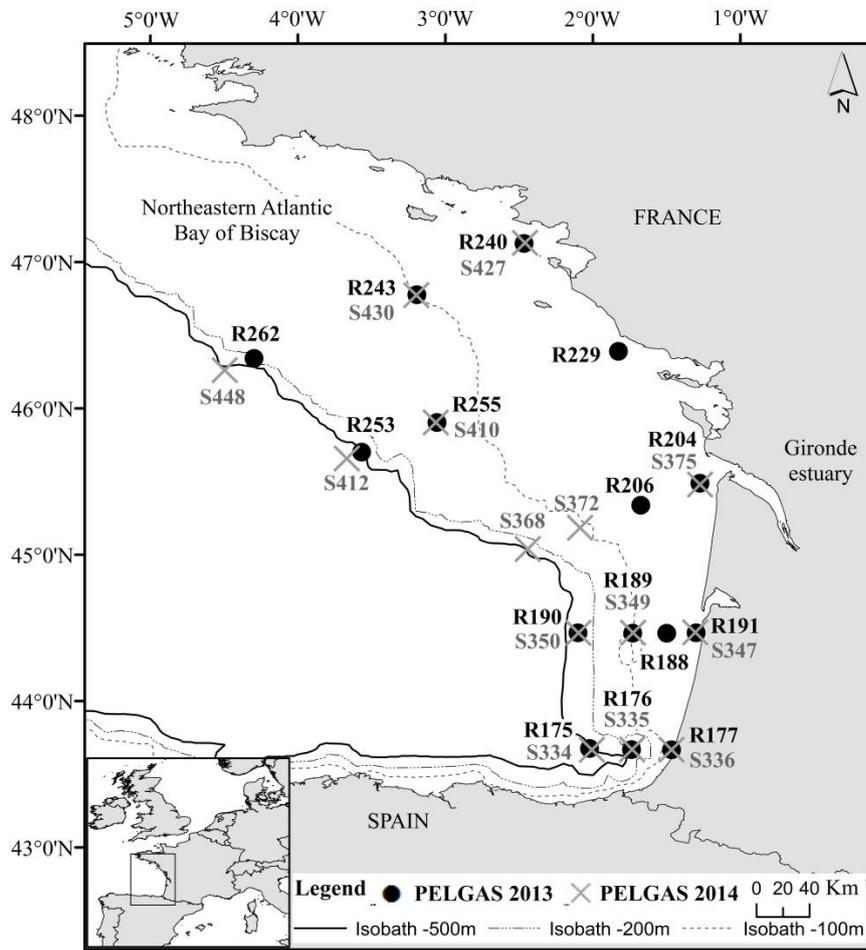
569 **Figure 4:** Boxplot of gross energy measured of several organisms (copepods: only on adult  
570 stages and non ovigerous females) in the Bay of Biscay at springtime. The box and the line  
571 represent the lower quartile, median and upper quartile. The dotted line represents the mean  
572 energy density ( $2.60 \pm 1.32$  kJ/g ww) content considering all measures. Outliers are represented  
573 by black circle. Asterisk represented significant difference between two species (Tuckey-HSD,  
574 p-value= 0.05).

575

576 **Figure 5:** Interpolation map of spring energy density (kJ/g ww) of *C. helgolandicus* sampled  
577 in the Bay of Biscay. Sampling stations are represented by black circle which are in a size  
578 proportional to the energy density measured.

579 Figure 1

580



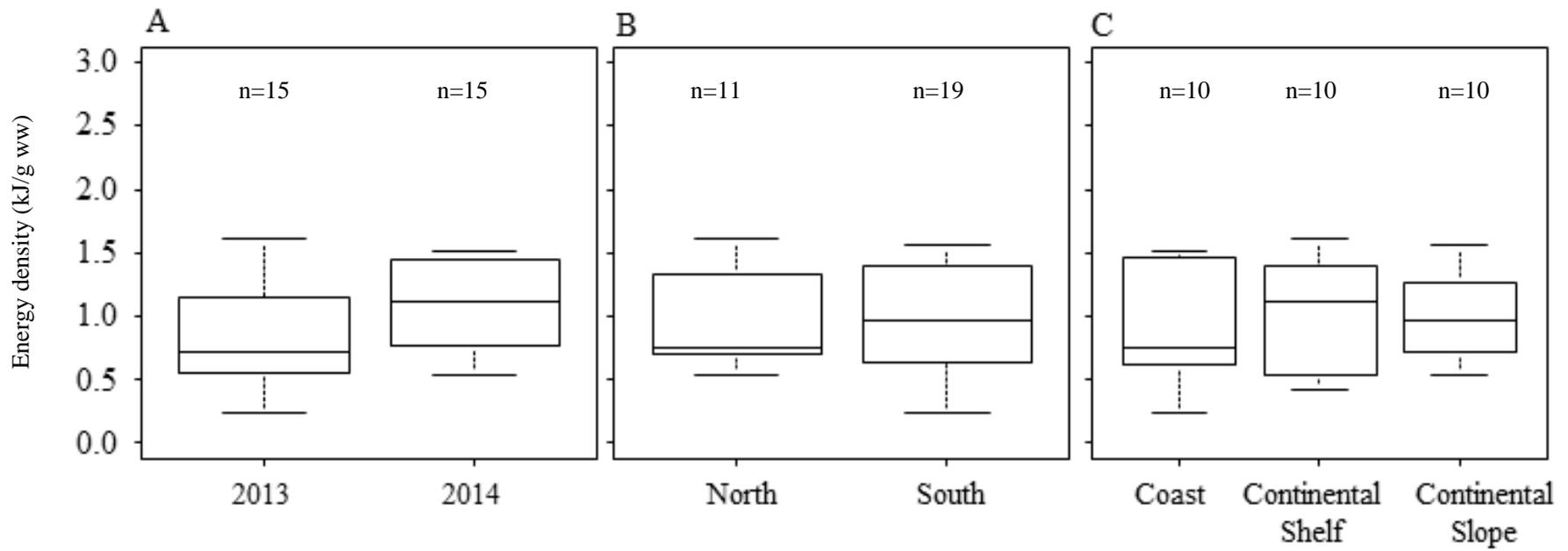
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583 Figure 2

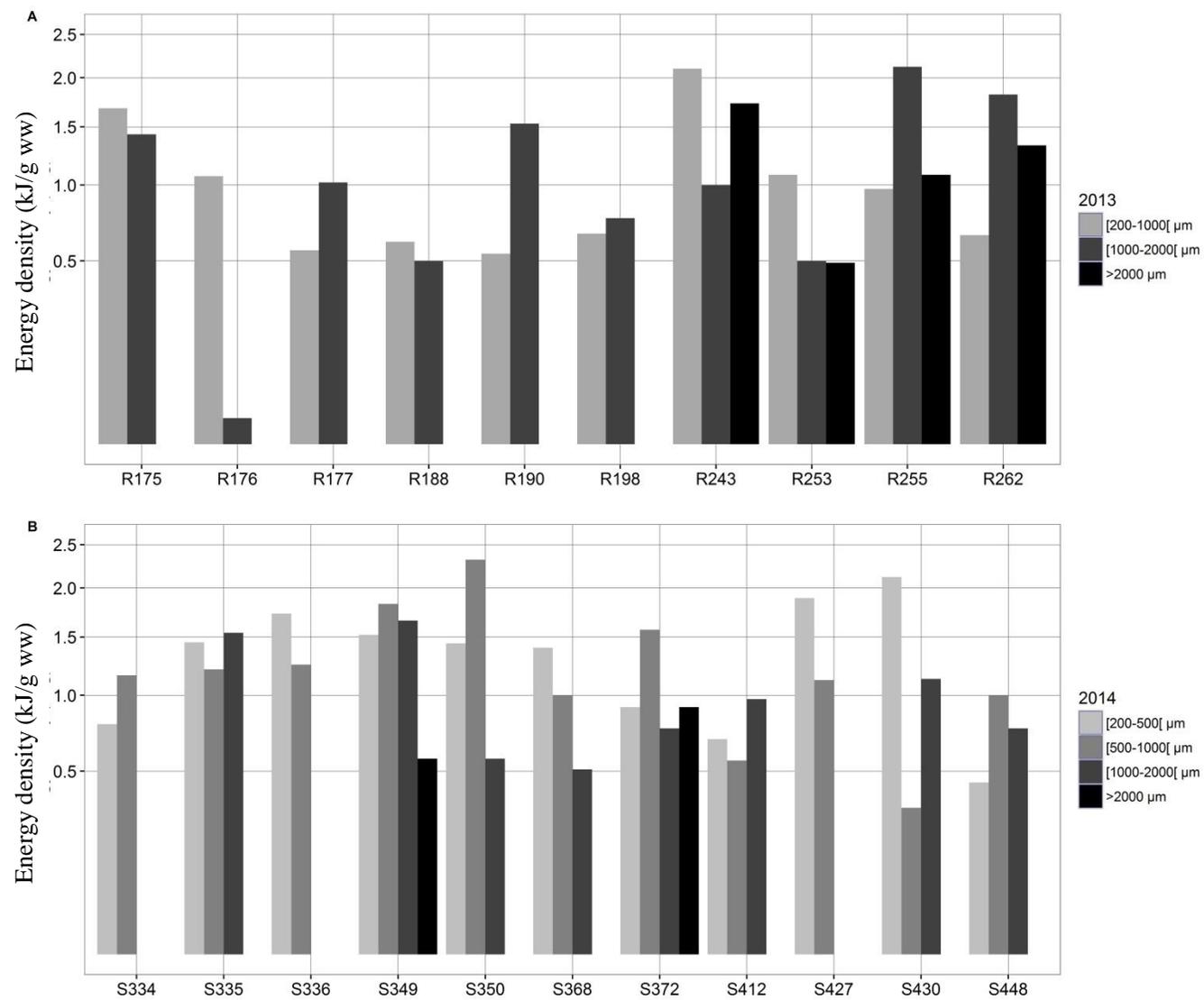
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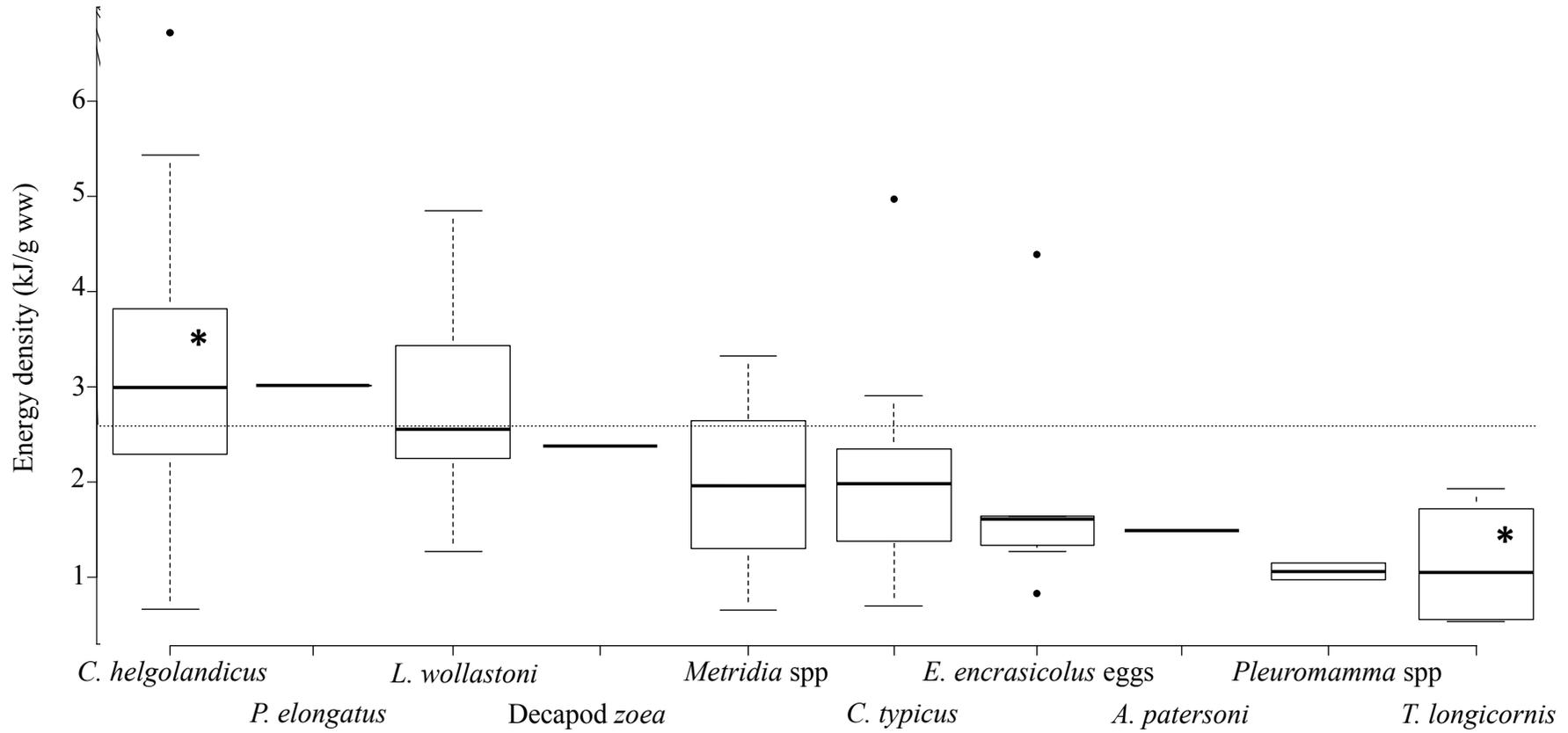
586 Figure 3

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588 Figure 4

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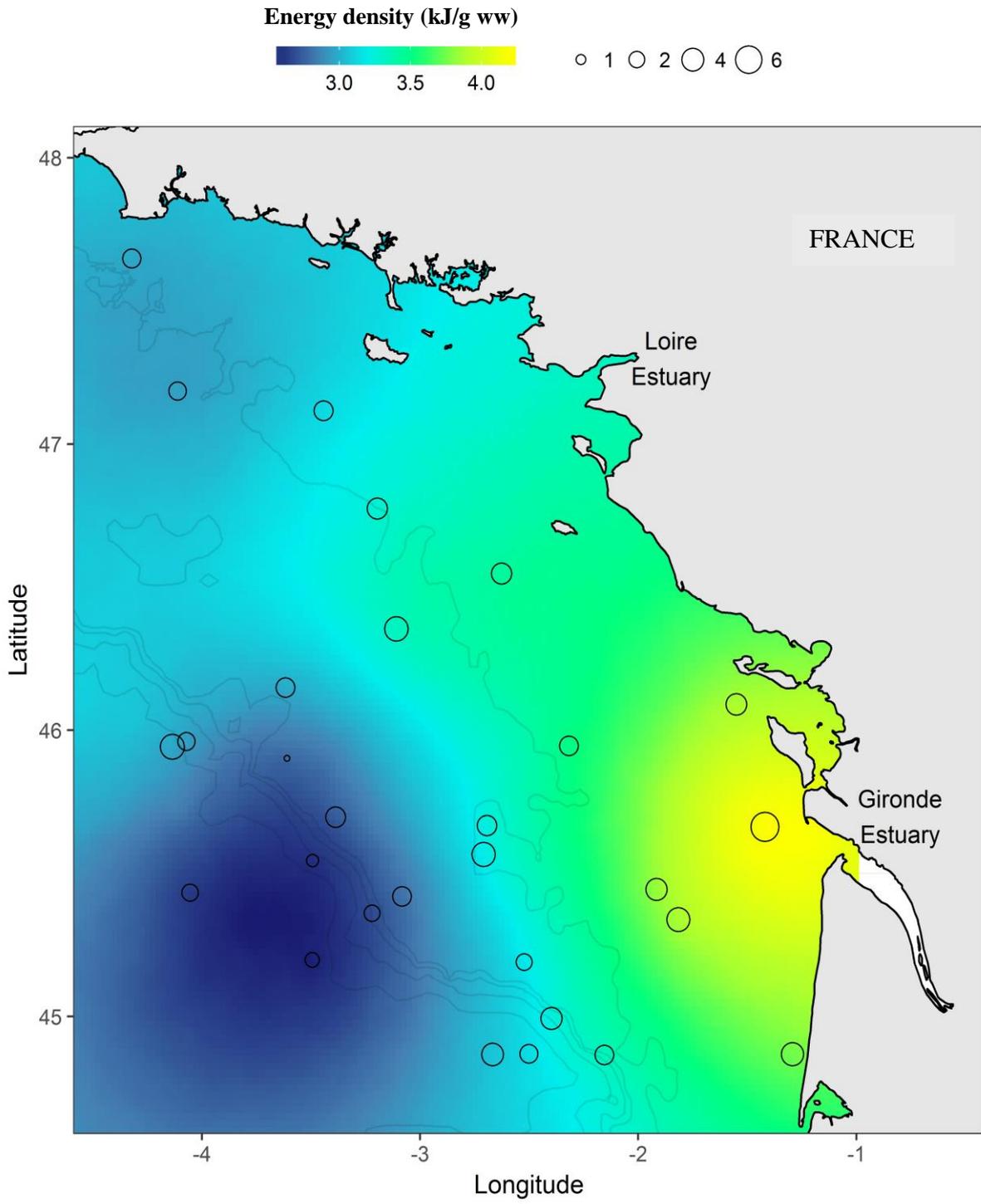
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592 Figure 5

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595 **List of tables**

596

597 Table 1: Mean energy density in wet mass ( $\pm$  SD, kJ/g ww) by size-classes for spring 2013,  
598 2014 and averaged data of both springs studied. The number of stations was represented by “n”.  
599 Energy density of [200-1000[  $\mu\text{m}$  size-classes (identified by \*) was obtained averaged energy  
600 density of [200-500[ and [500-1000[ $\mu\text{m}$  size-classes of spring 2014.

601

602 Table 2: Mean energy density in wet mass ( $\pm$  SD), minima and maxima of gross energy content  
603 expressed in kJ/g of twelve planktonic groups sampled, associated with number of replicates  
604 ( $N_{\text{replicates}}$ ) and total number of organisms ( $N_{\text{organisms}}$ ), in the Bay of Biscay at springtime.  
605 Taxonomic presentation was established following ([www.copepodes.obs-banyuls.fr/en](http://www.copepodes.obs-banyuls.fr/en)).  
606 Measures on *Acartia* and *Oithona* genus (\*) are below the detection limit and presumed to be  
607 smaller than the smaller values recorded (see results). The sampling tool is specified as WP2  
608 net and/or CUFES for each line.

609

610

611 Table 1

612

Size classes ( $\mu\text{m}$ )	Spring 2013		Spring 2014		Spring 2013/2014	
	mean $\pm$ SD	n	mean $\pm$ SD	n	mean $\pm$ SD	n
[200-500[	/	/	1.26 $\pm$ 0.53	12	/	/
[500-1000[	/	/	1.15 $\pm$ 0.56	12	/	/
[200-1000[	0.82 $\pm$ 0.47	16	1.20 $\pm$ 0.53 <sup>▲</sup>	24 <sup>▲</sup>	1.05 $\pm$ 0.54	40
[1000-2000[	1.06 $\pm$ 0.65	10	1.04 $\pm$ 0.43	9	1.05 $\pm$ 0.55	19
>2000	1.15 $\pm$ 0.51	4	0.74 $\pm$ 0.23	2	1.02 $\pm$ 0.46	6

613

614

615 Table 2

	Order	Family	Genus and/or species	Mean $\pm$ SD	minima	maxima	N <sub>replicates</sub>	N <sub>organisms/sample</sub>	WP2 net / CUFES
	Calanoida	Centropagidae	<i>Centropages typicus</i>	2.2 $\pm$ 1.2	0.7	5.0	13	130	CUFES
	Calanoida	Pontellidae	<i>Anomalocera patersoni</i>	1.50			1	40	WP2 net
	Calanoida	Temoridae	<i>Temora longicornis</i>	1.1 $\pm$ 0.7	0.5	1.9	5	250	WP2 net
	Calanoida	Calanidae	<i>Calanus helgolandicus</i>	3.1 $\pm$ 1.3	0.7	6.7	70	80	CUFES and WP2 net
Copepods	Calanoida	Acartiidae	<i>Acartia</i> spp.	<0.5*				600	WP2 net
	Calanoida	Pontellidae	<i>Labidocera wollastoni</i>	2.87 $\pm$ 1.2	1.3	4.9	7	80	CUFES
	Calanoida	Clausocalanoidae	<i>Pseudocalanus elongatus</i>	3.0	2.7	3.3	2	100	CUFES
	Calanoida	Metridinidae	<i>Metridia</i> spp.	2.0 $\pm$ 1.3	0.7	3.3	3	130	WP2 net
	Calanoida	Metridinidae	<i>Pleuromamma</i> spp.	1.1 $\pm$ 0.1	1.0	1.2	3	70	WP2 net
	Cyclopoida	Oithonidae	<i>Oithona</i> spp.	<0.5*				800	WP2 net
Fish	Clupeiformes	Clupeidae	<i>Engraulis encrasicolus</i>	1.8 $\pm$ 1.2	0.8	4.4	13	500	CUFES
Crabs	Decapoda	NA	Zoea larvae	2.4	2.2	2.6	2	100	CUFES

616

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618

619 **List of supplemental figure**

620

621 **Supplemental figure 1:** Boxplot of gross energy estimates in dry mass (kJ/g dw) of several  
622 organisms in the Bay of Biscay at springtime. The box and the line represent the lower quartile,  
623 median and upper quartile. The dotted line represents the mean energy density ( $23.78 \pm 4.97$   
624 kJ/g in dm) content considering all measures. Outliers are represented by black circle. The  
625 number of each species is reporting using “n=”. Asterisk represented significant difference  
626 between two species (Tuckey-HSD, p-value= 0.05).

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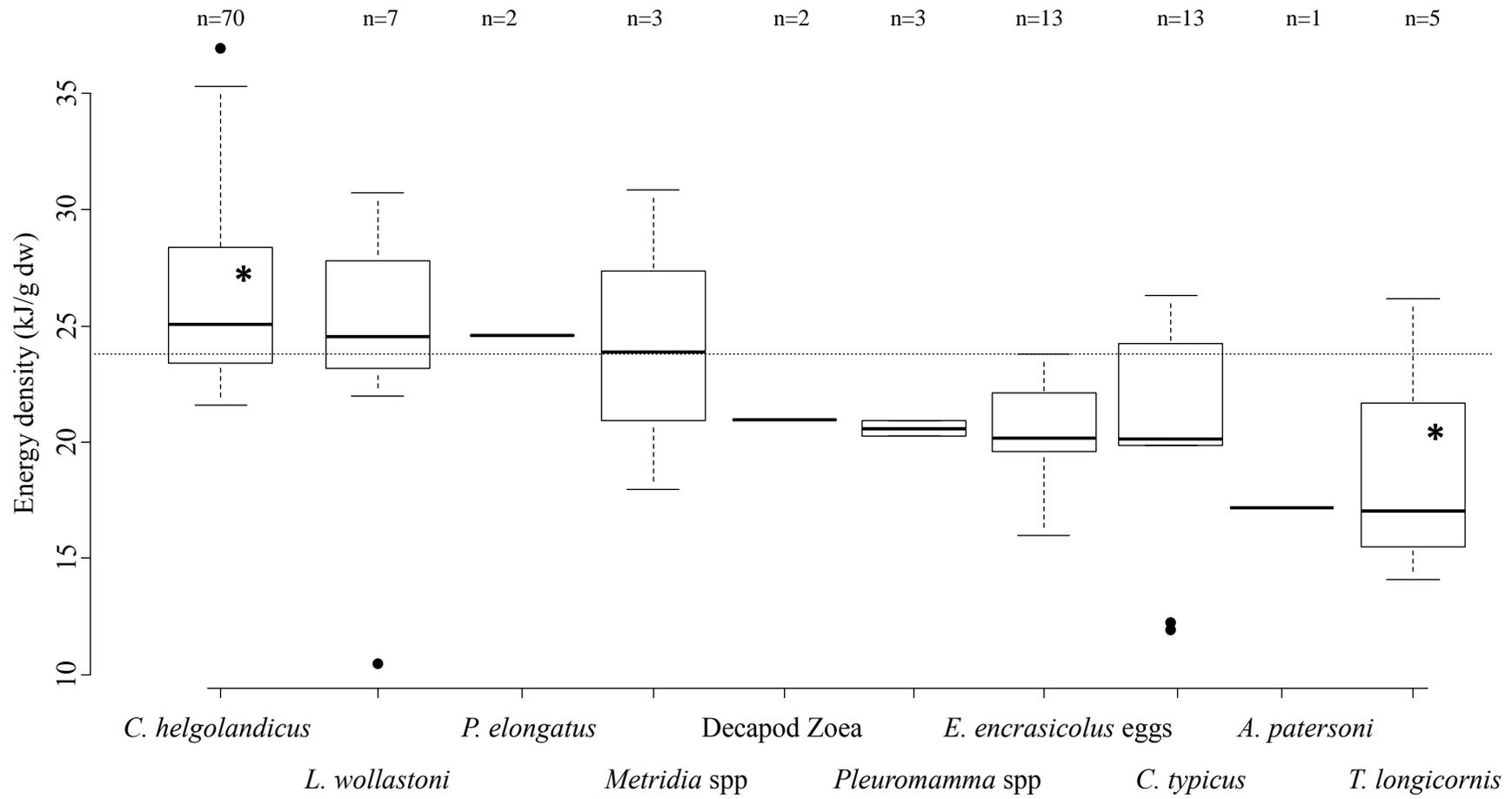
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629 Supplemental figure 1

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633 **List of supplemental tables**

634

635 Supplemental table 1: List of spring mesozooplankton size-classes ( $\mu\text{m}$ ) available ( $\checkmark$ ) for each  
636 station in 2013 and 2014 sampled in the Bay of Biscay. Absence of certain class-sizes reveals  
637 a lack of material to accomplish analyzes or/and absence of organisms belonging to specified  
638 size-class.

639

640 Supplemental table 2: Mean energy density in dry mass ( $\pm$  SD, kJ/g dm) by size-classes for  
641 spring 2013, 2014 and compiling data of both springs studied. The number of stations was  
642 represented by “n”. Energy density of [200-1000] $\mu\text{m}$  size-classes (identified by  $\blacktriangle$ ) was obtained  
643 combining energy density of [200-500] and [500-1000] $\mu\text{m}$  size-classes of spring 2014.

644

645 Supplemental table 3: P-values of ANOVA tests of mean energy density (kJ/g ww) by size-  
646 classes of mesozooplankton comparisons following latitudinal and longitudinal gradients (A),  
647 and between each size-class (B) in 2013 and 2014 (C: coastal stations, Sh: continental shelf  
648 stations, Sl: continental slope stations). Size-classes of mesozooplankton are expressed in  $\mu\text{m}$ .

649

650 Supplemental table 4: Some ecological observations relative to the presence of quiescent or  
651 resting eggs, the diet, the spatial distribution and the length of adults along different copepods  
652 (species or genus). Length adults were established using observations of (Rose, 1933)<sup>23</sup>  
653 including measures on both males and females.

654

655 Supplemental table 1

656

Stations	2013			Stations	2014			
	200-1000	1000-2000	>2000		200-500	500-1000	1000-2000	>2000
R175	✓	✓		S334	✓	✓		
R176	✓	✓		S335	✓	✓	✓	
R177	✓	✓		S336	✓	✓		
R188	✓	✓		S347			✓	
R189	✓			S349	✓	✓	✓	✓
R190	✓	✓		S350	✓	✓	✓	
R191	✓			S368	✓	✓	✓	
R204	✓			S372	✓	✓	✓	✓
R206	✓			S375	✓			
R229	✓			S410		✓		
R240	✓			S412	✓	✓	✓	
R243	✓	✓	✓	S427	✓	✓		
R253	✓	✓	✓	S430	✓	✓	✓	
R255	✓	✓	✓	S448	✓	✓	✓	
R262	✓	✓	✓					

657

## 658 Supplemental table 2

659

Size classes ( $\mu\text{m}$ )	Spring 2013		Spring 2014		Spring 2013/2014	
	mean $\pm$ SD	n	mean $\pm$ SD	n	mean $\pm$ SD	n
[200-500[	/	/	20.30 $\pm$ 5.38	12	/	/
[500-1000[	/	/	22.74 $\pm$ 8.29	12	/	/
[200-1000[	21.50 $\pm$ 3.96	16	21.52 $\pm$ 6.95 <sup>♠</sup>	24 <sup>♠</sup>	21.51 $\pm$ 5.87	40
[1000-2000[	24.38 $\pm$ 4.57	10	20.25 $\pm$ 8.21	9	22.42 $\pm$ 6.69	19
>2000	23.42 $\pm$ 3.49	4	17.00 $\pm$ 5.25	2	21.28 $\pm$ 4.88	6

660

661 Supplemental table 3

662

663 A

	2013	2014
North - South	0.186	0.201
C- Sh	0.293	0.259
Sh - SI	0.691	0.702
SI - Sh	0.564	0.367
Interannual	0.133	

664

665 B

2013			
	[200-1000[	[1000-2000[	>2000
[200-1000[			
[1000-2000[	0.106		
>2000	0.070	0.395	

2014				
	[200-500[	[500-1000[	[1000-2000[	>2000
[200-500[				
[500-1000[	0.456			
[1000-2000[	0.157	0.209		
>2000	0.601	0.378	0.301	

666

	Dormancy / Resting Eggs	Diet	Spatial distribution	Length adults (mm) 23
<i>Acartia</i> spp.	✓ <sup>1,2</sup>	Herbivorous <sup>3</sup> Omnivorous <sup>4</sup>	Coastal / Neritic <sup>5</sup>	0.8 – 1.2 <sup>1</sup>
<i>Oithona</i> spp.		Carnivorous, herbivorous, omnivorous <sup>6</sup> detritivorous <sup>8</sup>	Coastal Neritic or Oceanic <sup>2,5,7</sup>	0.4 – 1.0 <sup>2</sup>
<i>Centropages typicus</i>	✓ <sup>9</sup>	Very omnivorous <sup>10</sup>	Coastal / Neritic <sup>2,11</sup>	1.4 – 2.0 <sup>3</sup>
<i>Anomalocera patersonii</i>	✓ <sup>12</sup>	Carnivorous <sup>4</sup> , omnivorous <sup>13</sup>	Neritic/Oceanic <sup>4,13</sup>	3.0 – 4.1 <sup>4</sup>
<i>Calanus helgolandicus</i>	✓ <sup>7</sup>	Essentially herbivorous <sup>10,17</sup>	Oceanic/Neritic <sup>3,14</sup>	2.8 – 3.0 <sup>5</sup>
<i>Labidocera wollastoni</i>	✓ <sup>9</sup>	Very omnivorous <sup>10</sup>	Oceanic <sup>11</sup>	2.2 – 2.4 <sup>6</sup>
<i>Pseudocalanus elongatus</i>		Herbivorous <sup>15</sup>	Neritic-Oceanic <sup>3,16</sup>	1.2 – 1.6 <sup>7</sup>
<i>Metridia</i> spp.		Omnivorous <sup>17</sup>	Neritic <sup>18</sup>	2.3 – 3.3 <sup>8</sup>
<i>Pleuromamma</i> spp.		Omnivorous <sup>4</sup>	Neritic <sup>18</sup>	2.2 – 4.3 <sup>9</sup>
<i>Temora longicornis</i>	✓ <sup>9,19,20</sup>	Very omnivorous <sup>3</sup> , Opportunist <sup>21</sup>	Coastal <sup>22</sup>	1.0 – 1.3 <sup>10</sup>

680 <sup>1</sup> Katajisto, T., Viitasalo, M., Koski, M., 1998. Seasonal occurrence and hatching of calanoid eggs in sediments of the northern Baltic Sea. *Mar. Ecol. Prog. Ser.* 163, 133–143.  
681 doi:10.3354/meps171133

682 <sup>2</sup> Uye, S., 1985. Resting eggs production as a life history strategy of marine planktonic copepods. *Bull. Mar. Sci.* 37, 440–449.

683 <sup>3</sup> Sautour, B., Castel, J., 1993. Distribution of zooplankton populations in Marennes-Oléron Bay (France), structure and grazing impact of copepod communities. *Oceanol. Acta*  
684 16, 279–290.

685 <sup>4</sup> Kouwenberg, J.H.M., 1994. Copepod Distribution in relation to seasonal hydrographics and spatial structure in the North-western Mediterranean (Golfe du Lion). *Estuar.*  
686 *Coast. Shelf Sci.* 69–90. doi:10.1006/ecss.1994.1005

687 <sup>5</sup> Valdés, L., Moral, M., 1998. Time-series analysis of copepod diversity and species richness in the southern Bay of Biscay off Santander, Spain, in relation to environmental  
688 conditions. *ICES J. Mar. Sci. J. Cons.* 55, 783–792. doi:10.1006/jmsc.1998.0386

689 <sup>6</sup> Castellani, C., Irigoien, X., Harris, R.P., Lampitt, R.S., 2005. Feeding and egg production of *Oithona similis* in the North Atlantic. *Mar. Ecol. Prog. Ser.* 288, 173–182.  
690 doi:10.3354/meps288173

691 <sup>7</sup> Irigoien, X., Head, R.N., Harris, R.P., Cummings, D., Harbour, D., Meyer-Harms, B., 2000. Feeding selectivity and egg production of *Calanus helgolandicus* in the English  
692 Channel. *Limnol. Oceanogr.* 45, 44–54. doi:10.4319/lo.2000.45.1.0044

693 <sup>8</sup> Gonzalez, H.E., Smetacek, V., 1994. The possible role of the cyclopoid copepod *Oithona* in retarding vertical flux of zooplankton faecal material. *Mar. Ecol. Prog. Ser.*  
694 *Oldendorf* 113, 233–246. doi:10.3354/meps113233

695 <sup>9</sup> Lindley, J.A., 1990. Distribution of overwintering calanoid copepod eggs in sea-bed sediments around southern Britain. *Mar. Biol.* 104, 209–217. doi:10.1007/BF01313260

- 696 Lindley, J.A., 1986. Dormant eggs of calanoid copepods in sea-bed sediments of the English Channel and southern North Sea. *J. Plankton Res.* 8, 399–400.  
697 doi:10.1093/plankt/8.2.399
- 698 <sup>10</sup> Arnaud, J., Brunet, M., Mazza, J., 1980. Structure et ultrastructure comparées de l'intestin chez plusieurs espèces de Copépodes Calanoides (Crustacea). *Zoomorphologie* 95,  
699 213–233. doi:10.1007/BF00998123
- 700 <sup>11</sup> Gaudy, R., 1984. Biological Cycle of *Centropages typicus* in the North-Western Mediterranean Neritic Waters. *Crustac. Suppl.* 200–213. doi:10.2307/25027553
- 701 <sup>12</sup> Ianora, A., Santella, L., 1991. Diapause embryos in the neustonic copepod *Anomalocera patersoni*. *Mar. Biol.* 108, 387–394. doi:10.1007/BF01313647
- 702 <sup>13</sup> Kerambrun, P., Champalbert, G., 1995. Diel variations of gut fluorescence in the pontellid copepod *Anomalocera patersoni*. *Comp. Biochem. Physiol. A Physiol.* 111, 237–  
703 239. doi:10.1016/0300-9629(95)00008-U
- 704 <sup>14</sup> Bonnet, D., Richardson, A., Harris, R., Hirst, A., Beaugrand, G., Edwards, M., 2005. An overview of *Calanus helgolandicus* ecology in European waters. *Prog. Oceanogr.*  
705 65, 1–53. doi:10.1016/j.pocean.2005.02.002
- 706 <sup>15</sup> Breteler, W.M.K., Gonzalez, S.R., Schogt, N., 1995. Development of *Pseudocalanus elongatus* (Copepoda, Calanoida) cultured at different temperature and food conditions.  
707 *Mar. Ecol. Prog. Ser.* 119, 99–110. doi:10.3354/meps119099
- 708 <sup>16</sup> Kovalev, A.V., Mazzocchi, M.G., Kideys, A.E., Skryabin, V.A., 2006. Neritization of the plankton fauna in the Mediterranean basin. *МОРСЬКИЙ ЕКОЛОГІЧНИЙ*  
709 *ЖУРНАЛ*
- 710 <sup>17</sup> Graeve, M., Hagen, W., Kattner, G., 1994. Herbivorous or omnivorous? On the significance of lipid compositions as trophic markers in Antarctic copepods. *Deep Sea Res.*  
711 *Part Oceanogr. Res. Pap.* 41, 915–924. doi:10.1016/0967-0637(94)90083-3
- 712 <sup>18</sup> Albaina, A., Irigoien, X., 2007. Fine scale zooplankton distribution in the Bay of Biscay in spring 2004. *J. Plankton Res.* 29, 851–870. doi:10.1093/plankt/fbm064
- 713 <sup>19</sup> Glippa, O., Souissi, S., Denis, L., Lesourd, S., 2011. Calanoid copepod resting egg abundance and hatching success in the sediment of the Seine estuary (France). *Estuar.*  
714 *Coast. Shelf Sci.* 92, 255–262. doi:10.1016/j.ecss.2010.12.032
- 715 <sup>20</sup> Martynova, D.M., Graeve, M., Bathmann, U.V., 2009. Adaptation strategies of copepods (superfamily Centropagoidea) in the White Sea (66°N). *Polar Biol.* 32, 133–146.  
716 doi:10.1007/s00300-008-0513-1
- 717 <sup>21</sup> Niehoff, B., Kreibich, T., Saborowski, R., Hagen, W., 2015. Feeding history can influence physiological responses of copepods: an experimental study comparing different  
718 cohorts of *Temora longicornis* from the Southern North Sea. *J. Exp. Mar. Biol. Ecol.* 469, 143–149. doi:10.1016/j.jembe.2015.04.008
- 719 <sup>22</sup> Seuront, L., Lagadeuc, Y., 2001. Multiscale patchiness of the calanoid copepod *Temora longicornis* in a turbulent coastal sea. *J. Plankton Res.* 23, 1137–1145.  
720 doi:10.1093/plankt/23.10.1137
- 721 <sup>23</sup> Rose, M., 1933. Faune de France - Copépodes Pélagiques, Fédération française des sociétés des sciences naturelles - Office central de Faunistique.  
722

