

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

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2	functional diversity to forage fish
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22 Abstract

23 To assess one of the dimensions of mesozooplankton functional diversity, this study quantifies energy density during the springtime in the Bay of Biscay considering both 24 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
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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 purse, 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 correlated with profitability (Scharf et al., 1998). Prey quality defined here as energy content 56 57 per unit of prey mass consumed, as individual prey potential energy, is an 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 (Kitaysky et al., 2001; Rosen and Trites, 2000). A collapse of fat and energy-rich prey 60 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.

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

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

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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.

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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.

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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 m²). 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 were stored frozen at -20°C until further analysis. 124

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.

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141 Calorimetric analyses

Energy density was estimated, following Spitz et al. (2010), using a Parr[®] 1266 semi-142 143 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%).

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155 Data treatment

156 Statistical analyses were conducted with R v.3.1.2 (R Core Team, 2014). Nonparametric analyses were conducted to compare energy density by size-classes of 157 158 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 $3/_{2}$ (Juntunen et al., 2012). Model fitting was done via the software STAN v.2.5.0 (Stan 168 169 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

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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 µm 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 µm 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 1000-2000µm 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

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

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

218

219 **Discussion**

Previous studies on mesozooplankton quality focused mostly on *Calanus* species (Davies et al., 2012; Michaud and Taggart, 2007). Our objective was specifically to consider the sizes and the specific energy density in a diversified community (only on adult stages and non ovigerous females copepods). This study is the first to investigate mesozooplankton quality both at a broad taxonomic and at size scales across a major European fishing ground. This approach 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

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 ± 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 ± 3.7 kJ/g dw.

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264 Ecological observations of mesozooplanktonic organisms and energy density

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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).

A. *patersoni* was the largest species of our sampling but have a low energy density. A.
 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.

The breeding season of organisms could also impact the observed patterns of energy density among copepods species (Ventura and Catalan, 2005). Despite a short life-cycle due to their strong metabolic activity, it is possible that breeding cycles are synchronous among copepod species. Springtime is a highly dynamic season that can offer various and rapids change of 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). Variations in mesozooplankton biomass fail to explain alone the recruitment variability of 305 306 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 anchovies and pilchards, are mechanically constrained through their filter-size features
(Bachiller and Irigoien, 2013). Consequently, low quality mesozooplanktonic organisms, even
if they are abundant, should negatively impact the fitness of some planktivorous consumers.
Physiology and digestion rates would not compensate the ingestion of low prey quality by
higher consumption rates. A lower quality food induces lower reserves and less energy to
immediate swimming activity, to forage and to produce high quality gamets.

317

318 Conclusion

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

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Figure 1: Map of the continental shelf of the Bay of Biscay showing sampling sites where sizeclasses of mesozooplankton were sampled in spring 2013 and in spring 2014. Stations around 500 meter isobaths were considered as continental slope stations, stations near coastline were considered as coastal stations and other stations, in the center of the shelf as continental shelf 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

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

568

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



583 Figure 2













595 List of tables

596

597 Table 1: Mean energy density in wet mass (± 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] μ m size-classes (identified by ⁴) was obtained averaged energy

600 density of [200-500] and [500-1000[µm size-classes of spring 2014.

601

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_{replicates}) and total number of organisms (N_{organisms}), in the Bay of Biscay at springtime.

605 Taxonomic presentation was established following (<u>www.copepodes.obs-banyuls.fr\\en</u>).

606 Measures on Acartia and Oithona genus (*) are below the detection limit and presumed to be

- smaller than the smaller values recorded (see results). The sampling tool is specified as WP2
- 608 net and/or CUFES for each line.

611 Table 1

	Spring		Spring		Spring	
	2013		2014		2013/2014	
Size classes (µm)	$mean \pm SD$	n	mean \pm SD	n	mean \pm SD	n
[200-500[/	/	1.26 ± 0.53	12	/	/
[500-1000[/	/	1.15 ± 0.56	12	/	/
[200-1000[0.82 ± 0.47	16	1.20 ± 0.53 [♠]	24 *	1.05 ± 0.54	40
[1000-2000[1.06 ± 0.65	10	1.04 ± 0.43	9	1.05 ± 0.55	19
>2000	1.15 ± 0.51	4	0.74 ± 0.23	2	1.02 ± 0.46	6

615 Table 2

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

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 ± 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).

627



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633 List of supplemental tables

634

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

639

Supplemental table 2: Mean energy density in dry mass (\pm SD, kJ/g dm) by size-classes for spring 2013, 2014 and compiling data of both springs studied. The number of stations was represented by "n". Energy density of [200-1000[µm size-classes (identified by *) was obtained combining energy density of [200-500] and [500-1000[µm 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),

and between each size-class (B) in 2013 and 2014 (C: coastal stations, Sh: continental shelf
stations, Sl: continental slope stations). Size-classes of mesozooplankton are expressed in μm.

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)²³

653 including measures on both males and females.

	20	013				2014		
Stations	200-1000	1000-2000	>2000	Stations	200-500	500-1000	1000-2000	>2000
R175	\checkmark	\checkmark		S334	\checkmark	\checkmark		
R176	\checkmark	\checkmark		S335	\checkmark	\checkmark	\checkmark	
R177	\checkmark	\checkmark		S336	\checkmark	\checkmark		
R188	\checkmark	\checkmark		S347			\checkmark	
R189	\checkmark			S349	\checkmark	\checkmark	\checkmark	\checkmark
R190	\checkmark	\checkmark		S350	\checkmark	\checkmark	\checkmark	
R191	\checkmark			S368	\checkmark	\checkmark	\checkmark	
R204	\checkmark			S372	\checkmark	\checkmark	\checkmark	\checkmark
R206	\checkmark			S375	\checkmark			
R229	\checkmark			S410		\checkmark		
R240	\checkmark			S412	\checkmark	\checkmark	\checkmark	
R243	\checkmark	\checkmark	\checkmark	S427	\checkmark	\checkmark		
R253	\checkmark	\checkmark	\checkmark	S430	\checkmark	\checkmark	\checkmark	
R255	\checkmark	\checkmark	\checkmark	S448	\checkmark	\checkmark	\checkmark	
R262	✓	\checkmark	\checkmark					

658 Supplemental table 2

	Spring		Spring		Spring	
	2013		2014		2013/2014	
Size classes (µm)	mean \pm SD	n	$mean \pm SD$	n	mean \pm SD	n
[200-500[/	/	20.30 ± 5.38	12	/	/
[500-1000[/	/	22.74 ± 8.29	12	/	/
[200-1000[21.50 ± 3.96	16	21.52 ± 6.95*	24⁴	21.51 ± 5.87	40
[1000-2000[24.38 ± 4.57	10	20.25 ± 8.21	9	22.42 ± 6.69	19
>2000	23.42 ± 3.49	4	17.00 ± 5.25	2	21.28 ± 4.88	6

661 Supplemental table 3

663 A

	2013	2014
North - South	0.186	0.201
C- Sh	0.293	0.259
Sh - Sl	0.691	0.702
Sl - Sh	0.564	0.367
Interannual	0.1	33

В

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								

667 Supplemental Table 4

				660
	Dormancy /	Diet	Spatial distribution	Length
	Resting			adults (mm)
	Eggs			23 670
Acartia spp.	✓ 1, 2	Herbivorous ³ Omnivorous ⁴	Coastal / Neritic ⁵	0.8 - 621
Oithona spp.		Carnivorous, herbivorous, omnivorous ⁶	Coastal Neritic or Oceanic ^{2, 5, 7}	0.4 - 692
		detritivorous ⁸		673
Centropages typicus	✓ ⁹	Very omnivorous ¹⁰	Coastal / Neritic ^{2, 11}	1.4 - 2.0
Anomalocera patersonii	✓ 12	Carnivorous ⁴ , omnivorous ¹³	Neritic/Oceanic ^{4,13}	$3.0 - 4.1^4$
Calanus helgolandicus	✓ 7	Essentially herbivorous ^{10, 17}	Oceanic/Neritic ^{3, 14}	2.8 - GØ 5
Labidocera wollastoni	√ ⁹	Very omnivorous ¹⁰	Oceanic ¹¹	$2.2 - 2.4_{6}$
Pseudocalanus elongatus		Herbivorous ¹⁵	Neritic-Oceanic ^{3, 16}	1.2 - 1.6
Metridia spp.		Omnivorous ¹⁷	Neritic ¹⁸	2.3 - 537
Pleuromamma spp.		Omnivorous ⁴	Neritic ¹⁸	$2.2 - 4.3_{\circ}$
Temora longicornis	✓ 9, 19, 20	Very omnivorous ³ , Opportunist ²¹	Coastal ²²	$1.0 \ 1.3 \ 679$

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