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

Aurélie Dessier¹*, Christine Dupuy¹, Anaïs Kerrie¹, Françoise Mornet², Matthieu Authier³,
Paco Bustamante¹, Jérôme Spitz³

¹Littoral Environnement et Sociétés (LIENSs), UMR 7266, CNRS-Université de La Rochelle,
2 rue Olympe de Gouges, 17042 La Rochelle Cedex 01, France

²IFREMER, Unité Halieutique Gascogne Sud (HGS), Station de La Rochelle, Place Gaby Coll, F-17087 L’Houmeau, France

³Observatoire PELAGIS – Système d’Observation pour la Conservation des Mammifères et Oiseaux Marins, UMS 3462, CNRS-Université de La Rochelle, 17071, La Rochelle, France

*Corresponding author. E-mail address: dessier.aurelie@gmail.com
Fax: +33-(0)546 507 663 / Tel: +33-(0)546 458 38
Abstract

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 taxonomic and size-classes diversity. Energy density among copepods species (*Centropages typicus*, *Anomalocera patersoni*, *Calanus helgolandicus*, and *Labidocera wollastoni*), as well as anchovy eggs (*Engraulis encrasicolus*) ranges from 0.5 to 6.7 kJ/g on a taxonomic basis.

Considering size-classes, energy density varies from 0.74 to 1.26 kJ/g. *C. helgolandicus* exhibits with average energy density estimates generally higher in the plume of the Gironde estuary. In contrast, no spatial coherence is found in the variability of mesozooplankton energy density by size-classes. Our results show that the mesozooplanktonic resource is not homogeneous in terms of quality in the Bay of Biscay. During spring, some species and some geographical areas seems thus to be more profitable to predators than others. We argue that the energy density is a key functional trait of mesozooplankton, but the assessment of mesozooplankton quality should be preferentially based on taxonomy rather than on size-classes. We conclude that interspecific and spatial variability of energy density among the mesozooplankton community can have important implications on fish population dynamics.

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

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

Profitability is the net energy intake from food less the net energy allocated for a predator to purse, capture and consume their target prey (Pulliam, 1974). In marine ecosystem, diet composition was traditionally based on stomach content analyses (Hyslop, 1980), whereas profitability was based on prey availability and capturability (Garrido et al., 2007; Wirtz, 2012). More recently, profitability has been investigated with respect to prey functional characteristics 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 per unit of prey mass consumed, as individual prey potential energy, is another functional trait investigated to understand predators’ energetic needs (Spitz et al., 2014) that can explain 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 associated with an increase of low quality prey biomass (“junk-food,” Österblom et al. 2008) has negatively impacted some populations of marine top predators (the common murre seabird or Stellers sea lions for instance) around the world (Kadin et al., 2012). The role of prey energy densities was mainly investigated on high trophic-level species such as marine mammals or seabirds (Shoji et al., 2014; Spitz et al., 2012). Hence, the quality of prey such as forage fish, cephalopods or crustaceans has been investigated (Spitz, et al., 2010; Spitz & Jouma’ a, 2013; Schrimpf et al., 2012), but the variability of energy density in low trophic-level prey, such as 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, climate-mediated 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).

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

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

Sampling

Mesozooplankton samples were collected in the Bay of Biscay on the R/V Thalassa during the PELGAS surveys in spring (April-May 2013 and 2014). PELGAS are ecosystemic surveys conducted every year since 2003 by the Institut Français de Recherche pour l’Exploitation de la Mer (IFREMER - Doray et al., this issue). Size-class sampling of mesozooplankton was performed using WP2 nets along five transects covering the continental shelf from the coastline to the continental slope (Fig. 1). North versus South limit was the Gironde estuary. This sampling was conducted during nighttime by vertical tows (maximum 100 m depth for continental shelf and slope stations, mesh size of 200 µm and mouth area of 0.25 m²). Three size-classes of mesozooplankton were analyzed in 2013 corresponding to successive filtrations (washed with distilled water) on three sieves with different mesh size: 200, 1000 and 2000 µm. In 2014, four size-classes were conducted with mesh size of sieves corresponding to 200, 500, 1000 and 2000 µm. In total, thirteen stations were sampled reaching 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.

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

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

Data treatment

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

To predict energy density of Calanus helgolandicus (the most abundant species) at unsampled locations, ordinary kriging was performed (Wikle, 2003). The geodetic distance between pairs of locations where measurement were taken was computed and used for 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 Development Team, 2013) and interpolations were done with R v.3.1.2 (R Core Team, 2014). 4 chains were initialized with random starting values, and run for 6 000 iterations with a warm-up of 1 000 iterations. Model convergence was assessed with the Gelman-Rubin-Brook diagnostics. Weakly informative priors (Stan Development Team, 2013) were used to help parameter estimation given the small sample size. The latter feature motivated a Bayesian approach to avoid relying on asymptotic justifications, which are unlikely to hold in small sample analyses.
Results

Energy density by size-classes

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

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

Energy density by taxonomic diversity

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

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.

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

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

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

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

Ecological observations of mesozooplanktonic organisms and energy density

Feeding activities, reproduction, respiration and growth are energy demanding processes (Postel et al., 2000). Large copepods species suggesting a proportion of storage volume more important, oil sac, compared to other species (Lee et al., 2006; Davies and Taggart, 2012). Size cannot be also strictly used as a proxy of quality in mesozooplankton as suggested by our results on size classes or on some large species, i.e. A. patersoni and Pleuromamma spp (Supplemental table 4). This latter genus was constituted of large copepods which showed one of the lowest energy density in copepods. Pleuromamma spp. seems to be the deepest copepods species of our sampling suggesting possibly that deeper mesozooplankton 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
species suggesting diet composition may influence metabolic processes and energy storage based on protein intake (Supplemental table 4). Similarly, *T. longicornis* appears to be one of the energy-poorest species. This species cannot accumulate extensive energy because of its rapid metabolic and functional responses to food limitation (Niehoff et al., 2015). In experimental conditions, *T. longicornis* exhibits a rapid loss of lipids compared to *P. elongatus* (Martynova et al., 2009). Moreover, *Acartia* spp., *T. longicornis* and *C. typicus* present high metabolic rates implicating a limited lipid accumulation and in some cases (when unflavored conditions appear) resting eggs (Arts et al., 2009). Further studies should focus on relationship between the taxonomic composition of the mesozooplankton size-classes and their energy 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 rapid changes to the abiotic environment allowing the establishment of diverse ecological niches.

**Implications on fish population dynamics**

Energy fluxes between organisms depend on the relationships between environmental conditions (*e.g.* temperature), food consumption (*e.g.* abundance) and biologic factors (*e.g.* metabolic processes to reproduction) (Lambert et al., 2003). Bioenergetic models consider three compartments (food reserve, growth and reproduction); the variability of energy fluxes to these compartments can explain population dynamics (Brandt and Hartman, 1993). Energy density can be obtained using direct measures (as in our study), using the proximate composition, or using calculations from the percentage of the organic constituents from carbon called the ‘calorimetric equivalent’ (Postel et al, 2000). Existing models on fish population dynamics in the Bay of Biscay used mesozooplankton as a homogenous compartment in terms of energy density (Gatti et al., 2017). Mesozooplanktivorous species like pilchards and anchovies will be 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 anchovies in the Bay of Biscay (Irigoin et al., 2009). Politikos et al., (2015) suggested that the spawning spring spatial pattern of anchovies in the Bay of Biscay “is a result of the general southward movement of the population, as well as the associated better bioenergetic conditions as compared to the individuals remaining in the North”. Our hypothesis here is that the 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.

Conclusion

We showed mesozooplankton quality (measured here by the energy density) was variable among sizes, species and spatially. Mesozooplankton quality should be assessed according to taxonomic diversity rather than by size classes. Mesozooplankton 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.

Acknowledgments

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References


List of figures

Figure 1: Map of the continental shelf of the Bay of Biscay showing sampling sites where size-classes 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.

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

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.

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 ± 1.32 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).

Figure 5: Interpolation map of spring energy density (kJ/g ww) of C. helgolandicus sampled in the Bay of Biscay. Sampling stations are represented by black circle which are in a size proportional to the energy density measured.
Figure 1
Figure 2

Energy density (kJ/g ww)

A

2013 2014

n=15 n=15

B

North South

n=11 n=19

C

Coast Continental Shelf Continental Slope

n=10 n=10 n=10
Figure 3

A

Energy density (kJ/g ww)

R175  R176  R177  R188  R190  R198  R243  R253  R255  R262

B

Energy density (kJ/g ww)

S334  S335  S336  S349  S350  S388  S372  S412  S427  S430  S448

2013
- [200-1000] μm
- [1000-2000] μm
- >2000 μm

2014
- [200-500] μm
- [500-1000] μm
- [1000-2000] μm
- >2000 μm
Figure 4

Energy density (kJ/g ww)

C. helgolandicus  L. wollastoni  Metridia spp  E. encrasicolus eggs  Pleuromamma spp

P. elongatus  Decapod zoea  C. typicus  A. patersoni  T. longicornis
Figure 5

Energy density (kJ/g ww)

Loire Estuary

Gironde Estuary

FRANCE
List of tables

Table 1: Mean energy density in wet mass (± SD, kJ/g ww) by size-classes for spring 2013, 2014 and averaged 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 averaged energy density of [200-500] and [500-1000]µm size-classes of spring 2014.

Table 2: Mean energy density in wet mass (± SD), minima and maxima of gross energy content expressed in kJ/g of twelve planktonic groups sampled, associated with number of replicates (Nreplicates) and total number of organisms (Norganisms), in the Bay of Biscay at springtime. Taxonomic presentation was established following (www.copepodes.obs-banyuls.fr\en).

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 net and/or CUFES for each line.
### Table 1

<table>
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<th>Size classes (µm)</th>
<th>Spring 2013 mean ± SD</th>
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<th>Spring 2014 mean ± SD</th>
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<th>Spring 2013/2014 mean ± SD</th>
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<td>1.15 ± 0.56</td>
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## Table 2

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<th>maxima</th>
<th>Nreplicates</th>
<th>Norganisms/sample</th>
<th>WP2 net / CUFES</th>
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<td>Clupeidae</td>
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Supplemental figure 1: Boxplot of gross energy estimates in dry mass (kJ/g dw) of several organisms 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 (23.78 ± 4.97 kJ/g in dm) content considering all measures. Outliers are represented by black circle. The number of each species is reporting using “n=”.

Asterisk represented significant difference between two species (Tuckey-HSD, p-value= 0.05).
Supplemental figure 1

Energy density (kJ/g dw)

C. helgolandicus
P. elongatus
Decapod Zoea
E. encrasicolus eggs
A. patersoni
L. wollastoni
Metridia spp
Pleuromamma spp
C. typicus
T. longicornis

n=70
n=7
n=2
n=3
n=2
n=3
n=13
n=13
n=1
n=5
List of supplemental tables

Supplemental table 1: List of spring mesozooplankton size-classes (µm) available (√) 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.

Supplemental table 2: Mean energy density in dry mass (± 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.

Supplemental table 3: P-values of ANOVA tests of mean energy density (kJ/g ww) by size-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.

Supplemental table 4: Some ecological observations relative to the presence of quiescent or resting eggs, the diet, the spatial distribution and the length of adults along different copepods (species or genus). Length adults were established using observations of (Rose, 1933) including measures on both males and females.
### Supplemental table 1

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Supplemental table 2

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<td>[200-500]</td>
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<td>21.52 ± 6.95*</td>
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### Supplemental table 3

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<td>C - Sh</td>
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#### B

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### Supplemental Table 4

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<td>Acartia spp.</td>
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<td>Coastal / Neritic</td>
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<td>Oithona spp.</td>
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<td>3.0 – 4.1</td>
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