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

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Abstract :

To explore some aspects of mesozooplankton functional diversity, this study quantified energy density during the springtime in the Bay of Biscay both between different species and between different size-classes. Energy densities of copepod species (*Centropages typicus*, *Anomalocera patersoni*, *Calanus helgolandicus*, and *Labidocera wollastoni)*, as well as anchovy eggs (*Engraulis encrasicolus*) ranged from 0.5 to 6.7 kJ/g wet weight (ww). Considering size-classes, energy densities varied from 0.74 to 1.26 kJ/g ww. Energy density of *C. helgolandicus* exhibited a spatial pattern with the highest values in the plume of the Gironde estuary. In contrast, no spatial pattern of energy density has been detected considering size-classes. Our results showed that the mesozooplankton cannot be considered as a homogeneous resource in terms of quality. During spring, some species and some geographical areas seem thus to be more profitable to predators than others. We argued that the energy density is a key functional trait of mesozooplankton species. Finally, we discussed how interspecific and spatial variability of energy density among the mesozooplankton community can have important implications on fish population dynamics.

Highlights

► The nutritional quality is not homogeneous among the mesozooplanktonic community in the Bay of Biscay. ► Taxonomic approach is more relevant than size-classes approach to investigate mesozooplankton profitability. ► A clear spatial pattern of energy density is highlighted for *Calanus helgolandicus*.

Keywords : 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 associated with profitability (Scharf et al., 1998). Prey quality can be defined as energy content per unit of prey mass. Prey quality can thus be considered as a functional trait explaining some prey-predators relationships (Spitz et al., 2014). Decrease in prey quality can explain physiological stress at individual level, as well as some population declines (Kitaysky et al., 2001; Rosen and Trites, 2000). Some populations of seabirds and pinnipeds have been indeed negatively impacted by a collapse of fat and energy-rich prey associated with an increase of low quality prey biomass (Österblom et al. 2008; Kadin et al., 2012). The role of prey energy density 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 is relatively well-known (e.g., Spitz, et al., 2010; Spitz & Jouma'a, 2013; Schrimpf et al., 2012), however the variability of energy density among lower trophic levels, such as mesozooplankton, remains largely unknown.

Zooplanktonic organisms ranging between 200 and 2,000 µm (Sieburth et al., 1978) constitute a key compartment of marine food webs. Mesozooplankton communities participate in carbon recycling in the ocean (Mayzaud and Pakhomov, 2014), assure the transfer of energy from primary producers to the upper trophic levels. Mesozooplankton organisms constitute thus the main prey of many marine fish species including major commercial species, such as sardines and anchovies. Hence, changes in mesozooplankton

3

abundance and composition can impact the population dynamics of fish stocks (Batchelder et al., 2012; Beaugrand et al., 2003).

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, mackerels, horse mackerels or 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). Variability in the quality of available food to forage fish could be one factor contributing to explain the variability in the recruitment of these forage fish in the Bay of Biscay.

Our hypothesis is that mesozooplankton energy density should vary between different species, or also spatially, resulting in variability of the food quality available to forage fish. To this end, we explored in this study the variability of mesozooplankton energy density in the Bay of Biscay. We first investigated mesozooplankton energy density -1- between different size-classes, because prey size is crucial in trophic pattern of plankton feeders (Garrido et al., 2007); and -2- between different species because energy density can vary considerably between related species, as for fish or cephalopods (Doyle et al., 2007; Spitz et al., 2010). Finally, we explored the spatial variability of energy density both for different 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). The limit between the north part of the Bay of Biscay and the south part 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

4

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 sampled with mesh size of sieves of 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 CUFES was to estimate the abundance of pilchard and anchovy eggs (Petitgas et al., 2009). CUFES 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 adult stages and non ovigerous females), fish eggs and decapod *zoea* were identified on board at the lowest taxonomic level (see Table 2) with a Leica M3Z stereo microscope (x65 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, a total number of 40 to 5,600 individuals per species were analyzed. 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 CUFES were used here as tools to collect enough organisms for laboratory analysis. This sampling was not dedicated to estimate biomass abundance or vertical distribution 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. Results 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 were also expressed in kJ/g of dry mass (see

5

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 of size-classes ranged from 0.01 to 2.32 kJ/g ww (2013 and 2014). Energy density means were around 1.05 kJ/g ww, all size-classes combined (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 difference in

6

mean energy density was detected in spring (Fig. 2). No difference was detected within size-classes across the Bay of Biscay (Fig. 2). In both 2013 and 2014, no difference of mean energy density was observed between the northern and southern part of the Bay, or from coastal to continental slope areas.

For a given station, the values of energy density can largely vary between size-classes (Fig. 3). The 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 µm and 1000-2000 µm. No spatial pattern in energy density of size-classes was detected in the Bay of Biscay, 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 reached 2.7 kJ/g ww for undetermined decapod *zoea* (Table 2). No analytical measurement was obtained for *Acartia* spp. and *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). All organisms combined, average energy density in spring was 2.6 ± 1.3 kJ/g ww (Fig. 4). Without consideration of species 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-adj=0.051). Finally, the highest intraspecific variability were recorded for *C. helgolandicus* (from 0.68 to 6.74 kJ/g ww) and for *L. wollastoni* (from 1.28 to 4.87 kJ/g ww) at a lesser extent.

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).

7

Discussion

Previous studies on mesozooplankton quality focused mostly on *Calanus* species (Davies et al., 2012; Michaud and Taggart, 2007). Our objective was specifically to explore the variability of energy density among a diversified community composed only on adult stages and non ovigerous females copepods. This study is the first to investigate mesozooplankton quality both between species, and between size-classes in the Bay of Biscay. We demonstrated also the importance of assessing the profitability of mesozooplankton taking into account taxonomy rather than only size differences. The variability of energy density within size-classes is certainly related to difference in species composition and abundance. Further studies should focus on relationship between the taxonomic composition of the mesozooplankton size-classes and their energy density.

Nevertheless, several limitations are inherent in the methods used in this study. These limitations should be kept in mind in the present data interpretation, as well as in the future use of the present results. 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. Consequently, our sampling did not cover all species belonging to the spring mesozooplankton community in the Bay of Biscay (e.g. Valdés et al., 2007) and not consider the relative abundance of organisms. 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.

Mesozooplankton, and particularly copepods, have short life cycles involving a high metabolism (Allan, 1976) and possibly rapid changes of their energetic condition (Lee et al., 2006). Temporal changes of density energy can exist (Hagen and Auel, 2001), our results documented only the springtime combining data from two different years as a seasonal snapshot. Despite these sources of uncertainty, our study provided consistent results and a baseline data of mesozooplankton quality in the Bay of Biscay. Energy density of mesozooplankton species could be thus monitor to inform both on nutritional status of these organisms and on the quality of the underlying environmental conditions.

Variability of energy density among mesozooplankton community

The results showed broad variations in energy densities between species and between size classes. The range of energy density of mesozooplankton in the Bay of Biscay is

basically the same range observed between jellyfish (<4 kJ/g ww) and lipid-rich fish such clupeids (>6kJ/g ww) (Spitz et al., 2010). Thus, the mesozooplanktonic compartment in the Bay of Biscay can be qualified as low-quality resources (i.e. < 4 kJ/g ww) if we consider energy density based on size-classes, or moderate-quality resources (i.e. from 4 to 6 kJ/g ww) if we consider the most energetic copepods *C. helgolandicus* (Spitz et al. 2010).

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 data expressed in dry weight (dw) limiting their 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). Globally, our estimates were coherent with previous studies expressed in dry weight. 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.

Interspecific variability of energy density

Feeding activities, reproduction, respiration and growth are energy-demanding processes (Postel et al., 2000). Large copepods species should have a proportion of storage volume more important (oil sac) compared to other species (Lee et al., 2006; Davies and Taggart, 2012). However, size cannot be 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 of copepods was constituted of large individuals which showed a very low energy density. On the other hand, *Pleuromamma* spp. were the deepest copepod species of our sampling suggesting possibly that deeper mesozooplankton species could be less energy-rich than epipelagic species (Zarubin et al. 2014).

A. patersoni was the largest species of our sampling but have also 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 due to protein intake (Supplemental table 4). Similarly, *T. longicornis* appeared 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* exhibited 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).

The asynchrony of breeding cycles could also impact the observed patterns of energy density among copepod species (Ventura and Catalan, 2005). Despite a short life-cycle due to their strong metabolic activity, it is possible that breeding cycles, and so the maximum of lipid storage, are not synchronous among copepod species. Finally, springtime is a highly dynamic season that can offer various and rapid changes of abiotic environment exposing species to diverse ecological conditions.

Implications on fish population dynamics

Energy fluxes between organisms depend on the relationships between environmental characteristics (*e.g.* temperature), food availability and quality (*e.g.* prey abundance), and physiological factors (*e.g.* metabolic rates, breeding cycle) (Lambert et al., 2003). Bioenergetics models consider three compartments: food reserve, growth and reproduction. The energetic balance of these compartments can impact individual fitness and population dynamics (Brandt and Hartman, 1993). 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). However, mesozooplanktivorous species like pilchards and anchovies are certainly constrained by the intrinsic quality of their prey at a local scale (Bachiller and Irigoien, 2013). Variations in mesozooplankton biomass only fail to explain the recruitment variability of anchovies in the Bay of Biscay (Irigoien 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 bioenergetics conditions as compared to the individuals remaining in the North*". Our results highlighted that mesozooplankton species are not equally valuable to consumers. Consequently, changes in the nutritional quality of plankton could impact the fitness of some planktivorous fish. A decrease of food quality could indeed induce lower reserves and less energy to immediate swimming activity, to forage and to produce high quality gametes and eggs. Further bioenergetics models should incorporate variability of mesozooplankton quality to evaluate relationships between zooplankton quantity and quality, fish energetic requirements and fish feeding ecology (e.g., filtering vs. snapping) on fish population dynamics.

10

Conclusion

We showed mesozooplankton quality (measured here by the energy density) was variable between sizes, between species and spatially. Mesozooplankton species cannot be considered as interchangeable to satisfy energy requirements of forage fish. Ultimately, variability of some key functional traits, here energy density of mesozooplankton species, can play an important role to maintain the quality of some ecosystem services, as fish production to human consumption.

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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.
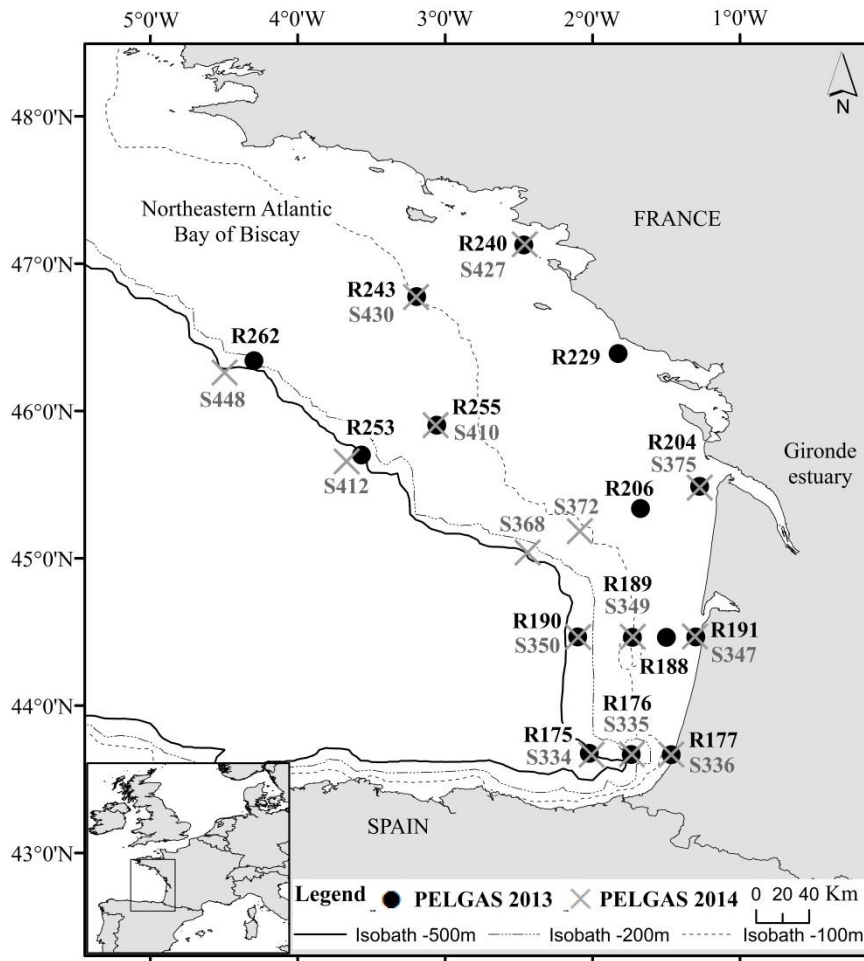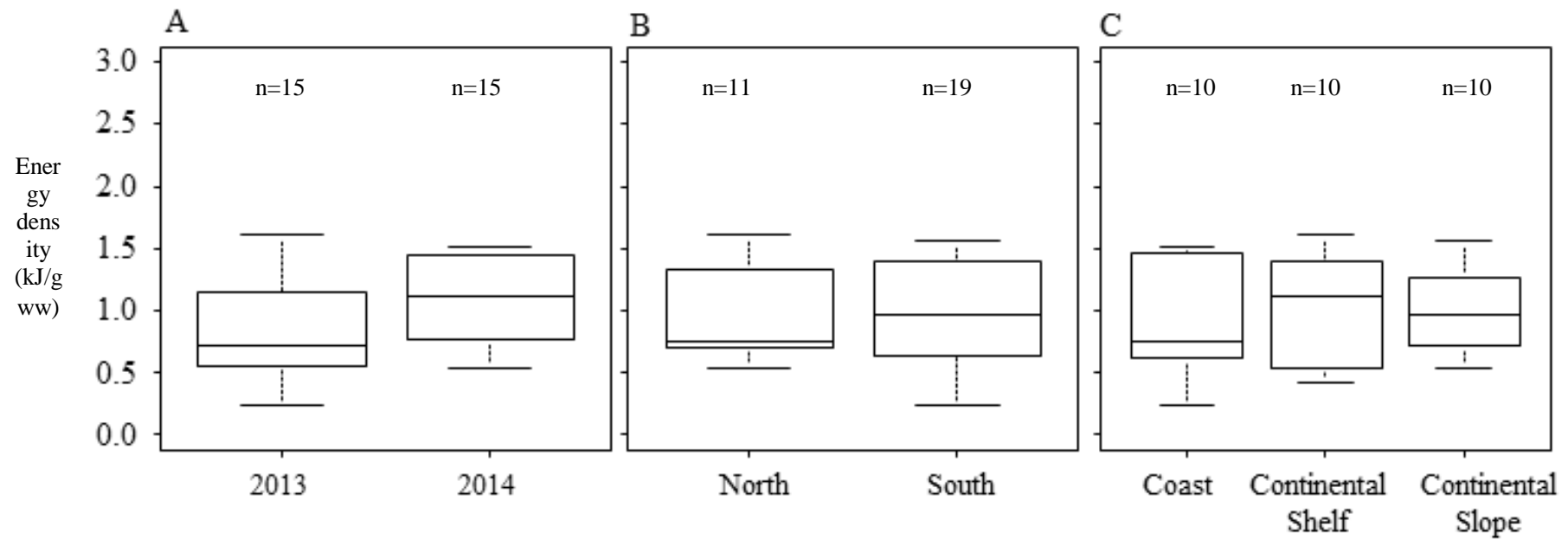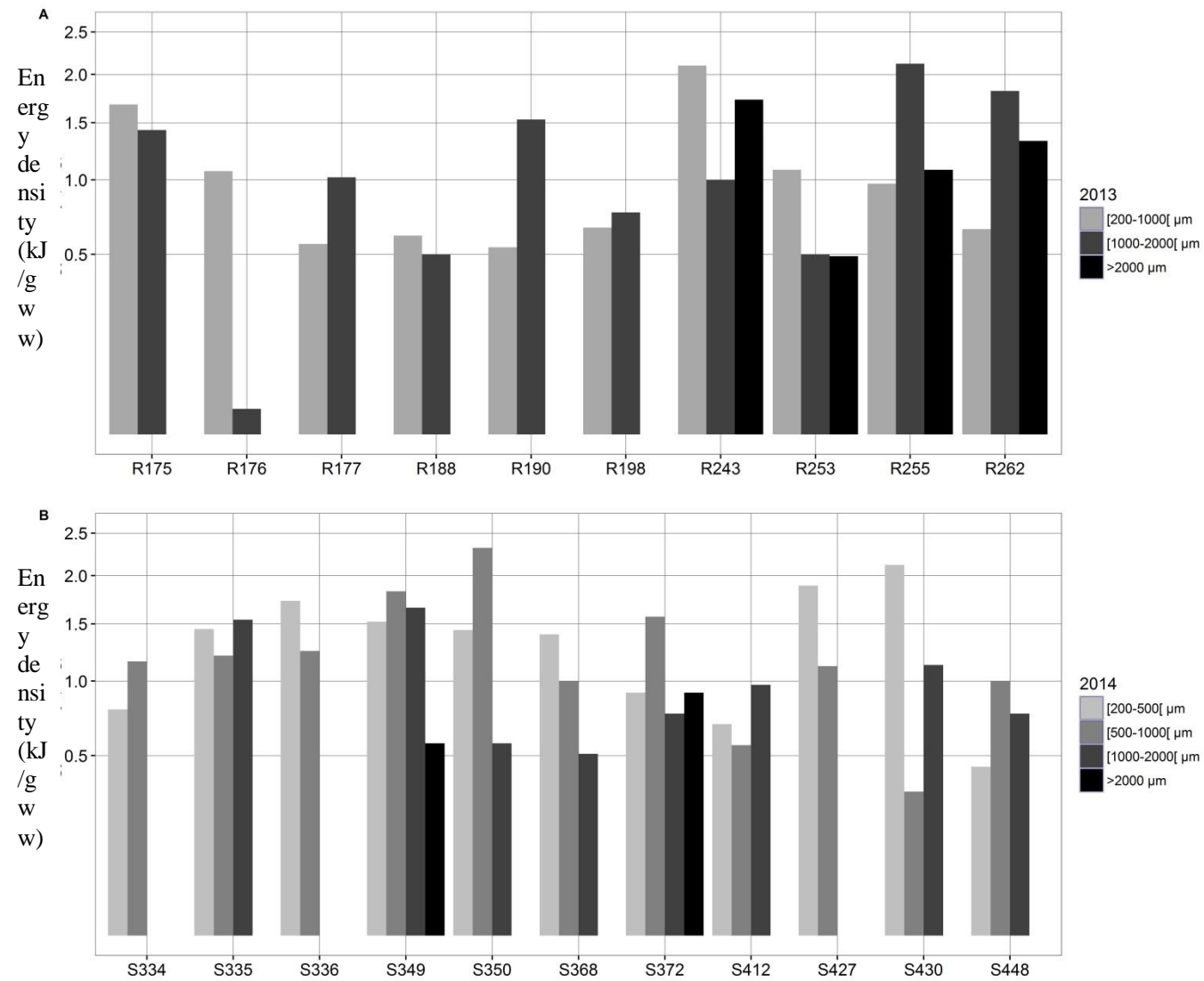
16

Figure 1

Figure 2
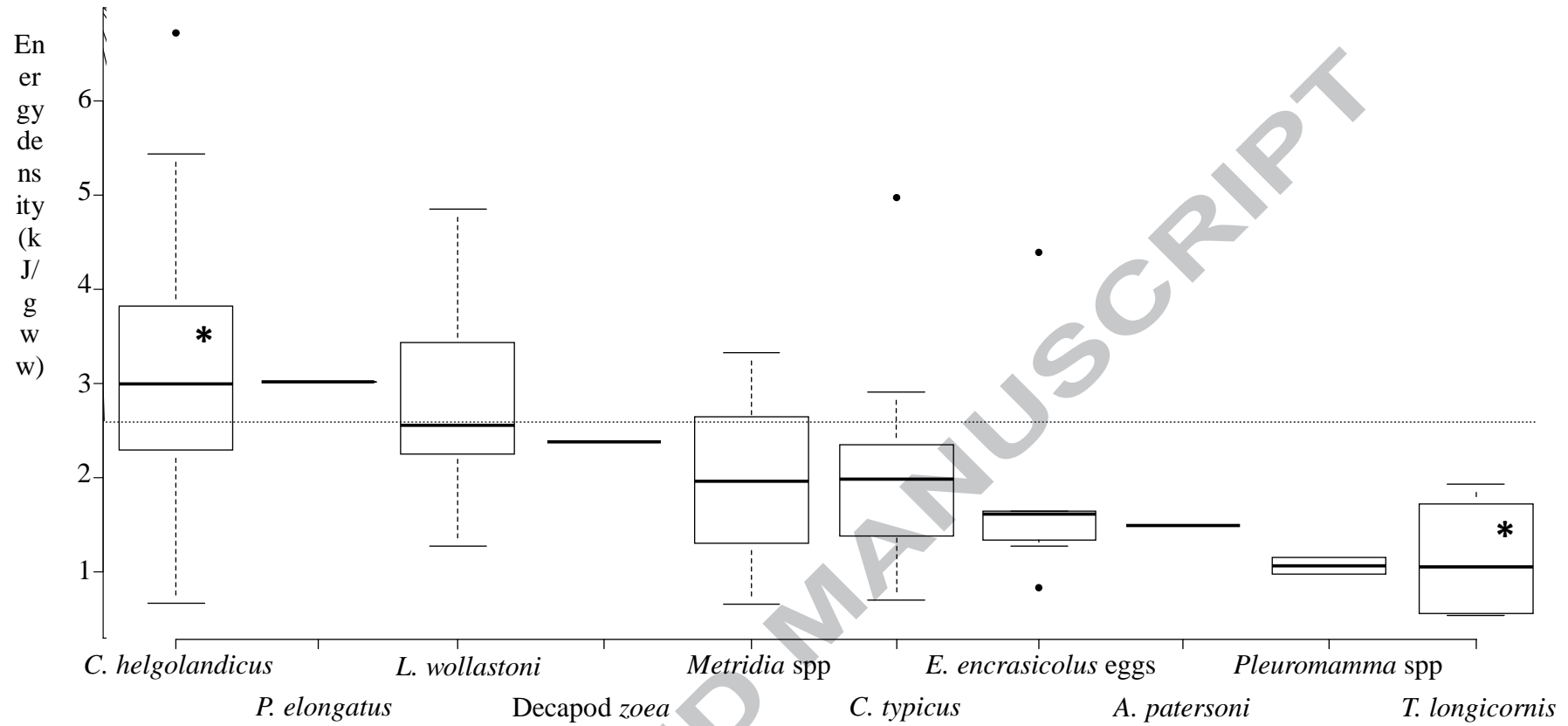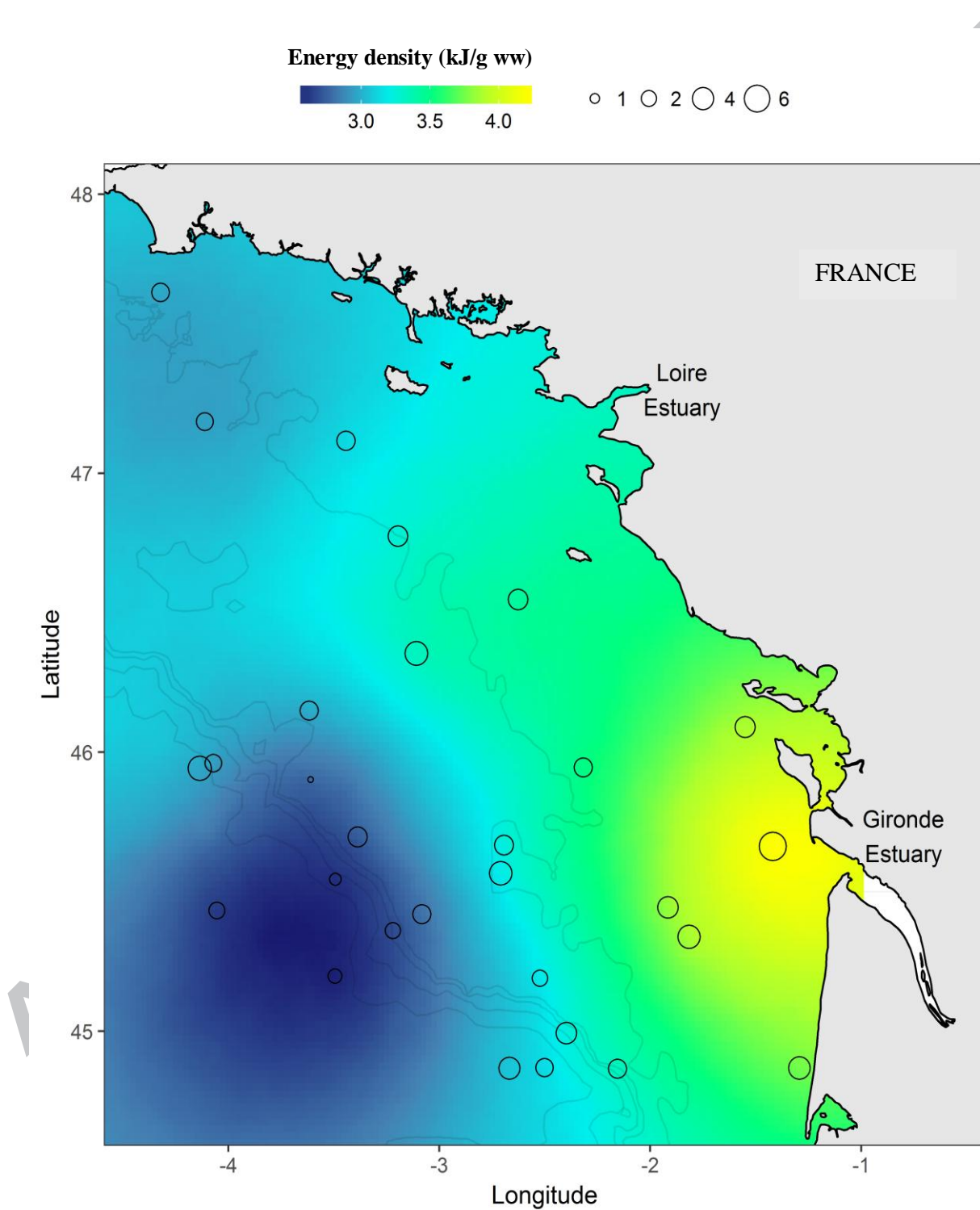
Figure 3

19

Figure 4

Figure 5

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 ($N_{replicates}$) and total number of organisms ($N_{organisms}$), 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.

22

Table 1

Size classes (μm)	Spring 2013 mean ± SD	n	Spring 2014 mean ± SD	n	Spring 2013/2014 mean ± 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

Table 2

	Order	Family	Genus and/or species	Mean ± SD	minima	maxima	$N_{replicates}$	$N_{organisms/sample}$	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± 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

25

List of supplemental figure

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

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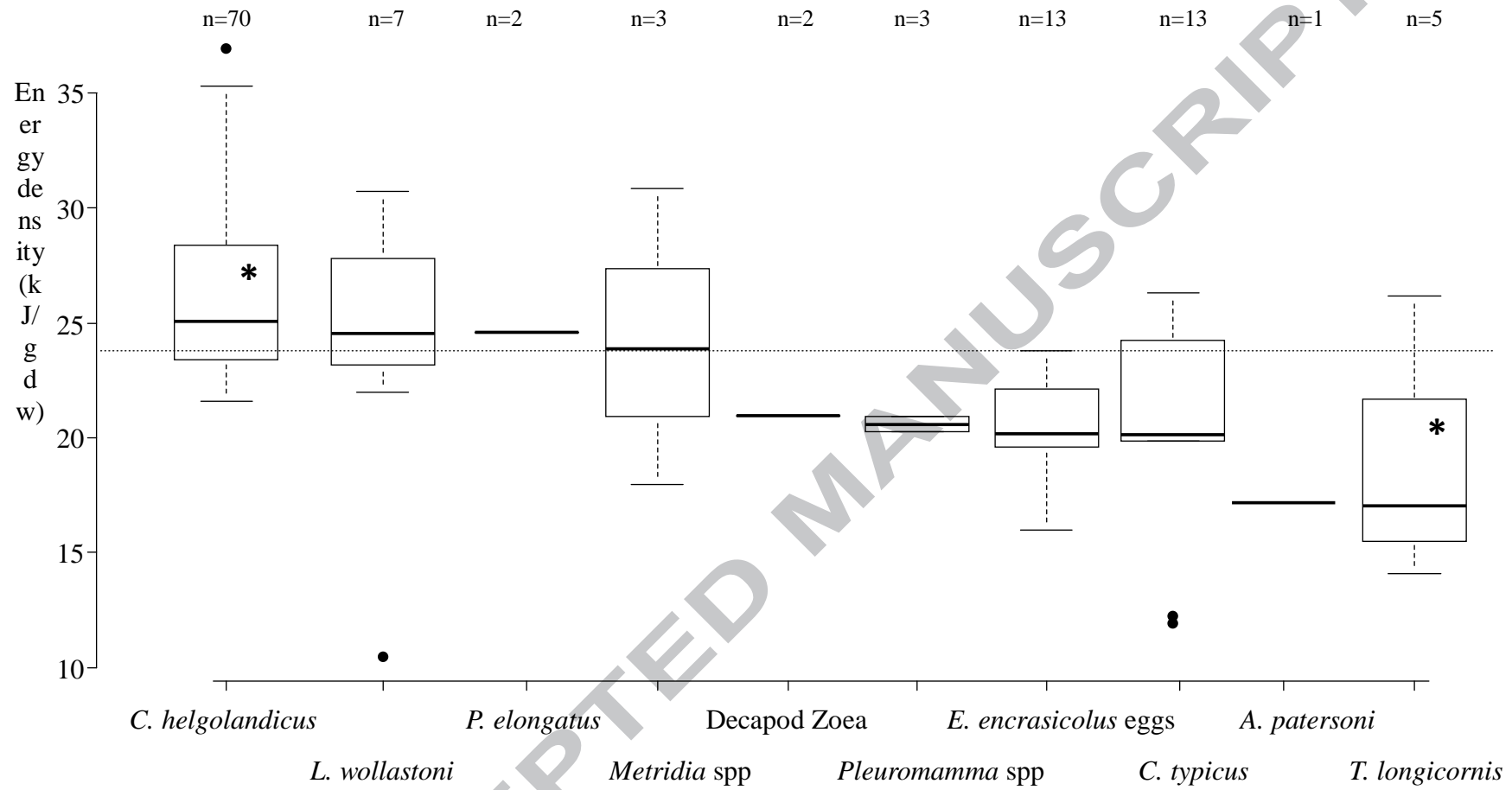
List of supplemental tables

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) [23] including measures on both males and females.

Supplemental table 1

	2013				2014			
Stations	200-1000	1000-2000	>2000	Stations	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	✓	✓	✓					

Supplemental table 2

Size classes (μm)	Spring 2013		Spring 2014		Spring 2013/2014	
	mean ± SD	n	mean ± SD	n	mean ± 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♠	24♠	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

Supplemental table 3

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	0.133	

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	

Supplemental Table 4

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

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33